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Tropical cyclones and the organization of mangrove forests: a review

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• **Background** Many mangrove ecosystems are periodically exposed to high velocity winds and surge from tropical cyclones, and often recover with time and continue to provide numerous societal benefits in the wake of storm events.
• **Scope** This review focuses on the drivers and disturbance mechanisms (visible and functional) that tropical cyclones of various intensities have on mangrove ecosystem properties around the world, as well as the potential ecosystem services role offered by mangroves along storm-ravaged coastlines. When viewed together, studies describe repeatable types of impact and a variety of responses of mangroves that make them ecologically resilient to high velocity winds, and which have served to advance the notion that mangroves are disturbance-adapted ecosystems.
• **Conclusions** Studies have documented massive tree mortality and forest structural shifts as well as high variability of spatial effects associated with proximity and direction of the tropical cyclone trajectory that influence biogeochemical processes, recovery of individual trees, and forest regeneration and succession. Mangroves provide coastal protection through surge and wind suppression during tropical cyclones, and yet are able to overcome wind effects and often recover unless some alternative environmental stress is at play (e.g. hydrological alteration or sedimentation). Structural elements of mangroves are influenced by the legacies imposed by past tropical cyclone injury, which affect their current appearance, and presumably their function, at any point in time. However, much is yet to be discovered about the importance of the effects of tropical cyclones on these fascinating botanical ecosystems, including the role of storm-based sediment subsidies, and much more effort will be needed to predict future recovery patterns as the frequency and intensity of tropical cyclones potentially change.

Key words: Mangrove wetlands, hurricane, regeneration, storm visible effects, surge, tropical storm, typhoon, recovery.

INTRODUCTION

Mangrove ecosystems occur throughout many tropical, subtropical and warm temperate regions of the world, and represent a unique botanical community comprised of a number of distinctive growth forms (Tomlinson, 2016). Mangroves have even expanded their distribution within warm temperate locations globally, facilitated by a prolonged post-Pleistocene recolonization period (Sherrod and McMillan, 1985; Woodroffe and Grindrod, 1991; Kennedy *et al.*, 2016), accentuated by higher minimum winter temperatures at progressively higher latitudes over the late Holocene and Anthropocene (Osland *et al.*, 2013; Saintilan *et al.*, 2014). Taxonomically, mangroves are comprised of approx. 70 species or putative hybrids (Duke *et al.*, 1998), and include tree, shrub, fern and palm life forms, collectively creating the potential for structural adaptability and resilience to major disturbances. In a recent review, 45 % of reported disturbances to mangrove area in the global literature were attributed to tropical cyclones (Sippo *et al.*, 2018), ranking tropical cyclones as perhaps the top non-anthropogenic disturbance they must endure.

Tropical cyclone effects on mangrove ecosystems, while disruptive, are often not long lived, as some tree species can re-sprout quickly (e.g. *Avicennia*), while others rely on advance regeneration strategies (e.g. seedlings present prior to storm events) or post-storm seeding. Mangroves are described as disturbance-adapted communities (Lugo *et al.*, 1981) and are often considered ecologically stable (Alongi, 2008), suggesting that they are able to take on structural disruptions from periodic storms and recover. Where tropical cyclone disturbance frequency is more intense (e.g. parts of the Caribbean region), mangrove structural complexity is reduced to lower statured canopies with few canopy emergents (Lugo and Snedaker, 1974). Where cyclone disturbance is rare (e.g. some Pacific islands, Panama), structural biomass and complexity can increase over time (Allen *et al.*, 2001; Simard *et al.*, 2019).

However, when the complexity of a mangrove is compromised by environmental modifications, especially those influencing tidal hydrological boundaries and characteristics, resistance to tropical cyclone disturbance is also compromised, making individual cyclone events potentially more impactful (Vogt *et al.*, 2012; Lewis *et al.*, 2016). Initial system properties matter tremendously, such that tropical cyclones with similar meteorological metrics affect the same mangrove

forest differently based on conditions imposed by past disturbance (Peters *et al.*, 2011). The legacy of past tropical cyclone disturbance and recovery in mangroves often defines the current ecosystem state, and this disturbance legacy is part of the ecology of mangrove forests in many locations.

Science programmes and policies have targeted mangrove ecosystems over the last few decades as structural protection afforded to coastal communities from wind, surge and tsunamis have become more evident (Danielsen *et al.*, 2005; Dahdouh-Guebas *et al.*, 2005; Das and Vincent, 2009). Along with protection for humans living in disturbance-prone environments, additional incentives for mangrove conservation related to carbon storage and flux have emerged as mangroves have also been identified as important components of the global carbon cycle (Bouillon *et al.*, 2008; Donato *et al.*, 2011). Because of these values attributed to mangroves, protection, rehabilitation and restoration activities have helped to reduce global mangrove area losses on an annual basis from the 1970s to the present (Friess *et al.*, 2019). While this is seemingly good news, reports are nuanced by very high annual mangrove losses in specific regions (e.g. Indonesia, Malaysia and Myanmar; Feller *et al.*, 2017), and an uncertain future for mangroves with climate change (Ward *et al.*, 2016). In some regions, climate change is expected to increase the frequency of the most intense tropical cyclones, increase the amount of rainfall produced by tropical cyclones near the cyclone centre and increase the poleward distribution of tropical cyclones (Knutson *et al.*, 2010, 2015; Christensen *et al.*, 2013; Sobel *et al.*, 2016; Kossin *et al.* 2017; Patricola and Wehner, 2018).

Tropical cyclones affect nearly every aspect of the ecosystem services that mangroves provide; for example, in protecting infrastructure, in provisioning of wildlife habitat and in carbon sequestration. Yet, storm influences on this ecosystem have not received comprehensive review. Here, we will define tropical cyclones, explain where they occur, describe their influences on mangrove ecosystem properties and relevant disturbance mechanisms, and describe cyclone–mangrove interactions with surge suppression, sea-level rise and climate change. We will end this review with a conceptual diagram detailing mechanistically what it means to be 'disturbance-adapted' and suggest avenues for impactful future tropical cyclone research on mangroves.

DEFINING TROPICAL CYCLONES

Across the world, tropical cyclones are described using several different names and classification systems. As a result, the literature describing cyclone effects on mangrove forests uses different terms that are location dependent (e.g. hurricane, typhoon or cyclone). Hurricane is the name used for powerful tropical cyclones (i.e. winds speeds that exceed 119 km h^{-1}) in the Atlantic Ocean and north-eastern Pacific Ocean. In contrast, typhoon is used to describe powerful tropical cyclones in the north-western Pacific Ocean. In the Indian Ocean and south-western Pacific Ocean, powerful tropical cyclones are called tropical cyclones, with the addition of a location-specific modifier to indicate intensity (e.g. severe or very intense). In many areas, less powerful tropical cyclones are called tropical depressions (low wind speeds) or tropical storms (moderate wind speeds). Cyclone classification systems typically use maximum sustained wind speeds to designate classification categories. For example, the Saffir–Simpson hurricane wind scale uses wind speeds to categorize hurricanes into five groups (nhc.noaa.gov): Category 1 (119–153 km h^{-1}), Category 2 (154–177 km h^{-1}), Category 3 (178–208 km h^{-1}), Category 4 (209–251 km h^{-1}) and Category 5 (≥252 km h^{-1}). In this review, we use the term 'tropical cyclone' in a general manner. However, when referring to intensity, we typically use the Saffir–Simpson categories.

WHERE DO TROPICAL CYCLONES AFFECT MANGROVES?

There are many regions of the world where mangrove forests are never affected by tropical cyclones due to climatic conditions that prevent tropical cyclone formation (Fig. 1; note the blue areas not crossed by red, orange or yellow tropical cyclone tracks). For example, tropical cyclones rarely affect mangrove forests in Africa, South America, Indonesia and Papua New Guinea. In contrast, there are certain cyclonic hot spots, where mangrove forests are greatly influenced by recurrent tropical cyclones (Fig. 1; note the blue areas surrounded by red, orange and yellow cyclone tracks). Hamilton and Casey (2016) provided a ranked list of the 20 countries with the largest mangrove areas. Our global map of tropical cyclone pathways (Fig. 1) indicates that the following seven of these 20 mangrove-rich countries are also affected by tropical cyclones: Australia, Mexico, Myanmar, Philippines, Bangladesh, Cuba and the USA (ranked in descending order according to mangrove area). In terms of aerial cover, these are the seven countries where the effects of tropical cyclones on mangroves are potentially largest. However, in terms of local effects, there are many smaller countries (e.g. Bahamas, Guadeloupe, Honduras, Belize and Haiti) where mangrove forest effects can be large due to their position within common cyclonic pathways.

INFLUENCES ON SYSTEM PROPERTIES

General descriptions of structural effects on forests from maximum sustained winds of specific intensities from tropical cyclones have been developed (Myers and van Lear, 1998). We have modified those for application to mangroves (Table 1). While difficulties arise when generalizing effects because of variation in geomorphology, tornadic wind downbursts, mangrove forest height and stand condition, two things should be noted from this table.

First, tropical cyclones with Category 3 windspeeds or higher (≥178 km h^{-1}) cause extreme visible effects on mangroves, almost without exception. Mangroves are positioned in wet soils and many species have dense wood (Chapman, 1976). Critical wind speeds >178 km h^{-1} often force tip-ups along with more prominent breakage of large trees (Roth, 1992; Aung *et al.*, 2013), which subsequently fall on small trees and break them. In spite of this, smaller trees and saplings missed by falling trees and branches, and sometimes inundated by storm surge, can survive cyclones. Thus, smaller statured mangrove forests and trees in canopy gaps can appear more resistant to structural effects because they are positioned lower within the vertical
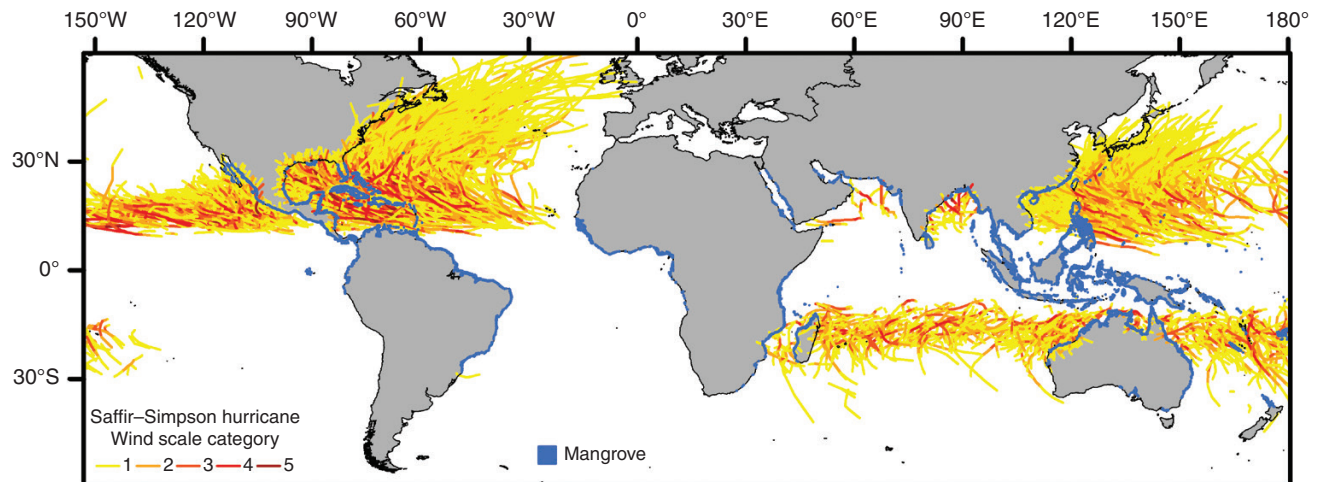
F<small>IG</small>. 1. G<small>LOBAL DISTRIBUTION OF TROPICAL CYCLONE STORM TRACKS IN THE NORTHERN AND SOUTHERN HEMISPHERES ALONG WITH</small> S<small>AFFIR–SIMPSON SCALE</small> C<small>ATEGORIES</small>. T<small>HE DISTRIBUTION OF MANGROVES IS DEPICTED BY BLUE SHADING</small> (<small>FROM</small> G<small>IRI</small> *<small>ET AL</small>.*, 2011), and reveals those mangrove areas that are subjected to tropical cyclone impact on a recurring basis. Saffir–Simpson scale wind speeds are as follows: Category 1, 119–153 km h^{-1}; Category 2, 154–177 km h^{-1}; Category 3, 178–208 km h^{-1}; Category 4, 209–251 km h^{-1}; Category 5, ≥252 km h^{-1}. Tropical cyclone track data are from Knapp *et al.* (2010).

boundary layer to allow some wind buffering (Smith *et al.*, 1994). However, if Category 4 wind speeds (>210 km h^{-1}) or higher are realized, dominant forest trees are often laid down (broken or tipped-up) and buffering of smaller trees from the wind is no longer ensured. While smaller statured forests may appear less affected than taller forests at windspeeds of 178–208 km h^{-1}, post-storm recovery may be slower in forests with reduced growth potential.

Secondly, visible tropical cyclone effects on mangroves can be striking before they become extreme (Fig. 2A, B). The physical change imposed by storm-generated surges vs. the protection provided by complete submergence from surge can lead to swathes of visible effects in some fringing locations but not others, confounding spatial resolution of impact. While damage to built structures might even be light in some cases, injury to mangroves, especially those in poor condition prior to the cyclone (Odum and Johannes, 1975; Lewis *et al.*, 2016), can be overwhelming to the casual observer (Fig. 2C). Thus, reactions are often negative (Smith *et al.*, 1994), but herein we offer context; most mangroves within the repetitive storm-track areas shown in Fig. 1 have sustained cyclone impacts previously, and they have already recovered to what they are now. When left in their natural and unaltered state, mangroves often recover from tropical cyclones.

Tree mortality

Tree mortality was 25–100 % over a mangrove area of approx. 40 000 ha from Hurricane Donna, which made landfall in south Florida in 1960 (Craighead and Gilbert, 1962). Likewise, mangrove tree mortality from tropical cyclone events ranged from zero to 100 % among published accounts since (Table 2). Tree mortality can continue for months (delayed mortality) after a cyclone makes landfall (Smith *et al.*, 1994), so post-assessment dates need to be considered. Notable among mortality accounts are the muddled correlations between the intensity of a tropical cyclone based on simple descriptors (e.g. maximum sustained

wind speeds) and realized mortality in any specific mangrove stand. For example, mortality ranged from 0 to 86 % from Typhoon Haiyan as it affected the Philippines with some of the strongest winds ever recorded in mangroves (Primavera *et al.*, 2016). Structural complexity, hydrogeomorphic setting, antecedent environmental change, orographic positioning and angle of cyclone trajectory relative to forest location generate a spatial signature of response to (or effects of) tropical cyclones that not only translates into differences in recovery and regeneration, but also confounds cause–effect predictability. That a single site in Primavera *et al.* (2016) registered no visible effects from such an intense storm is notable. Modelling has sorted some of this complexity by incorporating better storm wind characteristics at finer resolutions (e.g. Doyle and Girod, 1997), but it is clear that generalizing degrees of responses from tropical cyclones should be cautioned.

Differences in tolerances among mangrove species to wind throw also contribute to disparity of effects. This is expected, as tropical cyclones are not considered a stressor *per se*, but rather wind, rain, surge and excessive sedimentation are the stressors, and those are spatially delivered in vastly different ways during tropical cyclone events. Among neotropical mangroves, historical accounts suggested that *Laguncularia racemosa* was more susceptible to tropical cyclone effects than *Rhizophora mangle* (Wadsworth and Englerth, 1959); however, this trend has not always held up in the greater Caribbean region (Table 2). Accounts of differential tree species mortality from Cyclone Nargis, which affected the Ayeyarwady Delta in Myanmar as a Category 3 storm, were much more distinct than the multiple accounts from the Caribbean region. *Bruguiera sexangula* and *Rhizophora apiculata* trees experienced >90 % mortality, while mortality was far less for *Excoecaria agallocha*, *Sonneratia caseolaris*, *Heritiera fomes* and *Avicennia officinalis*, all of which had >85 % survival (Aung *et al.*, 2013). Results from the Caribbean region suggest that the characteristics of the cyclone vs. site conditions greatly influence species-ranked susceptibility outcomes during tropical cyclones (Table 2). In contrast, results from the old world tropics generally support suggestions

TABLE 1. Generalized mangrove forest damage descriptions relative to Saffir–Simpson tropical cyclone intensity ratings (after *Myers and van Lear, 1998*).

| Category	Wind speed, km h⁻¹	Description
1	119–153 (74–95 miles h⁻¹)	Shrubby mangroves, trees and foliage are damaged, but lightly, with few being fully susceptible to mortality through stem breakage or tip-ups. Litter and small branch fall limited to weaker structures or species with less dense wood, and is probably compensatory to what would fall ordinarily in the coming months. Seedlings and saplings with minor damage, but not generally from wind vs. woody debris, tree/branch fall and surge. Surge to 1.2–1.5 m above normal. Wrack deposition limited but notable, probably containing re-deposited mangrove seeds (when applicable) and propagules. Sedimentation low with minimal contributions from re-suspended estuarine components. Coastal built structures (e.g. piers and signs) sustain minor damage. Roads that are low lying are inundated, especially if storm impacts at high tide. No peat collapse expected after the storm.
2	154–177 (96–110 miles h⁻¹)	Shrubby mangroves, trees and foliage damaged considerably, with many large trees blown down through stem snapping (especially trees of lighter wood densities) and tip-ups. Litter and branch fall extensive and includes compensatory and additive components to what would fall ordinarily in the coming months. Seedlings and saplings with moderate damage, sustaining only small portion of that damage from wind vs. woody debris, tree/branch fall and surge. Surge to 1.8–2.4 m above normal. Wrack deposition extensive, containing re-deposited mangrove seeds (when applicable), propagules, wood, seagrass, shells, human-sourced debris, etc. Sedimentation moderate and would include re-suspended estuarine components, especially if surrounding estuaries are shallow (<2–3 m deep). Considerable damage to coastal built structures, with many roads being inundated 2–4 h in advance of the approaching storm. Peat collapse expected after the storm only in forests of lower productivity from previous human impact.
3	178–208 (111–130 miles h⁻¹)	Mangroves of all sizes highly susceptible to wind fall as they reach a wind velocity threshold established by Category 3 designation (Doyle *et al.*, 1995), especially species with lighter wood densities; nearly all large trees blown down or snapped, and smaller trees and shrubs sustaining moderate to heavy damage, often having damage to vascular structures if they do not break. Litter and branches ripped from trees, with extensive additive volumes of debris fall, affecting growth phenology of surviving mangrove trees into the next few growing seasons. Seedlings with moderate damage and saplings with heavy damage from wind, woody debris, tree/branch fall and surge. Surge to 2.7–3.6 m above normal. Wrack deposition extensive, containing similar elements to Category 2 storms but also including larger debris (e.g. trees) and larger human-sourced debris capable of physically damaging the mangrove forest. Sedimentation extensive (up to 40 mm) from upland, resuspended and autochthonous sources capable of covering emergent root lenticels. Great damage to coastal built structures, with debris from that damage infiltrating mangrove forests from wind throw and water. Most roads are inundated 3–5 h in advance of the approaching storm. Peat collapse expected in some forests after the storm, and imminent in forests of lower productivity from previous human impact.
4	2109–251 (131–155 miles h⁻¹)	All trees are affected extensively, with most trees and shrubs blown down or snapped, and saplings and smaller trees often sheared off (Craighead and Gilbert, 1962) in lieu of simply sustaining damage to vascular structures. Canopy loss of foliage and small branches extensive, both leading to delayed mortality of small surviving trees from foliage loss and affecting growth phenology for surviving mangrove trees into the next few growing seasons. Seedlings and saplings with moderate to heavy damage from all sources, often having to re-adjust to post-storm light intensities through new leaf development in order to ensure survival. Surge to 3.9–5.5 m above normal, submerging small statured mangrove forests aligning fringe locations with ocean water and serving (paradoxically) to buffer those small trees from wind damage in some cases. Terrestrial flooding extending to approx. 10 km inland. Wrack deposition extensive, containing similar elements to Category 2 storms but also including larger debris (e.g. trees) and larger human-sourced debris that physically damages the mangrove forest. Sedimentation even more extensive (up to 40–60 mm) from upland, resuspended and autochoctanous sources capable of covering emergent root lenticels and, in some cases, facilitating deposition of intact sections of soil from nearby damaged wetlands on top of the forest floor. Catastrophic damage to coastal built structures (including many homes), with debris from that damage infiltrating mangrove forests from wind throw and water. Roads are inundated 3–5 h in advance of the approaching storm. Beach erosion extensive, with new channels being forged through creeks and barrier islands, especially those areas without significant mangrove colonization. Peat collapse imminent after storm.
5	≥252 (> 155 miles h⁻¹)	Catastrophic damage incurred by mangrove forests, with 90–100 % destruction being noted in eyewall and immediate right quadrat areas in the northern hemisphere or left quadrat areas in the southern hemisphere. Shrubby mangroves, trees and saplings destroyed with only a few remaining seedlings, probably damaged by debris falling from broken canopies and debris in surge. Surge to >5.5 m above normal, submerging small statured mangrove forests aligning fringe locations with ocean water and serving (paradoxically) to buffer trees from wind damage in some cases. Terrestrial flooding extending to approx. 16 km inland. Wrack deposition extensive, containing similar elements to Category 2 storms but also including larger debris (e.g. trees) and larger human-sourced debris that physically damages the mangrove forest. Sedimentation extensive (>60 mm) from upland, resuspended and autochoctanous sources capable of covering lenticels on large segments of prop roots and entire pneumatophore structures, and facilitating deposition of intact sections of soil from nearby damaged wetlands deposited on top of the forest floor. Catastrophic damage to coastal built structures (including many homes, municipal structures and roads), with debris from that damage infiltrating mangrove forests from wind throw and water. Roads are inundated 4–7 h in advance of the approaching storm. Extensive beach erosion with and without established vegetation, with new channel formation through barrier islands and mangrove forests. Extensive surge and wave scouring evident, undermining mangrove roots. Peat collapse guaranteed after storm.
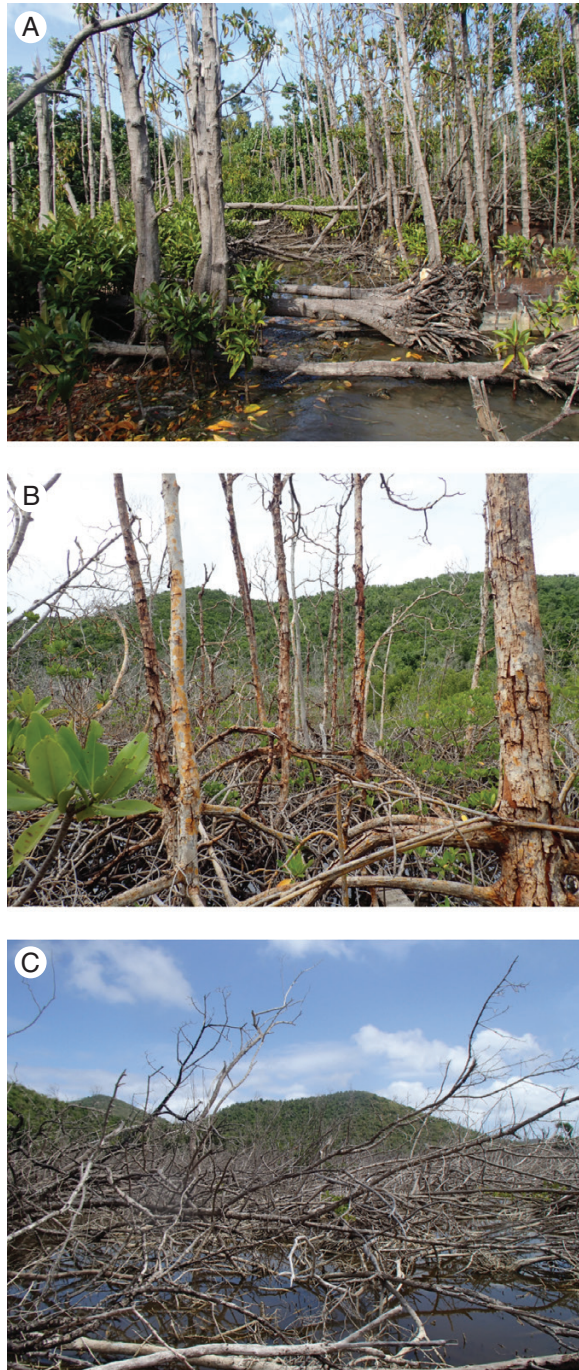
Fig. 2. Examples of the visual damage incurred by mangrove forests from tropical cyclones. (A) Depicts a *Bruguiera gymnorrhiza* forest at the mouth of Saddok Tasi Stream on the Pacific island of Saipan approx. 15 months after Typhoon Soudelor affected the island on 2 August 2015 showing individual tree damage, some re-sprouting and seedling regeneration (photo: K. W. Krauss, U.S. Geological Survey). (B and C) Photographs depict predominantly *Rhizophora mangle* forests along the fringes of Princess Bay (Hurricane Hole) and Leinster Bay (Annaberg Swamp), respectively, on the Caribbean island of St. John (US Virgin Islands) approx. 14 months after Hurricane Irma affected the island on 7 September 2017, showing a range of responses from (B) defoliation, some mid-storey tree survival and limited regeneration, to (C) large structural effects, ponding and few signs of regeneration (photos: Andrew S., From U.S. Geological Survey).

by Woodroffe and Grime (1999) that mangrove species in the family Rhizophoraceae (*Rhizophora* and *Bruguiera*) may be more susceptible to tropical cyclone effects than families such as Avicenniaceae. Perhaps the greater number of species in these families within the old world tropics allow for more prominent species-level trends to emerge at specific threshold wind intensities.

Forest structure

Plot-level assessments of mortality and basal area reductions after a tropical cyclone make use of at least three different approaches: (1) plots are established before the cyclone affects the mangrove forest, with effects being measured in time after the cyclone (e.g. Sherman *et al.*, 2001); (2) plots are established after the cyclone affects the mangrove forest, with pre-effect structure surmised by re-constructing structure from tipped-up or broken stems (e.g. Smith *et al.*, 1994); and (3) plots are established in different locations relative to storm trajectory, controlling for cyclone influences in space (e.g. Kauffman and Cole, 2010). Some assessments combine these approaches (e.g. Doyle *et al.*, 1995). Those techniques that include spatial variability in cyclone effects are likely to be most useful overall because they will translate as new remote-sensing technologies are developed, possibly even leading to less reliance on post-cyclone field surveys in the future.

Mangrove forest structure can be substantially altered by cyclone-induced mortality. In some cases, for example stands with smaller statured trees, lower forest structure can buffer stands against major wind pulses. Taller trees were more likely than shorter trees to suffer breakage from Hurricane Joan in Nicaragua (Roth, 1992), and 70 % of larger adult mangrove trees suffered broken stems in lieu of being uprooted during Cyclone Nargis in Myanmar (Aung *et al.*, 2013). Both McCoy *et al.* (1996) and Smith *et al.* (1994) suggested that taller trees were more susceptible to windthrow in their post-hurricane surveys, but Sherman *et al.* (2001) suggested that size influences among these same mangrove species were more difficult to discern in the Dominican Republic during Hurricane Georges. Species present on site also matter for recovery; snapped stems of *R. mangle* (and *Rhizophora* spp.) equate to mortality, as they are not able to coppice or sprout in other ways (Gill and Tomlinson, 1969), while mangroves of genera *Avicennia*, *Sonneratia*, *Xylocarpus*, *Excoecaria*, *Lumnitzera*, *Laguncularia* and *Conocarpus* readily coppice or sprout (Snedaker, 2002).

Roth (1992) described structural effects and tracked recovery of mangroves for 17 months after Hurricane Joan affected Nicaragua in 1988. There, 45 % of mangroves had broken trunks, and only 41 % of the mangroves began to re-foliate 17 months after the storm. Because larger trees had a greater frequency of broken stems than smaller trees, Hurricane Joan significantly altered the basal area of the mangroves. Re-foliation was registered by smaller trees, suggesting some wind resilience by smaller size classes (Roth, 1992), which would spark recovery. Doyle *et al.* (1995) assessed mangrove forest structure after Hurricane Andrew affected south Florida in 1992 by stratifying data collection into eyepath, right quadrat and

TABLE 2. Summary of mangrove forest mortality from tropical cyclones.

Location	Cyclone name	Category	Maximum sustained windspeed, km h⁻¹	Location*	Species†	Mortality, %‡	Reference
Isla del Venado, Nicaragua	Joan	4	217	Transects 1–3	AVGE	37	Roth (1992)
Southwest Florida, USA	Andrew	4	232	Transects 1–3	LARA	53	Doyle et al. (1995)
				Transects 1–3	RHMA	56	
				Eyepath	AVGE, LARA, RHMA	16–61	
South Florida, USA	Andrew	4	232	Right quadrat	AVGE, LARA, RHMA	3–28	
				Left quadrat	AVGE, LARA, RHMA	2–15	
				Everglades National Park	AVGE	12–66	Smith et al. (1994); Baldwin et al. (1995); McCoy et al. (1996)
				Everglades National Park	LARA	18–90	
				Everglades National Park	RHMA	21–90	
Guadeloupe Island	Hugo	4	160–230	Coastal fringe	RHMA	59	Imbert et al., 1996
				Mixed dwarf	RHMA, LARA, AVGE	26	
				Tall mixed	RHMA	78	
				Black	AVGE	3	
Dominican Republic	Georges	3	194	Los Haitises National Park	AVGE	64	Sherman et al. (2001)
				Los Haitises National Park	LARA	26	
				Los Haitises National Park	RHMA	50	
Pacific coast, Mexico	Rosa	2	167	Agua Grande	RHMA, LARA, AVGE	27	Kovacs et al. (2001)
				Ilsa La Palma	RHMA, LARA, AVGE	37	
				Canas	RHMA, LARA, AVGE	31	
				Chantilla	RHMA, LARA, AVGE	28	
				Punta Burro	RHMA, LARA, AVGE	30	
Bay Islands, Honduras	Mitch	4	188–260	High impact, Fringe	RHMA, LARA, AVGE	100	Cahoon et al. (2003)
				High impact, Basin	RHMA, LARA, AVGE	100	
				Medium impact, Fringe	RHMA, LARA, AVGE	0–94	
				Medium impact, Basin	RHMA, LARA, AVGE	0–50	
				Low impact, Fringe	RHMA, LARA, AVGE	0–5	
				Low impact, Basin	RHMA, LARA, AVGE	0–15	
Yap, Micronesia	Sudal	3 - 4	177 - 209	Windard sites	RHAP, SOAL, BRGY	10–27	Kauffman and Cole (2010)
			119 - 151	Leeward sites	RHAP, SOAL, BRGY	3–8	
Cape Bolinao, Philippines	Chan-hom	2	85–150	11-year-old plantation	RHMU	61	Salmo et al. (2014)
Eastern Samar, Philippines	Haiyan	5	305	18-year-old plantation	RHMU	69	Primavera et al. (2016)
				Maslog, Lawaan	RHAP, RHMU	30	
				Sto. Nino, Quinapondan	BRGY, RHAP, AECO	7	
				Anahaw, General MacArthur	SOAL, AEFL	20	

TABLE 2. Continued

Location	Cyclone name	Category	Maximum sustained windspeed, km h⁻¹	Location*	Species†	Mortality, %‡	Reference
Save River Delta, Mozambique	Eline§	3–4	168–212	Maliwaliw, Salcedo	RHAP, RHST	73	Macamo *et al.* (2016)
				Batang, Hernani	SOAL, AEFL, AVMA	86	
				Abejao, Salcedo	SOAL, RHAP, LULI	0	
				Bagombaua, Guiuan	SOAL, AEFL, RHST	72	
				Creek forests	AVMA, RHMU, CETA, SOAL, BRGY, XYGR	3–29	
				Seaward forests	AVMA, RHMU, CETA, XYGR	21–100	

*Location refers to specific distinctions made by the authors of the manuscript. Please consult the original article for details.

†AECO, *Aegiceras corniculatum*; AEFL, *Aegiceras floridum*; AVGE, *Avicennia germinans*; AVMA, *Avicennia marina*; BRGY, *Bruguiera gymnorrhiza*; CETA, *Ceriops tagal*; LARA, *Laguncularia racemosa*; LULI, *Lumnitzera littorea*; RHAP, *Rhizophora apiculata*; RHMA, *Rhizophora mangle*; RHMU, *Rhizophora mucronata*; RHST, *Rhizophora stylosa*; SOAL, *Sonneratia alba*; XYGR, *Xylocarpus granatum*.

‡When the percentage mortality was unreported, reductions in stem densities were used for its estimation.

§Other cyclones also impacted this study area, including Japhet in 2003 (157 km h⁻¹) and Favio in 2007 (222 km h⁻¹), but Eline caused the most damage in 2000.

left quadrat sections relative to the path of the hurricane. On average, basal area was reduced from 26.4 to 12.2 m² ha⁻¹, or by approx. 54 %, within eyepath plots compared with approx. 17 % in right and left quadrat plots (Doyle *et al.*, 1995).

Basal areas were reduced from 18.3 to 7 m² ha⁻¹ on three of four mangrove forest sites on Guadeloupe Island when Hurricane Hugo made landfall in 1989. Imbert *et al.* (1996) divided the mangrove zone into coastal fringe, mixed dwarf, tall mixed and black (i.e. referring to the black mangrove species: *A. germinans*). While the black mangrove zone was nearly unaffected by the tropical cyclone (3 % reduction), overall basal area reductions to the other three zones averaged 23–68 %. The lower percentage was registered in the dwarf stand of lower height. Surveyed upland forests also had fewer visible effects than the mangroves, with Guadeloupe's upslope rainforests averaging 11 % and semi-evergreen forests averaging 12 % basal area reductions (Imbert *et al.*, 1996). Sherman *et al.* (2000) divided the mangrove forests of the Dominican Republic into *R. mangle*-, *L. racemosa*- and *A. germinans*-dominated zones along two transects. Plots were established in 1994 and Hurricane Georges made landfall 4 years later in 1998. Basal areas were reduced by 68 % in the three plots dominated by *A. germinans* (from 20.4 to 6.6 m² ha⁻¹), by 44 % in the 12 plots dominated by *R. mangle* (from 23.8 to 13.4 m² ha⁻¹) and by 19 % in the four plots dominated by *L. racemosa* (from 40.9 to 33.0 m² ha⁻¹) (Sherman *et al.*, 2001). Visible effects were less on the *L. racemosa* forest in that instance, presumably because wind resistance was provided by an even *L. racemosa* canopy (Sherman *et al.*, 2001). Canopy structuring potentially explains discrepancies in interspecies susceptibilities found among studies (e.g. Smith *et al.*, 1994; Imbert *et al.*, 1996). Collectively, these studies reiterate that the effects of tropical cyclones on mangroves can be highly case specific.

Kovacs *et al.* (2001) established five transects relative to the passage of Hurricane Rosa on the Pacific coast of Mexico and discovered that basal area was also reduced by 32–71 % depending on the location of the mangrove forest relative to the storm's track. Again, species presence was important and few small diameter trees were uprooted; when stems were broken, all *R. mangle* died and, when larger trees were uprooted, *L. racemosa* fared better (39 % dead) than *A. germinans* (77 % dead) (Kovacs *et al.*, 2001). On the Island of Yap (Micronesia), Typhoon Sudal affected the mangrove forests in 2004. Kauffman and Cole (2010) established study plots after the storm based upon cyclone trajectory and discovered that plots established on the leeward side of the storm had very high basal areas of 72 m² ha⁻¹ but, in comparison, plots established on the windward side of the storm had lower basal areas of 54 m² ha⁻¹. Tropical cyclone effects led to a 226 Mg ha⁻¹ reduction in total above-ground stand biomass in Yap, or >52 % loss of what was standing before Typhon Sudal hit (Kauffman and Cole, 2010). Tropical cyclones do not affect Yap very often, so there was a lot of biomass available to be lost from a single event. Mangroves in Panama were noted to attain twice as much biomass as the mangroves of south Florida and Puerto Rico, which are affected by tropical cyclones more frequently (approx. 50 per century for Puerto Rico if cyclones of all intensities are tallied: Lugo, 2000). Cyclones can also pose a risk to commercial mangrove forestry operations in regions with high tropical cyclone frequencies. For example, Typhoon Chan-hom

reduced above-ground biomass of mangroves growing in 11- and 18-year-old plantations in the Philippines by 70–79 % (Salmo *et al.*, 2014). Commercial forestry operations often produce mangrove forests with more uniform canopies, which could theoretically reduce wind influences from lower intensity cyclones through this type of stand management.

Litter and woody debris fall

Annual litterfall of leaf, twig and reproductive debris in mangrove forests ranges globally from 1.3 to 27.6 Mg ha^{-1} year^{-1} (Saenger and Snedaker, 1993; Krauss *et al.*, 2014), the full balance of which can be deposited on the forest floor from any single tropical cyclone event in less than a few hours. Adame *et al.* (2013) even suggested that, with all else being equal, mangrove stands with moderate frequency of tropical cyclone effects develop higher rates of litterfall production over time vs. stands unaffected or heavily affected by cyclones. Litter and coarse woody debris stores can be high after a cyclone and, particularly in the case of woody debris, can persist for decades. Ten years after Hurricane Andrew, woody debris volume on the mangrove forest floor still ranged from 20 to 181 m^3 ha^{-1} in south Florida (Krauss *et al.*, 2005). Fine woody debris (<7.5 cm diameter) represented approx. 36 % of that total woody debris volume, which would have been deposited in the years after the cyclone. These woody debris volumes equate to a biomass of approx. 23.8 Mg ha^{-1}. In comparison, woody debris biomass ranged from 9.5 to 33.9 Mg ha^{-1}, respectively, in an Australian mangrove forest without major disturbance (Robertson and Daniel, 1989) and a Micronesian mangrove forest undergoing heavy harvesting pressure (Allen *et al.*, 2000).

The ecological role of litter and woody debris after a tropical cyclone has not been systematically assessed in mangrove forests. On the one hand, woody debris movement during a cyclone can cause physical damage to seedlings, saplings and trees. However, on the other hand, woody debris decomposes more slowly than leaf litter, suggesting a role in modulated delivery of nutrients to forests as woody debris decomposition ensues over time (Harmon and Hua, 1991). Different stores decompose at different rates, and all of these components would release nutrients akin to slow-release fertilizers. Leaves on the mangrove forest floor decompose the fastest (0.57 ± 0.08 % d^{-1}) followed by wood (0.10 ± 0.02 % d^{-1}), and both of these sources of nutrients and mineralized carbon are augmented by root decomposition (0.15 ± 0.02 % d^{-1}) (averages from Middleton and McKee, 2001; Romero *et al.*, 2005; Poret *et al.*, 2007), which would mineralize nutrients from below-ground as their supporting stems and canopies are also killed and soils become compacted (Lang'at *et al.*, 2014). Woody debris further serves a role in erosion control, soil pedogenesis, nursery beds for seeds and propagules, structure to trap propagules in large quantities near debris stores, and habitat for heterotrophic communities (Harmon *et al.*, 1986; Allen *et al.*, 2000; Pinzón *et al.*, 2003).

Spatial distribution of effects

When reporting structural effects on mangrove forests, maximum sustained winds and duration of sustainment from tropical cyclones are not always available for specific forests, which might be many kilometres from the nearest weather station. This is a major limitation as these are important details (Lugo *et al.*, 1983) and, where available, would help to describe specific cyclonic influences on the spatial distribution of forest injury. The strongest sustained winds are typically registered in a cyclone's eyewall (Jordan *et al.*, 1960), although, in the northern hemisphere, effects can sometimes be most severe in the storm's right quadrant (Shea and Gray, 1973), spawned by a higher probability of unpredictable wind downbursts and tornadoes in eyewall and immediate right quadrat areas (Novlan and Gray, 1974). Note that the right quadrant in the northern hemisphere corresponds to a left quadrant in the southern hemisphere due to hemispheric differences in cyclone rotation. During Hurricane Andrew in south Florida, the direction of mangrove tree fall corresponded very nicely to model-projected tropical cyclone wind directions from all except one location ($0.26 < r^2 < 0.75$); plots located in right quadrat areas immediately fringing the Gulf of Mexico had substantially lower correlations perhaps because of tornadic activity ($r^2 = 0.05$) (Doyle *et al.*, 2009). Aerial transects revealed greater storm effects along the fringe than from an inland transect, related to greater structural development of mangroves along the fringe, with the majority of those trees being felled by the forewinds of Hurricane Andrew (Doyle *et al.*, 2009). For subsequent tropical cyclones in south Florida, spatially consistent wind damage was most evident among trees over 4 m tall and nearest the coast (Zhang *et al.*, 2016).

Shielding of cyclone winds can occur. For example, mangroves located on the leeward side of Yap were shielded from Typhoon Sudal's major effect relative to windward stands (Kauffman and Cole, 2010), while tree mortality and major pulses of sedimentation were reduced through wind shielding on Roatan, Honduras, during Hurricane Mitch (Cahoon *et al.*, 2003). However, the 3-D structure of mountains can cause wind vortices and vertical sheer that contribute to wind-related injury. Although this type of effect may be more common in upland forests (e.g. Lugo *et al.*, 1983), even there, aspect and exposure were not strong predictors of forest response among Caribbean hurricanes (Brokaw and Walker, 1991). Windward slopes were, however, typically more affected than leeward slopes, but it is uncertain how this would relate uniformly to mangroves developing on flat intertidal planes corresponding to those slopes.

In addition to slope and aspect, mangrove trees developing in canopy gaps tended to be less affected than trees positioned in the canopy during Hurricane Andrew (Smith *et al.*, 1994). This related to average tree size in that trees in gaps were smaller. Such gaps have also been shown to contribute to spatial variability in structure and diversity in upland tropical forests (Brokaw and Grear, 1991; Vandermeer *et al.*, 2000). Considering that many mangrove forests within the Caribbean and other parts of the world have a number of lightning gaps in some stage of recovery (Whelan, 2005; Amir, 2012), gaps would provide significant legacies that contribute to resulting spatial structure of mangrove forests after a tropical cyclone.

The spatial signature of mangrove forest effects from tropical cyclones may be less when viewed across the landscape vs. through the lens of individual plots. Dutta *et al.* (2015) described the spatial effects of three tropical cyclones on

a series of mangrove islands in the Sundarbans of India and Bangladesh from 2007 to 2009. Cyclones SIDR (windspeeds of 46–212 km h^{-1}), Rechmi (windspeeds of 46–83 km h^{-1}) and Aila (windspeeds of 37–111 km h^{-1}) all created major structural change in very small areas of the mangrove forest, but, overall, these tropical cyclones affected the majority of the forest with <10 % effects (Fig. 3). Individual plots would have revealed greater structural effects (>60 %) in some locations, but, overall, visible effects were moderate and varied spatially by cyclone trajectory and size (Dutta *et al.*, 2015). Among the approx. 8568 ha of mangrove area affected by Typhoon Haiyan in the Philippines as it made landfall with windspeeds >252 km h^{-1} (Long *et al.*, 2016), 870 ha were initially severely affected (i.e. trees uprooted and broken, or complete defoliation), 1820 ha were moderately affected (i.e. broken branches, partially broken tree trunks still standing but defoliated) and 5900 ha were minimally affected (i.e. mostly intact with minor defoliation). These damage areas were reduced significantly within 18 months of the initial post-cyclone assessment from recovery (Long *et al.*, 2016).

Hurricane Vance, the strongest storm ever to affect the Australian mainland, removed 5700 ha of the 12 800 ha of mangroves in one region, but within 6 years 68 % of the affected area was recovering (Paling *et al.*, 2008). Finally, 47.8 % of the mangrove forests of Mozambique were affected by Cyclone Eline across a spatial landscape, but mangroves dominated by *Rhizophora mucronata* along the seaward fringes experienced upwards of 100 % mortality, while those forests of different species located along tidal creeks were often intact and recovering (Macamo *et al.*, 2016). Therefore, the development of mangroves along different ecogeomorphic settings (*sensu* Lugo and Snedaker, 1974) seems to have a role in tropical cyclone resilience to wind energy, making it even more difficult to develop surveys that isolate the spatial effects of singular cyclone events on spatially diffuse mangrove forests. Tropical cyclones are often more frequent along some coasts (Fig. 1). Typhoon Eline caused the most effects in Mozambique, but two subsequent cyclones contributed to additional effects (Typhoon Japhet in 2003 and Typhoon Favio in 2007) and, collectively, the effects from these tropical cyclones are difficult to separate (Macamo *et al.*, 2016). Other cases of frequent effects from tropical cyclones include, but are not limited to, the greater Caribbean region (including Florida), parts of Central America, the Philippines and the Northern Marianas Islands.

Biogeochemical effects

The biogeochemical effects of tropical cyclones on mangrove forests are diverse and often context dependent. In some cases, tropical cyclones can improve abiotic conditions, increase nutrient availability and stimulate biotic productivity (Lovelock *et al.*, 2011). However, in extreme cases, tropical cyclones can lead to forest mortality, rapid carbon losses and, while uncommon, the conversion of mangrove forests to an entirely different ecosystem (Wanless and Vlaswinkel, 2005; Smith *et al.*, 2009). Positive biotic effects of cyclones are most pronounced in hypersaline and/or nutrient-poor environments, where the freshwater and nutrient subsidies provided by tropical cyclones

have the potential to alleviate physiological stress and stimulate productivity. For example, in an arid, hypersaline mangrove forest in north-western Australia, Cyclone Pancho increased nutrient availability and enhanced plant growth (Lovelock *et al.*, 2011). Similarly, in the oligotrophic, phosphorus-limited Florida Everglades (USA), phosphorus-rich storm sediments transported by tropical cyclones can increase forest productivity (Chen and Twilley, 1999; Davis *et al.*, 2004; Castañeda-Moya *et al.*, 2010). Karstic-mangrove ecosystems, like those in the Everglades and the Yucatan Peninsula (Mexico) that have developed on calcareous substrates without large terrigenous sediment inputs, are often phosphorus limited (Rovai *et al.*, 2018; Twilley *et al.*, 2018); hence, storm-derived, phosphorus-rich sediments can trigger comparatively large biotic responses in these nutrient-limited systems (Rivera-Monroy *et al.*, 2011; Adame *et al.*, 2013). In contrast, the nutrient-enrichment effects of storm sediments are expected to be less pronounced in mangrove forests that have developed in deltas and other sediment- and nutrient-rich environments. Although storm-derived sediment additions are often beneficial, too much sediment has the potential to bury aerial roots and limit oxygen exchange, which, in extreme cases, can lead to anoxia and forest mortality (Ellison, 1998; Paling *et al.*, 2008). Tropical cyclone floodwaters that are impounded and retained by anthropogenic barriers or cyclone-transported sediments can also produce anaerobic conditions, high sulfide concentrations and/or hypersaline soils, which may lead to forest stress and mortality if the flooding persists or natural tidal connectivity is hindered for an extended period (i.e. months or years) (Lewis *et al.*, 2016). In an arid mangrove system in Baja California (Mexico), a tropical cyclone-transported sand dune hindered tidal exchange and resulted in mangrove degradation; hydrological restoration was subsequently used to restore tidal connectivity and improve abiotic conditions for mangrove recovery (Bashan *et al.*, 2013).

Tropical cyclone effects on carbon cycling in mangrove forests are largely understudied. In the most extreme cases, carbon may be permanently lost and exported from the system if mangrove peat collapses following forest mortality (Cahoon *et al.*, 2003; Wanless and Vlaswinkel, 2005; Smith *et al.*, 2009). Wind-induced leaf defoliation and loss of vegetation structure can result in temporary losses of above-ground carbon, due to reductions in above-ground biomass and productivity; however, these short-term carbon losses are often followed by periods of rapid carbon gains during forest regeneration and recovery (Odum, 1969; Barr *et al.*, 2012; Danielson *et al.*, 2017; Kominoski *et al.*, 2018). The tree heights and above-ground carbon stocks of mangrove forests in cyclone-free regions are often much larger than their counterparts along coasts that are affected by frequent tropical cyclones (Simard *et al.*, 2019), but we expect that the below-ground carbon stocks and soil burial rates in cyclone-active regions vs. cyclone-free regions would be more difficult to generalize.

MECHANISMS OF EFFECT

Structural effects on individual mangrove trees during tropical cyclones occur in three ways: (1) stems are broken; (2) trees are knocked over (tip-ups); or (3) trees remain standing
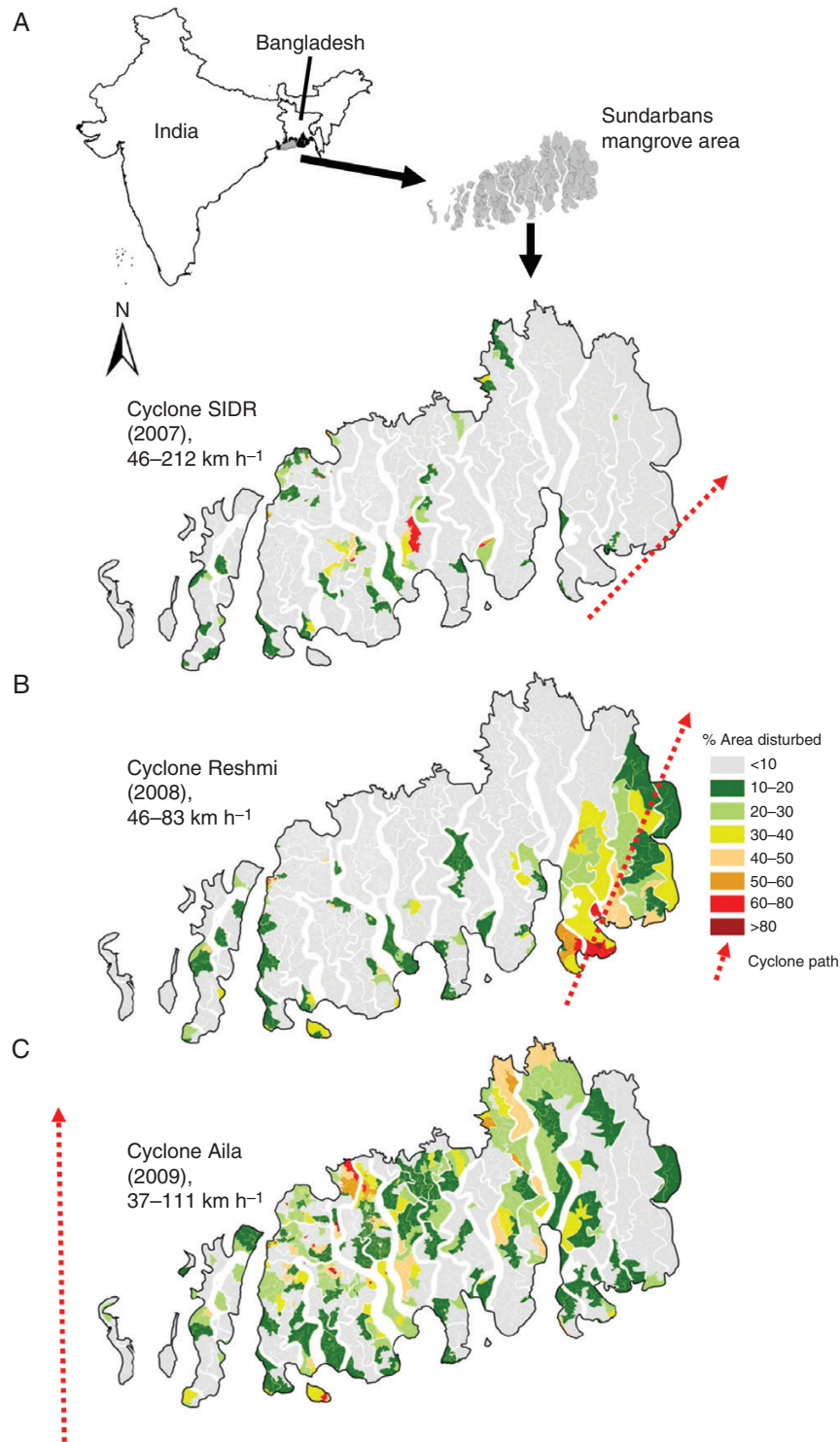
FIG. 3. SPATIAL DISTRIBUTION OF DAMAGE (% area disturbed) caused by three separate tropical cyclones (SIDR, Reshmi and Aila) affecting the Sundarbans mangrove forest of India and Bangladesh from 2007 to 2009. Approximate tropical cyclone storm tracks are depicted by red-dashed arrows. The figure modified is from Dutta *et al.* (2015). Reprinted by permission from Springer Nature Customer Service Centre GmbH: *Natural Hazards* [Assessment of ecological disturbance in the mangrove forest of Sundarbans caused by cyclones using MODIS time-series data (2001–2011)], D. Dutta, 2015.

but are whipped by the wind and sustain internal structural injuries and/or are defoliated. The first two categories are often considered together in post-cyclone effect surveys, as both are often, but not always, lethal. Some insight into the distribution

of each category from a major tropical cyclone event in south Florida can be inferred from McCoy *et al.* (1996), who separated effects according to uprooted vs. broken stems. Across three mangrove species, 49–81 % of the trees were uprooted or

broken, with 43–62 % of those trees being uprooted. A few of the trees with broken stems appeared to be still in good condition; however, most were judged to be dead or in poor condition (McCoy *et al.*, 1996). Roth (1992) reported that 37, 53 and 56 % of *A. germinans*, *L. racemosa* and *R. mangle* trees, respectively, were broken from Hurricane Joan in Nicaragua. Indeed, certain species do tend to have more wind-resistant structural characteristics as rated in survival terms. The mangrove species *Ceriops tagal*, *Rhizophora stylosa*, *Bruguiera parviflora* and *Excoecaria agallocha* were very susceptible to windthrow in Australia, while *Xylocarpus moluccensis*, *Aegiceras corniculatum*, *Aegialitis annulata* and *Lumnitzera racemosa* were not (Stocker, 1976).

Ecophysiology of individual trees

What characteristics of individual mangrove trees dictate relative susceptibility to tropical cyclone winds, or is this left more to chance? In a review, Saenger (2002) suggested that trees susceptible to windthrow are likely to be those with weakly developed cable root systems, or those with structures weakened by erosion, slumping or biological agents. Aerial root structures have long been hypothesized to provide storm resilience to forested wetland trees (Lamborn, 1890), and aerial root structures are diverse and abundant in mangroves (Tomlinson, 2016).

Crown alteration is the most common type of tropical cyclone effect described globally, as the morphological structure of many mangrove leaves (i.e. thick and large) often catch the wind and are ripped off trees (Saenger, 2002). Even during cyclones with lower wind velocities, substantial crown alteration can occur. For example, broken branches and twisted stems were found in 33–71 % of mangrove trees occurring in the Indian River Lagoon, Florida, from a combination of Hurricanes Frances (Category 2) and Jeanne (Category 3) (Vogt *et al.*, 2012). In order to ensure survival of the tree, the canopy must quickly re-grow leaves. A characteristic of *Avicennia* following a tropical cyclone is prolific stem re-sprouting on decurrently growing primary branches that once supported dominant crowns, perhaps serving as a mechanism to quickly re-establish photosynthesis and assist the tree with further structural repairs. Yet, we must keep in mind that in instances where all of the crown is lost, mortality can sometimes occur even in trees with the capacity for secondary lateral bud formation.

New growth from stems must be supported by at least a partially intact vascular structure (xylem) within the stem, and winds can affect the internal anatomical structuring (e.g. induce embolism) of mangrove trees to the point of mortality. Some mangrove trees show recovery of part of their canopy only, potentially related to the parts still supported by an intact vascular structure through the stem in the months following a tropical cyclone. Furthermore, individual branches and trees continue to die long after a cyclone hits, especially among those trees that are uprooted (Walker, 1995). Sherman *et al.* (2001) discovered that 6–9 % of the mangrove trees recorded to be alive 7 months after Hurricane Georges in the Dominican Republic were dead by 18 months. Additional mortality and morbidity occur from a combination of defoliation stress, reduction or alteration of vascular structures and limited carbohydrate stores, which are sometimes exacerbated by greater soil anaerobiosis

from prolonged flooding or sediment smothering post-cyclone. Steinke and Ward (1989) even discovered that physical stress of flooding from two cyclones contributed to the loss of a 75 m shoreline fringe of *Avicennia marina*, with larger trees being directly killed through scour along with the injury from wind. Prolonged flooding sufficient to result in barnacle growth on some mangroves after the cyclone also contributed to delayed mortality from altered soil conditions (greater anaerobiosis). Certainly, natural and human-sourced debris from flooding and storm surge routinely affect or injure mangrove stands and are especially prone to killing seedlings and saplings (Table 1).

The structure of the mangrove stand itself can dissipate tropical cyclone winds. *Laguncularia racemosa* stems experienced uncharacteristically greater survival during a tropical cyclone in the Dominican Republic because of the occurrence of *L. racemosa* within a uniform canopy (Sherman *et al.*, 2001). While the stand provides structural protection, individual *L. racemosa* trees in these stands may also have had a higher stem length to diameter ratio characteristic of many forest plantations; this ratio is suspected in reducing sway frequency during high winds (Sellier and Fourcaud, 2009). Thus, the structure of the mangrove stand can influence individual tree characteristics and survival during a tropical cyclone. Many naturally seeded mangrove forests over a certain height (>5 m), however, have uneven structural characteristics composed of emergent trees potentially more susceptible to initial tropical cyclone winds. While we know very little about patterns of anatomical injury to individual mangrove trees during wind events, studies from other forest types have indicated that material properties of wood (e.g. modulus of elasticity) can have only a limited influence on wind resistance; rather, small differences in individual tree morphology can cause extreme variation in stem oscillations during wind events that compound structural failures in various ways (Sellier and Fourcaud, 2009). Whether a mangrove tips-up or is broken may also be related to these small anatomical variations, position in a stand and substrate, and perhaps less on wood density *per se*. In firm soils in upland forests (Peltola *et al.*, 2000), wind effects occurred more often from stem breakage vs. tip-ups, such as when soils were looser (Coutts, 1986). Mangrove soils are often wet, but soils around mangrove trees can be very firm, providing structural support to mangroves far beyond storm resilience (e.g. McKee *et al.*, 2007). Appreciable soil strength may also contribute in some way to the percentages of broken vs. tipped-up mangrove trees. Crown characteristics also play a role. Trees with larger crowns and leaves that are more resistant to breakage at the petiole cause greater mechanical stress to stems during wind events (Sellier and Fourcaud, 2009).

Ecophysiology of mangrove stands

Mangrove canopies that do survive a tropical cyclone would be expected to encounter different environmental conditions after the storm as sunlight, heat and humidity are also altered. Hurricane Wilma, which passed through the mangrove forests of Everglades National Park in October of 2005 with maximum sustained winds of 176–190 km h^{-1}, caused complete defoliation of the upper canopy comprised of *A. germinans*, *L. racemosa* and *R. mangle* surrounding an established eddy

covariance tower. After the cyclone, soil temperatures down to 50 cm into the soil increased, variability in air temperature increased with higher peak temperatures and greater transport of water vapour from soil to the upper canopy drove latent heat flux increases and sensible heat flux decreases post-cyclone (Barr *et al.*, 2012). These conditions continued through at least 2009 (i.e. 4 years). Residual mangrove canopy trees would not only have to sustain and overcome structural reduction and injury incurred during the tropical cyclone, but would also have to survive a new transpirational diffusion gradient imposed by higher vapour pressure deficits to the canopy. This could press the need for greater stomatal control over canopy water losses.

Recall that the primary driver of water use in forests is the vapour pressure diffusion gradient between the canopy and atmosphere, and, as water is transpired from leaves, pressure builds in stem xylem, which prompts a greater need for water extraction through the stem and from the roots (Cohesion–Tension Theory; Dixon and Joly, 1894). Mangrove stands almost universally have two primary characteristics that allow them to survive these higher vapour pressure deficits after a cyclone: (1) mangroves have strong stomatal control of transpirational water losses (Clough and Sim, 1989); and (2) mangroves have very high rates of water use efficiency, meaning that they need to use very little water to support photosynthesis (Farquhar *et al.*, 1982; Reef and Lovelock, 2015), a characteristic being realized among mangroves at the leaf, stem and stand level (Lovelock *et al.*, 2016). Despite lower total water use of mangrove stands from structural losses after Hurricane Wilma (O'Halloran *et al.*, 2012), surviving mangrove trees might have still been pressed to use more water because of higher vapour pressure deficits in the months following the cyclone as many of the surrounding trees were broken or blown over. Therefore, residual trees may have to deal with additional desalination and less efficient use of water. For example, after Hurricane Wilma, sap flow from the outer sapwood (1.5–2.0 cm) of individual *R. mangle*, *A. germinans* and *L. racemosa* trees averaged 68–179 % higher in surviving trees of broken canopies vs. these same species growing in intact canopies a distance away (cf. Krauss *et al.*, 2015) (Fig. 4), perhaps at least partly reflecting a greater physiological demand for water loss and stomatal regulation from persistently high vapour pressure deficits or enhanced nutrient conditions post-cyclone.

Tropical cyclones impose changes to the net ecosystem exchange of CO_2 and radiative forcing from mangrove forests in line with what has been documented from other forest disturbances (Amiro *et al.*, 2010). Injury to the mangrove canopy from Hurricane Wilma caused a significant decrease in overall photosynthesis, an increase in respiration and a reduced albedo from the underlying dark peat-based soils, altering radiative forcing over the years following the tropical cyclone (O'Halloran *et al.*, 2012). This is not necessarily what happens in other forests as lighter understorey soils are exposed after passage of a cyclone to increase albedo. Tropical cyclone influences on mangrove air and soil temperatures are not consistent though. Among six tropical cyclones to influence mangroves in China, air and soil temperatures were not reduced after the storm, and in only one stand was evapotranspiration higher after the cyclone (Typhoon Megi). All other tropical cyclones imposed relative, though not significant, decreases in evapotranspiration after the cyclone (Chen *et al.*, 2014). While these study sites from China suggest caution when interpreting atmospheric change and stress to the residual canopy in mangroves post-cyclone, both stands assessed in China were located lower in the boundary layer, with canopy heights of 3–4 m, than sites in Everglades National Park, with canopy height averaging 19 m. The climate zone along with underlying soil type, state of forest succession and site index no doubt matter to this assessment (O'Halloran *et al.*, 2012; Chen *et al.*, 2014).
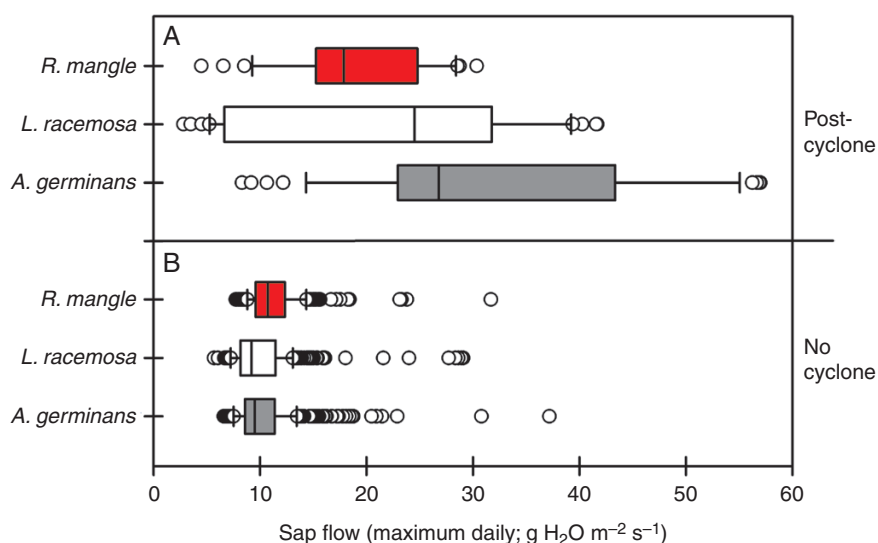

FIG. 4. Box plots with maximum daily individual tree sap flow rates as measured from the outer sapwood of three Neotropical mangrove tree species in Florida, USA. Plot (A) shows relatively high sap flow rates in June and July from individual trees left standing approx. 21 months after Hurricane Wilma damaged mangroves along the Shark River in Everglades National Park on 24 October 2005 (*n* = 2–3 trees per species; 16 d), and plot (B) shows lower sap flow rates from the same mangrove species in May and June of a previous year (2003) within an intact, undamaged canopy at Rookery Bay National Estuarine Reserve, Florida (*n* = 15–18 trees per species; 49 d). U.S. Geological Survey data (V. Engel and K. W. Krauss; after Krauss *et al.*, 2015).

Regeneration systems

Recovery of mangroves after a tropical cyclone by various means is often assured; however, challenges exist. For example, tree mortality from repetitive cyclone strikes can lead to rapid decomposition and compaction of peats, or 'collapse' (Snedaker, 1995; Lang'at *et al.*, 2014), and the increased standing water levels that result may stymie regeneration (Sherman *et al.*, 2000; Cahoon *et al.*, 2003). One obvious mechanism to overcome this (and previously covered) involves the ability of certain mangrove trees to re-sprout either from coppiced stems or from lateral stem sprouts of trees felled by cyclonic winds (Snedaker, 2002). However, data on the percentage of mangrove trees coppicing or re-sprouting after individual storms and their subsequent contribution to the regenerating forest are difficult to find, perhaps because coppicing or re-sprouting can take time and most post-cyclone assessments occur within 2 years of the event. Sherman *et al.* (2001) did report that most of the *L. racemosa* seedlings present 7 months after a tropical cyclone in the Dominican Republic were from basal sprouts, but there were very few *A. germinans* sprouts to be found at that point in time. Also, profuse re-sprouting from dormant epicormic buds was recorded for *L. racemosa* and *A. germinans* after Hurricane Andrew in south Florida (Baldwin *et al.*, 1995), but differentiation between sprout and seedling in-growth to the sapling or young tree stage was not made (Baldwin *et al.*, 2001).

Surge and high tides can serve to buffer and protect seedlings and saplings from wind effects during tropical cyclones. When Cyclone Tracy affected the mangrove forests around Darwin, Australia in 1974, forests were on a rising tide, leaving most saplings and small trees covered in water and unaffected by winds (Stocker, 1976). Ferwerda *et al.* (2007) suggested that flooding of the regeneration pool contributed significantly to a near-complete recovery of the mangrove forest within 10 years of Cyclone Tracy. Short-statured mangroves in Exmouth Gulf may have also been spared some wind and wave effects by being inundated up to one half of the average canopy height during Cyclone Vance (Paling *et al.*, 2008).

Many post-cyclone surveys provide counts of seedlings from two primary seedling-based regeneration systems inherent to mangroves. The first seedling-based regeneration system includes all of the seedlings or saplings that are rooted in the understorey before a tropical cyclone event. This is referred to as advance regeneration (Helms, 1998). Advance regeneration provides an opportunity for seedlings or saplings surviving in the understorey on seed or hypocotyl reserves, sparse side or overhead light, or sunflecks to grow into the mid-storey and eventually replace the mangrove forest that was blown over. While the concept of shade tolerance in mangroves has been questioned (Snedaker and Lahmann, 1988), it is clear that mangrove seedlings and, in some cases, saplings can survive in the understorey for a period of time overlapping cyclonic activity. Because mangrove seedlings and saplings must also balance salinity tolerance, high light levels are eventually required for growth and development in most mangroves (Lugo, 1986). For example, seedling survival in *A. germinans* was higher at low salinity, and increased light levels promoted greater survival under high vs. low salinity in a Venezuelan mangrove forest (López-Hoffman *et al.*, 2007). Mangrove seedlings benefit from higher light levels almost universally and would be stifled long term in the understorey (Krauss *et al.*, 2008).

Paradoxically, seedlings surviving in the understorey after a tropical cyclone would have to adjust to new and more intense light levels once the overstorey is partially or completely removed. This is a common issue in tropical forests as seedlings present in newly formed gaps or larger canopy openings must tolerate photosynthetic light induction and altered cellular metabolism as light levels increase acutely (Press *et al.*, 1996). Avoiding photoinhibition in high irradiance, saline environments is enabled through inherently low stomatal conductance, high photosynthetic water use efficiencies and low light-saturated rates of photosynthesis at the leaf level in order to protect photosystem II proteins, all of which are characteristics of mangroves (Farquhar *et al.*, 1982; Ball and Farquhar, 1984). Thus, photoinhibition is rarely noted in mangroves (Cheeseman, 1991); however, mangrove leaves developing in shaded environments often have high quantum yields (Björkman *et al.*, 1998; Krauss and Allen, 2003), which may indicate that such leaves would not be optimally designed for the higher light environments encountered immediately after a tropical cyclone removes overstorey shading.

The second seedling-based regeneration system includes dispersal of seeds and propagules to understorey locations within cyclone-affected mangroves, which can continue for months to years after a tropical cyclone. Roth (1992) even suggested that the production of propagules in some Caribbean mangrove species might coincide by design with higher hurricane frequencies in August through October, thus recognizing the potential evolutionary importance of dispersing mangrove propagules to post-cyclone recovery. Furthermore, dispersal of propagules can occur over considerable distances as some mangrove propagules can float for many months and remain viable. For example, propagules of *R. apiculata* and *R. mucronata* from Micronesia floated for up to 3 and 5 months, respectively (Drexler, 2001), and propagules of *B. sexangula* from introduced populations in Hawaii floated for >2 months (Allen and Krauss, 2006). Propagules of *R. mangle*, *L. racemosa* and *Pelliciera rhizophorae* floated for >100, 31 and 6 d, respectively, in experiments conducted in Panama (Rabinowitz, 1978), and, among 13 species of Australian mangroves subjected to flotation trials, most floated for >15 d (Clarke *et al.*, 2001). Indeed, some mangroves exhibit a greater capacity for dispersal than is realized in nature, e.g. the majority of *Ceriops tagal* propagules in northern Australia did not disperse >3 m from parent trees (McGuinness, 1996), despite the potential of having >80 % of propagules floating beyond 15 d (Clarke *et al.*, 2001). Thus, much of the seed and propagule base might also be very locally sourced after a tropical cyclone.

As a result of these two regeneration systems, regeneration of mangrove forest trees can be high after a tropical cyclone, and proceed rapidly in some cases (Ferwerda *et al.*, 2007). Some 17 months after Hurricane Joan affected mangrove forests in Nicaragua, 0.68–1.82 seedlings m^{-2} (6800–18 200 seedlings ha^{-1}) were established and represented all four mangrove species present there even though seedlings had to contend with shading from the mangrove-associated fern, *Acrostichum* sp. (Roth, 1992). A general theme among post-cyclone surveys in mangrove forests is variability in recovery (Stoddart, 1969), which might not always be predictable across an affected landscape. For example, in south Florida, mixed-species mangrove forests in Everglades City regenerated more heavily

with *A. germinans* vs. its pre-hurricane distribution, but Broad River mangrove forests regenerated more heavily with *R. mangle* and *L. racemosa* approx. 9 years after Hurricane Andrew affected south Florida (Fig. 5A, C). As further contrast, mixed-species mangrove forests along the Lostmans River regenerated with more equal representation among all three species (Fig. 5B); all three sites sustained large amounts of visible effects because of their location in the eyewall and right quadrats of tropical cyclone circulation (Doyle *et al.*, 1995). On two fringe mangrove forests in south Florida also affected by Hurricane Andrew, much of the regeneration pool for *R. mangle* was present before the cyclone, while densities of *L. racemosa* seedlings increased exponentially for 7 years after the cyclone (Baldwin *et al.*, 2001). Over this same period, regeneration of *A. germinans* increased on one site, but not on the other. In-growth to the sapling stage was prolific but variable by species on each site, with sapling heights increasing considerably between 1995 and 1999 (or 3–7 years after the tropical cyclone). Baldwin *et al.* (2001) concluded that moderate tropical cyclone effects on fringe mangrove forests tended to promote release via advance regeneration of *R. mangle* seedlings, while heavy effects necessitate more reliance on seedling recruitment, which may lead to mixed-species stands upon full recovery of these fringe mangrove forests (Baldwin *et al.*, 2001). Likewise, mangrove forests assigned as coastal fringe and interior fringe in south-eastern Florida were dominated by *R. mangle* stems after the same tropical cyclone in 1992, but both sites differed greatly in seedling numbers at specific heights by 2001 (Ross *et al.*, 2006). Piou *et al.* (2006), who assessed the recovery of mangrove forests in Belize some 41 years after Hurricane Hattie, suggested that early post-cyclone regeneration trajectories greatly influence the stand structure observed well into the future. In some extreme cases, mangrove seedlings are completely stripped from the understorey during tropical cyclones. For example, fringing mangrove forests within one study block were denuded of seedlings (≤40 cm tall) from Cyclone Eline in Mozambique (Macamo *et al.*, 2016). Likewise, Cyclone Vance took a massive toll on *A. marina* forests of north-western Australia in 1999, with the majority of initial post-cyclone regeneration being dominated by *R. stylosa* in lieu of *A. marina* (Paling *et al.*, 2008).

A large threat to post-cyclone recovery for mangroves globally is hydrological modifications incurred before a tropical cyclone event, which can often limit or altogether prevent advance regeneration or successful seeding after a storm because of improper hydrodynamic conditions established before the cyclone (Lewis *et al.*, 2016). For example, a greater number of seedlings were recruited in a tidally unrestricted (69.4 % change in seedling density) vs. tidally restricted (31.2 % change in seedling density) impoundment over a 2 year period following Hurricane Charley on Sanibel Island, Florida (Harris *et al.*, 2010).

SURGE SUPPRESSION AND COASTAL PROTECTION

Identifying the role of mangroves in surge suppression and damage abatement to anthropogenic structures is part of the underlying theme of coastal protection (Gedan *et al.*, 2011; Lee *et al.*, 2014); surge can also affect those protective forests, as

has been documented during past tropical cyclone and major tsunami events (Smith *et al.*, 1994; Kamthonkiat *et al.*, 2011). On the other hand, mangrove forests along estuarine fringes that are flooded by surge from approaching tropical cyclones are afforded some protection from wind (Smith *et al.*, 1994), perhaps even lessening the suppression role of mangroves as waters overtop small stands. Indeed, assigning a role to vegetation in suppression and identifying suppression rates use two very different approaches. The first set of evidence includes a series of empirical assessments from actual tropical cyclone events, whereby water level recorders are present in a cyclone's path. These are uncommon, and the first of these assessments probably did not include many mangroves; however, beach ridges and any marsh-dwelling scrub species would have contributed to an estimated storm surge suppression rate of approx. 6.9 cm km^{-1} (i.e. centimetres of surge suppression per linear kilometre of wetland) through the coastal wetlands of Louisiana along the northern US Gulf Coast (House Document, 1965). Additional published rates of surge suppression from a range of other coastal wetland types, including some that merely re-state previous sources, expand suppression to 4.2–18.9 cm km^{-1} (Krauss *et al.*, 2009), with very few observation points aligned to evaluate specific habitat types. In contrast, water level recorders were positioned just right for two tropical cyclone events affecting south Florida mangrove forests in 2004 (Hurricane Charley) and 2005 (Hurricane Wilma). One series of recorders was aligned inside mangrove forests along the Shark River, recording surge suppression of 4.2 cm km^{-1}, while the other series of recorders was aligned within interior mangrove forests not associated with a river, recording greater surge suppression of 9.5 cm km^{-1} (Krauss *et al.*, 2009).

The second set of evidence includes a series of models of both theoretical scenarios and actual tropical cyclone events. Three-dimensional vegetation structure, different plant types (woody vs. herbaceous), surge height, surge velocity, coastal geomorphology and storm characteristics (Resio and Westerink, 2008) all contribute to surge suppression and can be modelled with some degree of accuracy (Mazda *et al.*, 1997a, b; Sheng *et al.*, 2012). A meta-analysis using wave attenuation data from four mangrove and ten marsh environments indicated that wave height attenuation was similar in marshes and mangroves, despite the more complex vegetation structure in mangroves (Gedan *et al.*, 2011). Actual measurements of surge suppression from storm events assessed over larger distances were universally lower than suggested by modelled rates (Gedan *et al.*, 2011), but the immediate seaward fringe consistently provided the largest surge suppression (Narayan *et al.*, 2010; Zhang *et al.*, 2012).

Suppression of waves by mangroves is sensitive to the speed of the approaching tropical cyclone; reducing that speed by 6.7 m s^{-1} to 2.2 m s^{-1} is equivalent to the difference between a Category 3 and a Category 5 cyclone in terms of flooding (Liu *et al.*, 2013). The faster the storm moves inland the more effective mangroves are in attenuating surge. Thus, there are a large number of simulation scenarios to consider, so the most effective way to handle modelling is to consider actual scenarios of coastline geomorphology or characteristics of past tropical cyclone events. Mangroves (6–10 m tall) were found to decrease cyclone wave heights by 60 % under simulated conditions, suggesting that bands of mangroves just 300–800 m wide placed in front of surge will greatly reduce
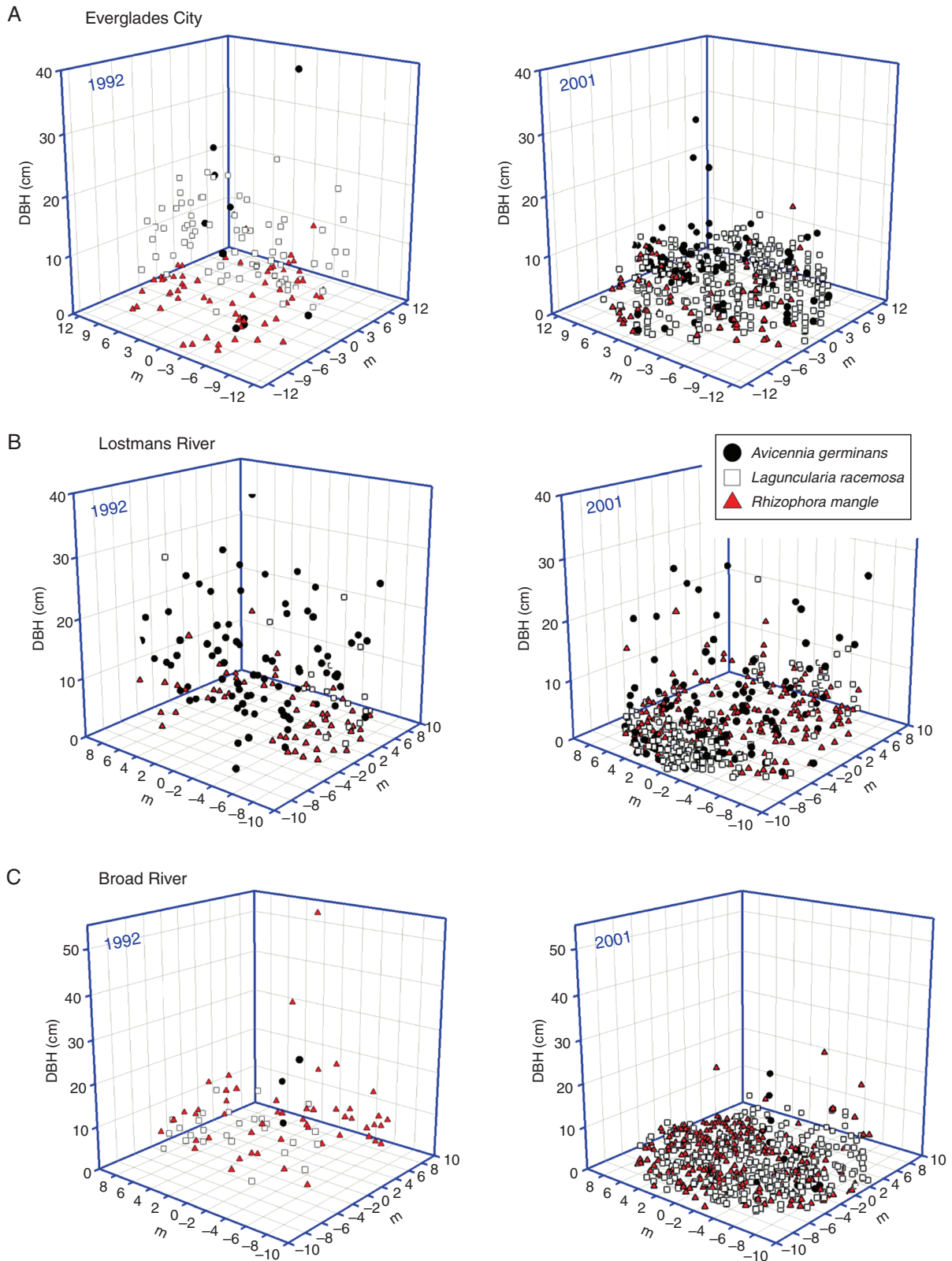
FIG. 5. SPATIAL DEPICTION OF INDIVIDUAL MANGROVE TREE DIAMETER AT BREAST HEIGHT (DBH: CM) DISTRIBUTIONS WITHIN 10–13 M RADIUS CIRCULAR PLOTS PRIOR TO SUSTAINING DAMAGE FROM HURRICANE ANDREW (GRAPHS LABELLED 1992) and 9 years after sustaining damage from Hurricane Andrew and showing regeneration (graphs labeled 2001). Hurricane Andrew barrelled through the Florida Everglades on 24 August 1992, with (A) Everglades City plots oriented to the north and outside of the eyewall but within the storm's right impact quadrat, and (B) Lostmans River and (C) Broad River plots oriented within the northern eyewall and central eyewall, respectively, of the storm. U.S. Geological Survey data (T. W. Doyle and T. J. Smith).

damage to built structures (Narayan *et al.*, 2010). Zhang *et al.* (2012), using hindcasts from storm readings, suggested that storm surge suppression from Hurricane Wilma could have been 20–50 cm km^{-1} for bands of mangrove 6–30 km wide. Much of the suppression documented by their modelling occurred within the first 3 km of the mangrove band from open water inland. Indeed, for the series of recorders aligned during Hurricane Charley's approach to the Ten Thousands Islands region of Florida, suppression was highest in the 2.3–3.2 km band (15.8 cm km^{-1}), intermediate in the 3.2–4.5 km band (9.4 cm km^{-1}) and lowest in the 4.5–5.5 km band (4.1 cm km^{-1}) from the open estuary, with the latter two bands dominated by marsh (Krauss *et al.*, 2009).

The specific differences associated with cyclones vs. normal waves and tsunamis have created some confusion in modelling. Tropical cyclone-generated storm surges act like a high tide event fostering a temporary increase in sea level (Lowe *et al.*, 2001). As that surge moves inland, barometric pressure decreases commensurate with the intensity of the tropical cyclone to allow for water volume expansion to add to surge intensity, and strong winds can create additional 'normal waves' superimposed on the top of surge to compound effects (Wells, 2012). Therefore, it is not appropriate to simply apply a normal wave model to surge suppression; energy, wave amplitude, pressure and velocity are different (von Storch and Woth, 2008). It is uncertain how some of the more notable models of surge waves account for this difference (see Baird *et al.*, 2009), or how 3-D vegetation structure is accounted for as water levels increase to higher vegetation layers during the surge, *sensu* Sheng *et al.* (2012). For example, using normal wave models, wave height is suppressed by 20 % over 100 m of mangrove (Mazda *et al.*, 1997a) and by 50 % over 150 m of mangrove when simulating *Rhizophora*-style prop roots (Brinkman *et al.*, 1997). This is not a reasonable expectation of suppression for tropical cyclone-generated surge events through mangroves. Likewise, a tsunami creates a different scenario. Despite the publication of 54 papers on the topic of coastal protection by mangroves between 1972 and 2005 (Dahdouh-Guebas and Jayatissa, 2009), protection offered by tropical cyclone surge suppression for specific events may still be overstated by modelling (Baird *et al.*, 2009).

SEDIMENTATION, SURFACE ELEVATION CHANGE AND RESPONSES TO SEA-LEVEL RISE

In the face of accelerated-sea level rise, the fate of mangrove forests will depend upon their ability to adjust their vertical and horizontal position in the landscape via local surface elevation change (Krauss *et al.*, 2014; Woodroffe *et al.*, 2016) as well as via horizontal migration into upslope and/or upriver ecosystems (Enwright *et al.*, 2016; Borchert *et al.*, 2018). The sedimentation and surface elevation changes that are triggered by tropical cyclones can affect local, soil surface elevation in positive and negative ways. Mangrove ecosystems are, in general, highly resilient ecosystems that can often tolerate or quickly recover from tropical cyclones, as discussed in previous sections. Nevertheless, there are a few examples throughout the Holocene where potent tropical cyclones have resulted in mass mangrove mortality followed by peat collapse, soil elevation losses and

conversion to mud flats (Jones *et al.*, 2019). One example of cyclone-induced peat collapse comes from the Cape Sable region of Florida's Everglades National Park (USA), where forest mortality and peat collapse triggered by the powerful 1935 Labor Day Hurricane – the most intense tropical cyclone to make landfall in the USA (Landsea *et al.*, 2015) – resulted in the local loss of mangrove forests, which were replaced by mudflat ecosystems (Bischof, 1995; Wanless and Vlaswinkel, 2005; Smith *et al.*, 2009). Another example of peat collapse occurred in the Bay Islands of Honduras, where mass mangrove mortality caused by Hurricane Mitch resulted in rapid elevation losses 18–33 months after the storm (11 mm year^{-1}) due to decomposition of root material and sediment compaction, and which were modelled to continue for at least another 8 years at a reduced rate (7 mm year^{-1}) (Cahoon *et al.*, 2003).

In contrast to these examples of negative cyclone effects, there are many examples of positive effects of tropical cyclones on soil surface elevation change. Tropical cyclones have the potential to deliver nutrient-rich sediments to mangrove forests (Castañeda-Moya *et al.*, 2010, 2013; Lovelock *et al.*, 2011; Smoak *et al.*, 2013; Breithaupt *et al.*, 2014, 2017). Although excessive sedimentation can bury roots and lead to mortality (Ellison, 1998; Paling *et al.*, 2008), moderate sediment deposits can stimulate plant growth and produce immediate gains in soil surface elevation. For example, in the Florida Everglades, Hurricane Wilma deposited up to 8 cm of sediment onto the forest surface; sediment deposition during this storm was negatively correlated with distance upstream and was estimated to be equivalent to between 18 000 and 27 000 dump truck loads of sediment (Smith *et al.*, 2009; Whelan *et al.*, 2009). While a portion of this storm sediment was lost due to erosion, much of it was quickly stabilized by the upward growth of mangrove roots. Using pre- and post-Wilma measurements at surface elevation table-marker horizon (SET-MH) stations, Whelan *et al.* (2009) found that some of the gains in elevation due to the storm sedimentation were later offset by compaction below the soil surface; however, the net elevation effect of the storm during the measurement period was positive, resulting in a net rate of change that was greater than the rate of relative sea-level rise (Whelan *et al.*, 2009; Feher *et al.*, 2019) (Fig. 6). In the Everglades, most of the cyclone-derived sediments come from the ocean; however, in watersheds that are more sediment rich, tropical cyclones also have the potential to deliver terrigenous sediments to mangroves from upstream ecosystems. Given the potential for future increases in storm intensity, it is possible that sediment delivery and elevation change in some mangrove forests could increase. However, long-term elevation change data from mangrove forests are rare, and there is clearly a need to advance understanding of the contribution of storm sediments to long-term elevation changes relative to rising sea levels.

In addition to affecting local responses to sea-level rise via elevation changes, tropical cyclones also have the potential to facilitate landward migration and adaptation to sea-level rise by transporting mangrove propagules long distances, into upslope and/or upriver locations. For example, in the south-eastern USA and the Caribbean, a portion of the hurricane season coincides with the timing of mangrove propagule production. As a result, cyclones and other tropical storms can transport propagules

longer distances than possible under normal tidal fluctuations. Peterson and Bell (2012, 2015) demonstrate the critical role of high water events, such as storm surges, for lifting mangrove propagules above vegetative barriers and across the mangrove ecotone, where they may become entrapped and established within an adjacent plant community. These cyclone-mediated, long-distance dispersal events can facilitate mangrove landward migration in response to sea-level rise.

CLIMATE CHANGE AND TROPICAL CYCLONE EFFECTS ON MANGROVES

In the coming century, the global frequency of tropical cyclones is expected either to decrease or remain essentially unchanged in response to climate change (Christensen *et al.*, 2013; Kossin *et al.*, 2017). However, at the global scale, climate change is expected to: (1) increase the frequency of the most intense tropical cyclones; (2) increase the amount of rainfall produced by tropical cyclones near the cyclone centre; and (3) increase the poleward distribution of tropical cyclones (Knutson *et al.*, 2010, 2015; Christensen *et al.*, 2013; Sobel *et al.*, 2016; Kossin *et al.* 2017; Patricola and Wehner, 2018). Collectively, these projections indicate that tropical cyclone effects on mangrove forests in some regions could be amplified in the future. However, future changes in cyclone activity are less consistent, and challenging to predict at the regional scale. Increases in cyclone intensity may increase the frequency of extreme events that result in local mangrove mortality, peat collapse and mangrove conversion to open water. Tropical cyclone effects will also be modulated by interactions with other aspects of climate and land use change (Osland *et al.*, 2018; Sippo *et al.*, 2018). For example, rising sea

levels and increased precipitation are expected to increase storm surge effects, and the poleward expansion of tropical cyclone pathways may enhance the long-distance poleward dispersal of mangrove propagules (Van der Stocken, 2019*a*, *b*; I. C. Feller, pers. commun.), which could facilitate the poleward expansion of mangrove forests in response to warming winter temperatures. Moreover, anthropogenic activities, such as urban and agricultural encroachment, can lead to habitat fragmentation and nutrient enrichment, which can affect mangrove responses to tropical cyclones (Feller *et al.*, 2015). As noted throughout this review, mangrove forests are highly resilient ecosystems that have continuously adjusted to dynamic, ever changing abiotic conditions at the land–sea interface. In response to past changes in climate and sea level, mangrove forests have used long-distance dispersal mechanisms to migrate to new positions in the landscape as well as biogeomorphic feedbacks to adapt locally. In the coming century, mangrove forests will use these same mechanisms to adapt to future change. From a coastal management perspective, humans can help facilitate mangrove adaptation to climate change by restoring favourable abiotic conditions in existing mangrove forest as well as ensuring that landward migration corridors are available for future migration into adjacent upland and upriver ecosystems (Enwright *et al.*, 2016; Borchert *et al.*, 2018).

CONCLUSIONS AND PERSPECTIVES FOR ADDITIONAL STUDY

The influence of tropical cyclones on structural characteristics of mangrove forests depends not only on storm characteristics, but also on ecogeomorphic location, stand structure, previous wind events, regeneration present before the storm, seed and propagule dispersal potential after the storm, nutrient conditions, the characteristics of individual species present in the mangrove forest being affected and whether hydrological processes have been altered before the cyclone (Fig. 7). With continued study, we may one day improve predictions of mangrove ecosystem responses to individual tropical cyclone events; however, we might also anticipate that wide-scale convergence in responses will be elusive given the variable trajectories of responses to tropical cyclones created by legacies inherent to any one forest (Fig. 7). Indeed, mangroves have an ability to recover from damage and reduce impacts of tropical cyclones, which limits many of the perceived negative effects over longer time frames contributing to their reputation for being 'disturbance adapted'. Cyclones are also a source of potentially important sediment amendments and can facilitate dispersal of mangroves far inland. It is evident that having mangroves along a coastline provides important protective roles from surge and winds. A greater understanding of surge suppression by mangroves could be facilitated by additional empirical assessments to include water-level observations after multiple tropical cyclone events to improve modelling.

Mangrove studies should also focus on establishing, measuring and re-measuring long-term forest plots after singular and repetitive tropical cyclones to understand recovery and resilience with iterative effect, a condition that may become more common in the future with climate change. Along with this is a fundamental need to measure, at the mangrove scale of study, the wind energy
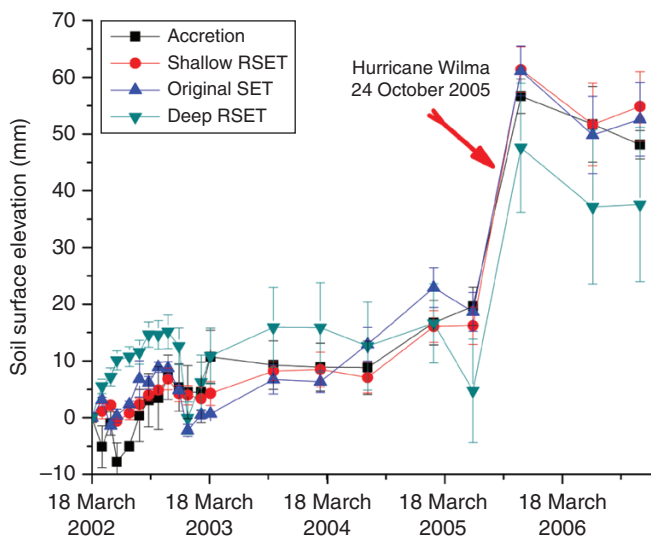
Fig. 6. Sedimentation patterns relative to various soil depths from Hurricane Wilma in a mangrove forest in Everglades National Park, Florida, USA (after Whelan *et al.*, 2009). 'Accretion' represents the deposition of sediment on the soil surface, and 'Shallow RSET', 'Original SET' and 'Deep RSET' represent the influence that sediment deposition had on different segments of the soil profile to include depths of approx. 0–0.35, 0–4 and 0–6 m, respectively. Reprinted by permission from Springer Nature Customer Service Centre GmbH: *Wetlands* [Hurricane Wilma's impact on overall soil elevation and zones within the soil profile in a mangrove forest], K. R. T. Whelan, 2009.
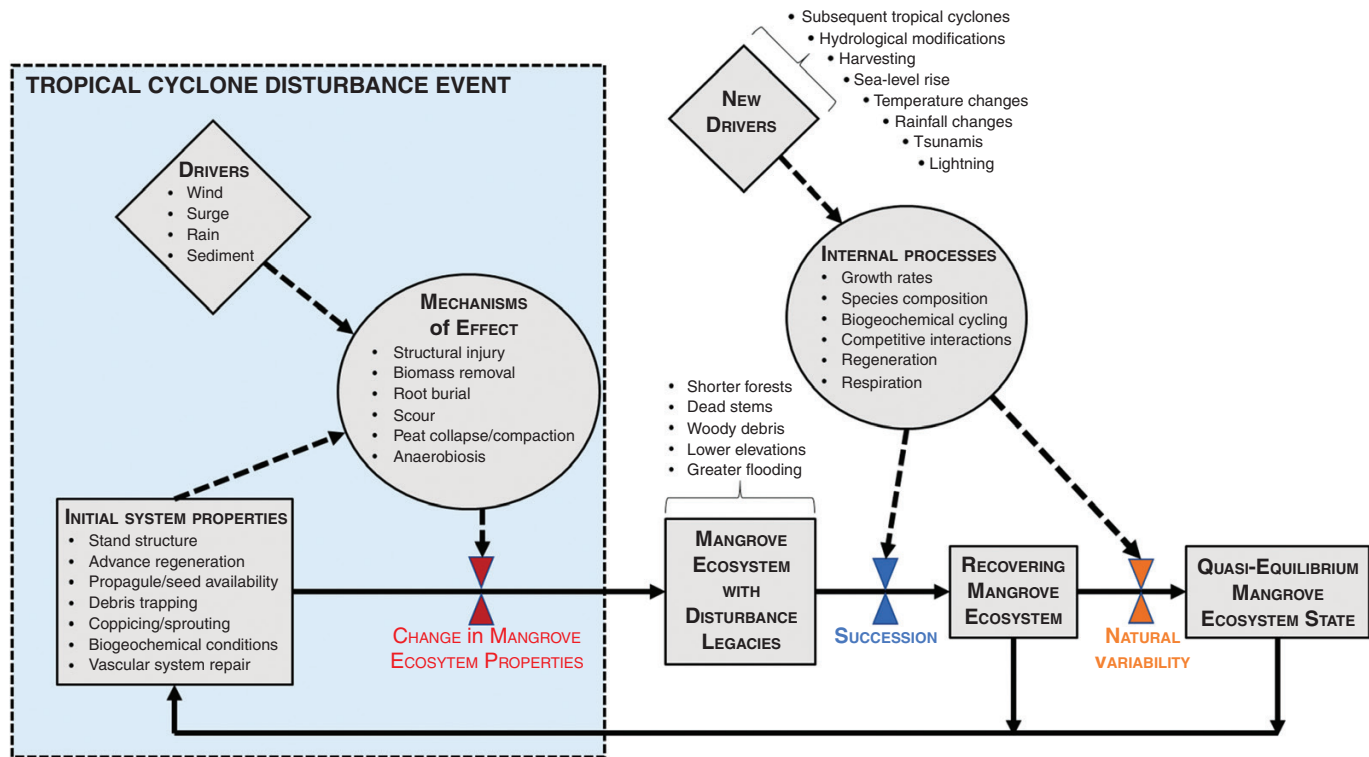
FIG. 7. AN INTEGRATED, DISAGGREGATED VIEW OF THE EFFECTS OF TROPICAL CYCLONE DISTURBANCES ON MANGROVE ECOSYSTEMS (ADAPTED FROM PETERS *ET AL.*, 2011). This conceptual framework includes the effects of an individual tropical cyclone event (large blue box) as well as the contributions of subsequent events and other environmental factors towards the ecosystem reaching a quasi-equilibrium state. In the large blue box, an individual tropical cyclone event consists of three measurable components: (1) the environmental drivers; (2) the initial system properties; and (3) the biological and physical mechanisms of effect. Together, these three components result in a change in ecosystem properties (red symbol and text) and a mangrove ecosystem state with disturbance legacies. Following the cyclone disturbance event (areas outside of the large blue box), subsequent environmental drivers and successional processes (blue symbol and text) will produce a recovering mangrove ecosystem. Ultimately, recurrent disturbance events may produce a quasi-equilibrium ecosystem state with natural variability in ecosystem dynamics (orange symbol and text). Examples are provided as bullets throughout the conceptual framework. Mangroves are especially adept at tolerating legacy effects of past disturbance through this disaggregated view, creating the notion that mangroves are disturbance-adapted ecosystems.

being dissipated by the event; not knowing the wind speed in relation to measurements of response will keep ecologists guessing forever. Efforts should be made to incorporate these long-term forest and wind observations into modelling efforts of post-cyclone recovery such that society can understand their requirements for recovery and availability for future storm shielding. Likewise, if society is to become increasingly dependent on the ecosystem services and recovery of mangrove ecosystems during and after tropical cyclones, more effort must be made to identify mangrove stress on large spatial scales far in advance of tropical cyclone impact so that they can be rehabilitated and remain resilient to storm effects (*sensu* Lewis *et al.*, 2016). Stress comes in many forms, intended and unintended, but all chronic stress affects recovery from acute events in mangroves.

It is also a point of curiosity to understand the unique microclimatic conditions faced by residual standing mangrove trees after a tropical cyclone, created by increased temperatures, reduced or enhanced albedo, greater vapour pressure deficits and larger fluxes of sunlight. Surviving the short-term effects of the tropical cyclone might not be enough. While mangroves are extremely tolerant of harsh environmental conditions within a forest stand setting, there may be thresholds to individual seedling, sapling or tree tolerances when short-term pulses of sunlight or alterations in microclimatic conditions

occur, potentially facilitating delayed mortality of residual plants, which would need to be included in tropical cyclone recovery models. Spatially expansive mangrove forests may be far more resilient to tropical cyclones than smaller stands because the effect is aligned with cyclone trajectory and is partial, with surviving areas serving as seed and propagule sources for affected areas. More information is also needed to determine whether sedimentation events from tropical cyclones have a true long-term positive influence on elevation trajectories in mangrove forests in partially offsetting sea-level rise. Finally, some effort should be directed toward understanding what causes mangroves to be most resilient to cyclones. Does maintaining hydrological connectivity matter most, or are disturbance legacies or other aspects of soil biogeochemistry as important? If the right aspects of the tropical cyclone response and recovery are known among multiple mangrove ecosystems throughout the world, then perhaps management action can target greater resilience of those ecosystems to tropical cyclone events.

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