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Better Resilient than Resistant—Regeneration Dynamics of Storm-Disturbed Mangrove Forests on the Bay Island of Guanaja (Honduras) during the First Two Decades after Hurricane Mitch (October 1998)

Thomas Fickert

Physical Geography, University of Passau, Innstraße 40, D-94032 Passau, Germany;
thomas.fickert@uni-passau.de; Tel.: +49-851-509-2737

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Abstract: Located at the interface of land and sea, Caribbean mangroves frequently experience severe disturbances by hurricanes, but in most cases storm-impacted mangrove forests are able to regenerate. How exactly regeneration proceeds, however, is still a matter of debate: does—due to the specific site conditions—regeneration follows a true auto-succession with exactly the same set of species driving regeneration that was present prior to the disturbance, or do different trajectories of regeneration exist? Considering the fundamental ecosystem services mangroves provide, a better understanding of their recovery is crucial. The Honduran island of Guanaja offers ideal settings for the study of regeneration dynamics of storm-impacted mangrove forests. The island was hit in October 1998 by Hurricane Mitch, one of the most intense Atlantic storms of the past century. Immediately after the storm, 97% of the mangroves were classified as dead. In 2005, long-term monitoring on the regeneration dynamics of the mangroves of the island was initiated, employing permanent line-transects at six different mangrove localities all around the island, which have been revisited in 2009 and 1016. Due to the pronounced topography of the island, different successional pathways emerge depending on the severity of the previous disturbance.

Keywords: Guanaja; mangrove regeneration; hurricane disturbance; successional pathways

1. Introduction

Located at the interface of land and sea, mangroves provide many important ecosystem services for (sub)tropical coastal regions and their population [1–5]. Of particular relevance is the protection against mechanical disturbances such as tropical storms [6–8]. While effectively slowing down wind and wave energy, mangrove forests often experience severe disturbances once a storm hits ([9], for the Caribbean see also [10–14]). How regeneration dynamics of storm disturbed mangrove forests proceed is still a matter of debate: does regeneration—due to the specific site conditions—happen as true auto-succession with exactly the same set of species driving regeneration that was present prior to the disturbance [4,15–18]? Or do different successional trajectories with respect to species composition and vegetation structure and/or disturbance intensity exist [11,19–21]? Can extreme disturbances even transform mangrove forests into different ecosystems [22]?

While there is no shortage of studies focusing on the regeneration of mangroves after hurricane impacts, insight on long-term mechanisms and processes is still poor [23] as most studies are singular studies at varying periods of time after the storm impact and with different study designs, not allowing for the deduction of general trends. Considering the fundamental ecosystem services mangroves provide, a better understanding of the recovery of those forests is crucial, in particular as an increase of the hurricane intensity and/or frequency with global warming is predicted by climate models (on this controversial discussion, see, e.g., [24–32]). The Honduran island of Guanaja provides an ideal setting for the study of long-term regeneration dynamics of storm-impacted mangrove forests. The island was hit in October 1998 by Hurricane Mitch, one of the most intense Atlantic storms of the past century [33]. Infrastructure on the island as well as several ecosystems suffered severe disturbances; amongst those affected were the mangroves [34]. Immediately after the storm, 97% of the mangroves were classified as dead by wind throw, breakage of stilt-roots, or removal of leaf buds [35]. However, five years after the passage of Mitch, differences in regeneration dynamics between windward and leeward mangrove localities became apparent. In 2005, a long-term monitoring project on the regeneration dynamics of the mangrove forests was initiated, employing permanent line-transects perpendicular to the shore from the supratidal zone to the seaward fringe of the mangroves at six different localities all around the island. The transects were GPS-tracked and flagged in 2005 and revisited in 2009 and 2016 to document changes in vegetation development and to allow for the deduction of general successional trajectories for Caribbean mangrove forests after variable preceding disturbance intensities.

2. Materials and Methods

2.1. Study Area

Guanaja is the second largest of the Bay Islands (in Spanish Islas de la Bahia) off the north coast of Honduras (Figure 1). The island has a pronounced relief reaching its highest point in Michael Rock Peak at 415 m a.s.l. According to its latitude of 16°28′ N, the climate of Guanaja is tropical, dominated by trade winds from E to NE for most of the year. The climate chart of the neighboring island of Roatan in Figure 1 depicts the general climatic situation of the Bay Islands [36]. Mean temperature is 27.3 °C, with little seasonal variation. The mean annual precipitation is around 1750 mm with a maximum in winter, when polar-continental cold fronts originating from the North American continent (the so-called "nortes") advance far south into the Caribbean and the Gulf of Honduras [36,37]. Between May and October, tropical low pressure systems regularly move in from the Atlantic, inducing a potential "hurricane season."

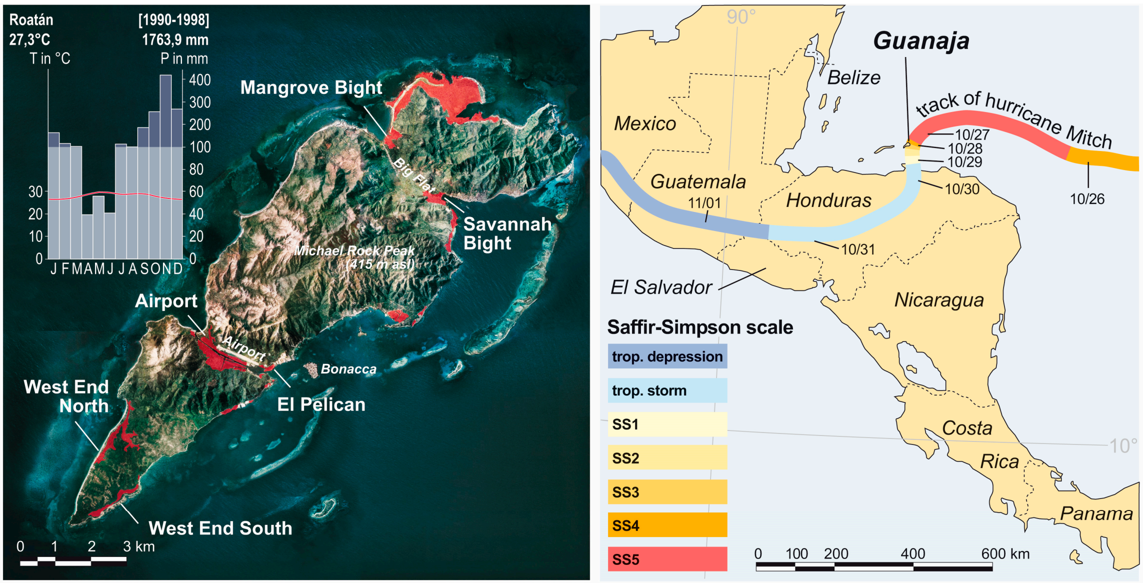


Figure 1. Aerial view of Guanaja (left); highlighted in red are mangroves, those studied are labeled; the climate diagram of the nearby island of Roatan illustrates the general climate of the Bay Islands [36]. To the right is the track of Hurricane Mitch; the different colors indicate the storm strength, the numbers the location of the storm center ("hurricane eye") at the respective dates in October 1998.

Controlled by relief and edaphic conditions, a variety of vegetation types occurs on Guanaja [34]. The mangroves are restricted to flat, poorly drained areas and lagoons along the coast with low wave action (Figure 1). As elsewhere in the Caribbean, *Rhizophora mangle* was (is) the most dominant species, often forming monospecific forests. Where inundation is slightly less, *Rhizophora mangle* is usually associated with *Laguncularia racemosa* and/or *Avicennia germinans* [38]. The transition to terrestrial ecosystems is commonly by a belt of *Conocarpus erectus* and/or the mangrove fern *Acrostichum aureum*.

2.2. Hurricane Mitch

Hurricane Mitch was one of the strongest and most destructive Atlantic hurricanes of the 20th century [33]. Like most hurricanes within the Caribbean Basin, Mitch originated from an easterly wave that developed offshore Western Africa on 8/9 October 1998. After crossing the Northern Atlantic and getting in contact with the warm waters of the Caribbean Sea, this low-pressure system developed into the 13th named tropical storm of the extraordinary storm season of 1998 on 23 October. A day later, the storm reached hurricane intensity, successively strengthening during the next days. On 26 October, the pressure of the storm system reached a minimum of 905 hPa with winds up to 305 km/h, making Mitch the strongest October hurricane ever to occur until that time [33]. Slightly weakening, Mitch made landfall on Guanaja on 27 October as a Category 4 hurricane (Figure 1) but still had very high wind speeds of 195 km/h. As track speed slowed to less than 8 km/h, the center of Mitch remained right off the north coast of Honduras between 27 and 29 October. Despite an ongoing weakening of wind speeds, Guanaja was exposed to heavy winds for about 70 h. Finally, in the night to 29 October, Mitch made landfall on mainland Honduras, where it quickly became a tropical storm, nevertheless causing severe destruction and high number of casualties due to massive rain and subsequent landslides in many Central American states [33].

2.3. Data and Methods

To assess the magnitude of disturbance within the mangrove forests on Guanaja by Hurricane Mitch, a change detection analysis was initially performed [39], employing satellite images prior to and after the passage of the storm (March 1986, Landsat 5 TM, ID: LT50170491986067XXX08; April 2000, Landsat 7 ETM$^+$, ID: LE70170492000098EDC00, respectively). Satellite images were downloaded from http://earthexplorer.usgs.gov/. Pixel values of the earlier image were normalized by linear regression related to the base image of 2000. The change detection analysis itself is based on NDVI-transformed images, and the image differencing was performed by simple subtraction of the two images. The resulting difference image shows the degree of change in vegetation density and/or vitality on the ground (high pixel values indicating a high degree of change). Satellite image analyses were performed by the software IDRISI Taiga.

In 2005, long-term monitoring on the regeneration dynamics of the mangroves on Guanaja was initiated, employing permanent line-transects (line-intercept method, see [40]) at six different mangrove localities all around the island (Figure 1). The transects run perpendicular to potential ecological gradients (as recommended by the authors of [41]) from the supratidal zone to the seaward fringe of the mangroves. According to size and outline of the mangrove area, the number of transects per site as well as their length is variable. Collectively, eleven transects were surveyed: four in West End North (50 m, 50 m, 50 m and 60 m), two in Mangrove Bight (250 m and 300 m), one in Savannah Bight (550 m), one in El Pelican (110 m), one in Airport (200 m), and two in West End South (150 m and 110 m), totaling almost 1900 m. Along the transects the sections of the measuring tape covered by living plant species (including seedlings) were recorded species-wise with a resolution of 0.1 m. Woody debris was recorded in the same manner. Those linear measures (in m) were converted afterwards to ground-cover values in % per 10 m segments for each species (see Figure 2). The taxonomy of species is in accordance with [42]. Additionally, lifeform affiliation for each taxon was determined (in accordance with [43], see also Table 1). The transects were GPS-located and flagged by colored ties to allow for exact relocation during subsequent resurveys. Resurveys took place in 2009 and 2016.

Table 1. Species list (incl. family and life-form affiliation) of all plant species encountered at different sites and dates. Figures are mean ground cover values for a particular site and date.

Species	**Family**	**Life-form**	**Westend North**			**Mangrove Bight**			**Savannah Bight**			**El Pelican**			**Airport**			**West End South**		
			2005	**2009**	**2016**	**2005**	**2009**	**2016**	**2005**	**2009**	**2016**	**2005**	**2009**	**2016**	**2005**	**2009**	**2016**	**2005**	**2009**	**2016**
unidentified climber	unknown	climber													1.3	0.95				
Acrostichum aureum	Adiantaceae	fern				22.26	22.07	19.65					0.36	0.4	9.05	37	23	9.3	9.57	8.42
Sesuvium portulacastrum	Aizoaceae	herb					0.25	1.4		0.11	0.13									
Blutaparon vermiculare	Amaranthaceae	herb					2.63	16.41		0.13										
Rhabdadenia biflora	Apocynaceae	climber													7.25	5.8	9.15	1.46	1.86	
Acoelorraphe wrightii	Arecaceae	palm										1.8	1.91	2.2						
Cocos nucifera	Arecaceae	palm																0.77	0.87	0.87
Eclipta prostrata	Asteraceae	herb					0.04													
Pachira aquatica	Bombacaceae	tree													3.9	5.05	4.85			
Cakile lanceolata	Brassicaceae	herb					0.4													
Tillandsia dasyrilifolia	Bromeliaceae	epiphyte	0.1			0.1									0.35	1.05	3.45	0.14	0.09	
Conocarpus erecta	Combretaceae	tree	1.99	2.49	2.95	0.92	0.87	1.4							22.1	18.75	11.25			
Laguncularia racemosa	Combretaceae	tree	6.2	8.2	9.29	0.68	1.62	15.47	0.67	5.15	8.33		3.82	6.9	15.85	25.55	36.45	2.64	4.02	9
Cyperus esculentus	Cyperaceae	herb	0.29	0.33	0.42			0.06							0.65					
Dalbergia cf. *brownei*	Fabaceae	climber													4.55	6.65	5.65			
Vigna luteola	Fabaceae	climber														0.9				
Myrmecophila tibicinis	Orchidaceae	epiphyte				0.02												0.05		
unidentified orchid	Orchidaceae	epiphyte														0.05	0.2			
Distichlis spicata	Poaceae	graminoid					0.54	0.24		4.35			0.73	1						0.5
Spartina spartinae	Poaceae	graminoid					0.29													
Rhizophora mangle	Rhizophoraceae	tree	70.29	77.86	75	0.26	1.74	20.18	1.78	6.38	43.13	15.2	17.36	46.1	47.65	41.1	46.25	6.43	9.76	39
Typha domingensis	Typhaceae	herb					4.76	4.76												
Avicennia germinans	Verbenaceae	tree						6.87		1.22	3.84	7.1	9.73	5.1						0.92
woody debris			5.89	4.41		16.06	2.42	1.2	8.41	1.73		1.08			7.93	0.6	0.28	22.37	2.59	0.27

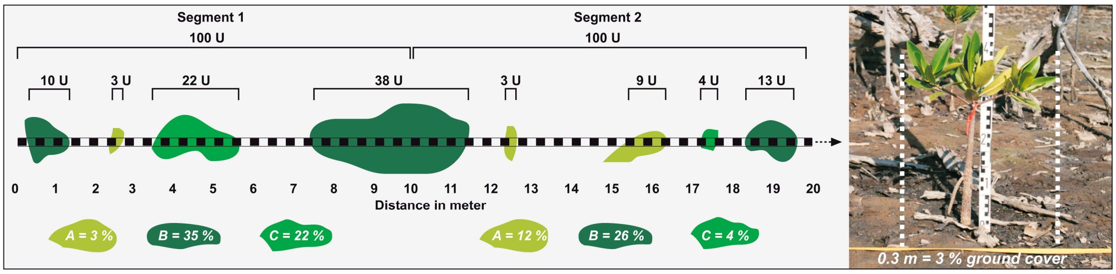


Figure 2. Sampling design of the line-transects employed; sampled distance measures (=units U) of each encountered species (here exemplified for three species A, B, and C) with a resolution of 10 cm were converted to ground cover values in % for 10 m transects segments afterwards.

Data analyses include standard uni- and multivariate statistical procedures. For the visualization of general trends of temporal change in ground cover of particular functional groups, bar plots of mean ground cover per site were employed. To detect (un)similarities concerning species composition and/or structural features between transect segments of different sites and different sampling dates, a multivariate gradient analysis (principle component analysis, PCA) is employed. PCAs are unconstrained ordination procedures calculated from species data only. The species data set used here consists of an assortment of true species (common mangrove taxa such as *Rhizophora mangle*, *Laguncularia racemosa*, *Avicennia germinans*, *Conocarpus erectus*, and *Acrostichum aureum*) as well as functional groups (such as climbers, graminoids, herbs, epiphytes, freshwater swamp trees, and palms; integrating mainly rare and uncommon taxa). The ordination axes of the resulting PCA represent theoretical gradients that explain the species data best [44]. Results are visualized by an ordination diagram, arranging samples along these meaningful gradients based on the interrelationships among a large number of interdependent variables. Graphical ordinations are displayed as scatter diagrams with samples as symbols and species as arrows, which point from the coordinate origin in the direction toward samples with above-average values of the respective species/functional group, while in the opposite direction samples with below-average values are located. The location of different transect segments within the ordination space allows for a spatio-temporal interpretation of the floristic and/or structural (dis)similarity between different segments or between the same segments of different sampling dates. As an ordination-plot including all transect segments of all three surveys (i.e., almost 600 entries) would be very crowded, data are displayed separately for particular locations and sampling dates to illustrate the direction of change. PCA analyses were performed with CANOCO 4.5, and the species data were log-transformed (x′ = log (x + 1)) to balance extreme values within the dataset [44,45].

3. Results

Prior to Hurricane Mitch mangroves covered an area of 243 ha on the island of Guanaja [37]. Exposed to the high wind and wave energy caused by Mitch, the mangroves were among the ecosystems hit most severely on the island [34]. The change detection analysis in Figure 3 illustrates that most of the mangroves of the island experienced a strong alteration caused by breakage of the delicate stilt roots of the dominating *Rhizophora mangle*, by windthrow of *Laguncularia racemosa* and *Avicennia germinans*, and/or by the removal of leaves and leaf buds in standing mangrove trees [36]. Immediately after the passage of Mitch, 97% of the mangroves were classified as dead [35]. However, during the initial survey in 2005, seven years after Mitch, obvious differences in the state of recovery were observable, most likely due to varying previous storm impacts related to location and topography of the island.

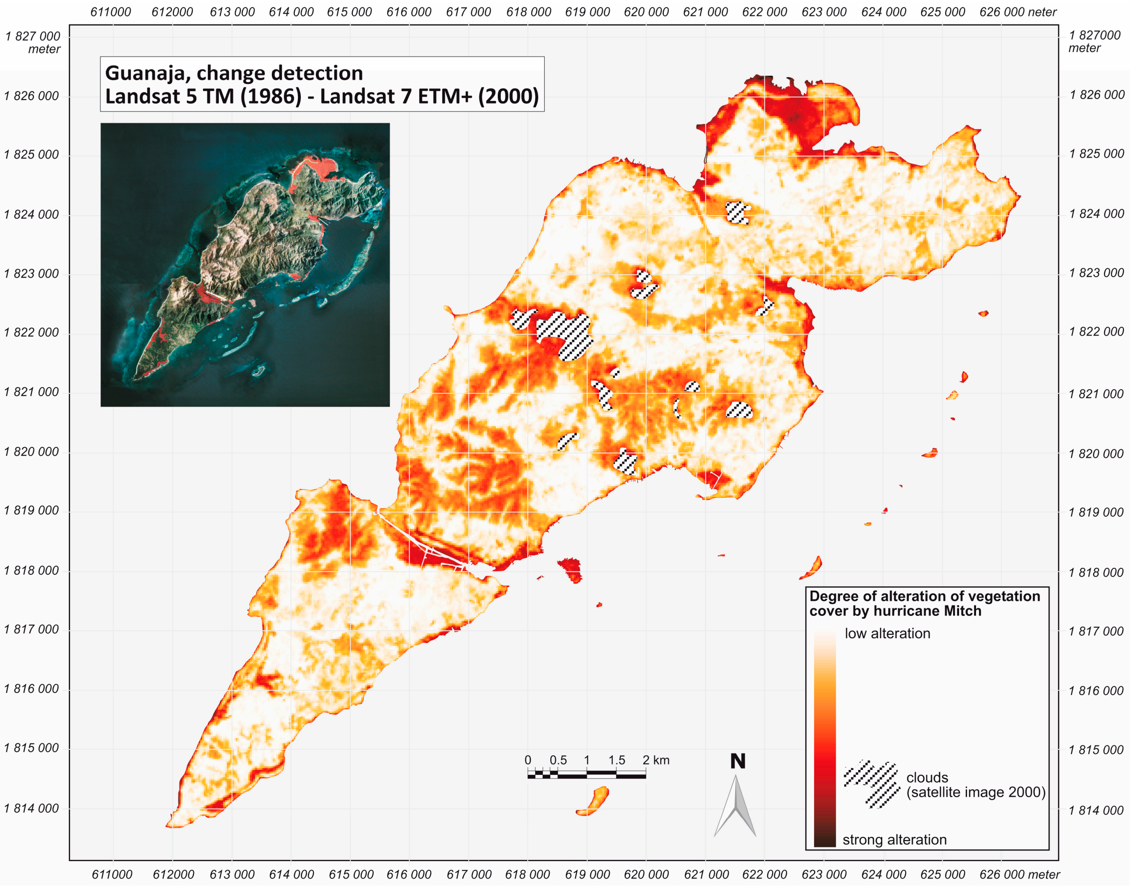
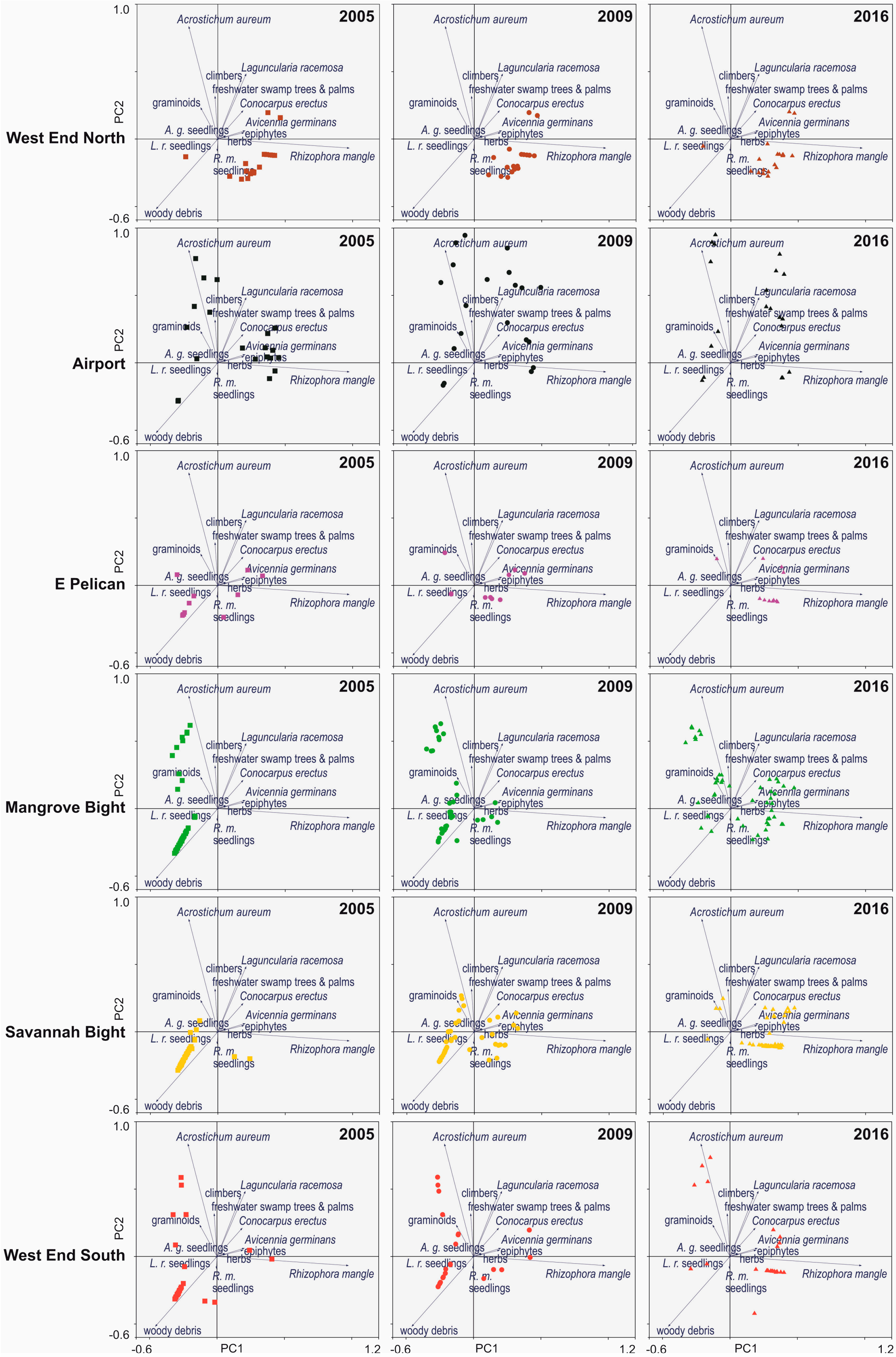


Figure 3. Difference image of two NDVI-transformed satellite images, one prior to (1986) and one after (2000) the passage of Hurricane Mitch. Areas of strong alteration correspond primarily with the mangroves (highlighted in red within the inserted aerial view of Figure 1; the other terrestrial formation strongly altered by Hurricane Mitch is the pine forest, see [34]).

Those differences in disturbance intensity and regeneration dynamics become apparent in the PCA analysis (Figure 4). The ordination space is primarily defined by living mangrove taxa (*Rhizophora mangle* and to a lesser degree by *Laguncularia racemosa* and *Avicennia germinans*) on the right side and by low or even absent cover of living mangrove species on the left, by the light-demanding mangrove fern *Acrostichum aureum* in the upper part of the ordination space as well as by woody debris in lower left corner. Simply speaking, transect segments without living mangrove vegetation are concentrated on the left side of the y-axis in Figure 4, while vital mangroves or those showing signs of regeneration are located on the right. Figure 4 illustrates that the *Rhizophora mangle*-dominated mangroves in West End North (see Table 1) had recovered from hurricane damage by 2005 (almost all transect segments are located in the right quadrants). In the subsequent surveys, there was not much further development going on except for local internal dynamics (e.g., the shift of one transect segment from the right side (in 2009) to the left side (in 2016) of Figure 4 due to the die-back of one adult *Rhizophora mangle* tree). Thus, a quick return to pre-Mitch conditions can be assumed for West End North. Little changes can also be observed for the Airport mangrove in Figure 4, with a continuous co-occurrence of vital (right quadrants), a few disturbed (left quadrants) and fern-dominated transect segments (in the upper left quadrant), and not much change between the three sampling dates. For all other sites, Figure 4 indicates a considerable change by the shift of transect segments from the left side (2005 and 2009) to the right side (2016), indicating a delayed but continuous regeneration of the mangrove forests.



Axes	1	2	3	4
Eigenvalues:	0.317	0.195	0.154	0.084
cum. percentage variance of species data:	31.7	51.2	66.7	75.1

Figure 4. Principal component analysis (PCA) including all transect segments of all sampling dates; for the sake of clarity, data are displayed separately for particular locations and sampling dates.

The differences in the state of regeneration in 2005 led to a rough classification in low, moderate, and high regeneration sites (Figure 5). In general, this classification was valid for the resurvey in 2009, too. During this four-year period, ground cover of mangrove tree species increased in high (West End North) to moderate regeneration sites (El Pelican, Airport, in the latter also the light-demanding mangrove fern *Acrostichum aureum* increased), and in the low regeneration sites (Mangrove Bight, Savannah Bight, and West End South) some developments become apparent, too (see bar graphs in Figure 5): Mangrove taxa increased to about 10% groundcover in Savannah Bight and West End South since the initial survey, while in Mangrove Bight a relatively high amount of salt-tolerant herbs and grasses (close to 10%) established between 2005 and 2009, but almost no mangroves. A strikingly different situation was present in 2016, in particular in the most severely disturbed sites West End South, Savannah Bight, and Mangrove Bight (Figure 6), where mangrove cover skyrocketed within the seven-year period starting from 2009. Moreover, in El Pelican, cover values for mangroves doubled in the same period of time. That a herb- and grass-rich understory does not preclude the establishment of mangrove seedlings (mainly *Rhizophora mangle*) becomes obvious in Mangrove Bight, where both mangrove cover and cover of halophilous herbs and grasses (mainly *Blutaparon vermiculare* and to a lesser degree *Sesuvium portulacastrum*, Table 1) increased.

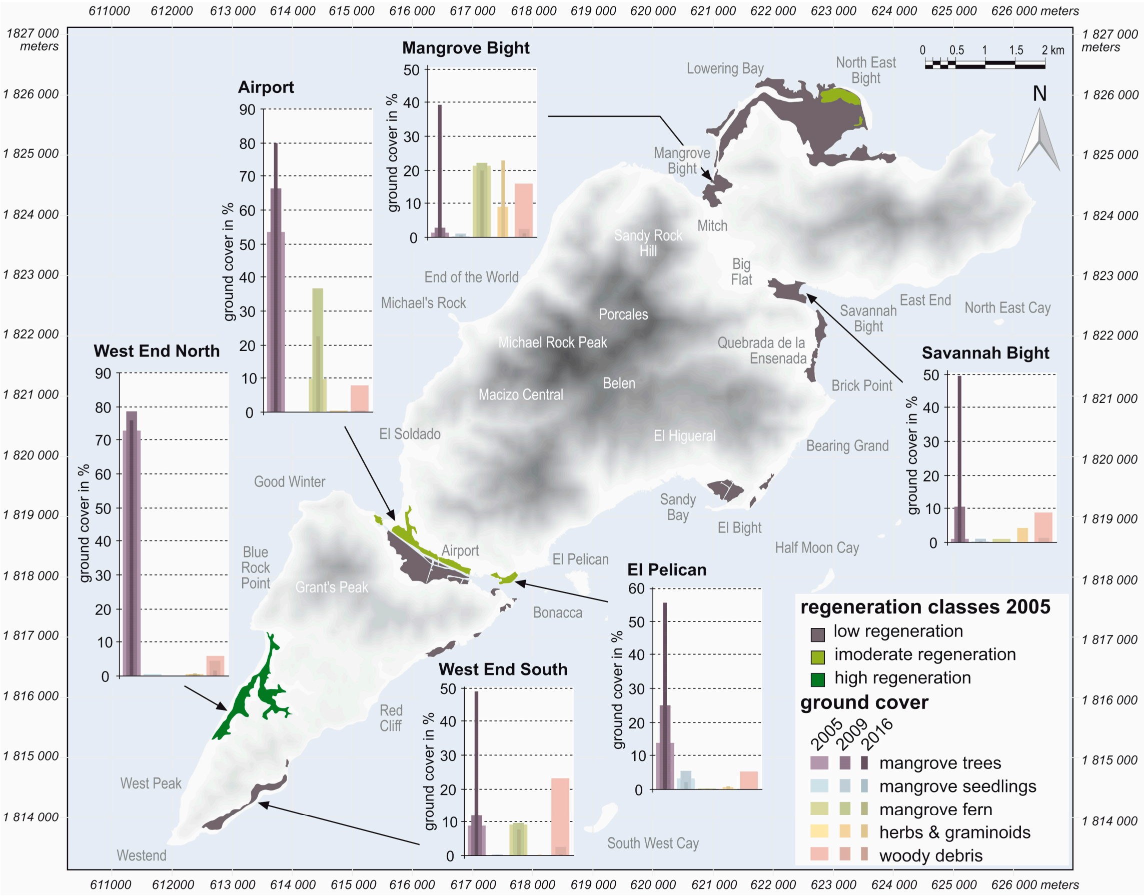


Figure 5. Digital elevation model of Guanaja (SRTM data) with location of sampling sites and initial classification of regeneration classes as represented in 2005; bar plots illustrate changes of mean cover values of particular functional groups within the different study sites for the three different sampling dates.

Figure 6. Repeated photographs of the three most severely hit mangrove sites studied on Guanaja, illustrating the substantial progress in regeneration between (2009) and (2016).

4. Discussion

Differences in the state of mangrove regeneration in 2005 that led to the rough classification in low, moderate, and high regeneration sites shown in Figure 5, most likely result from differences in the preceding disturbance by Hurricane Mitch. As Mitch approached the island from the Northeast (Figure 1), West End North on the leeward side of the island was effectively protected by the pronounced topography of the island. Wind energy was still strong enough to remove all leaves, so this locality was classified as dead immediately after the hurricane impact by the authors of [35], and the change detection analysis in Figure 3 indicates a strong alteration, too. Roots, trunks, and leaf buds, however, remained intact, so a swift return to pre-Mitch conditions was possible by the re-sprouting of leaves. To a lesser degree, such wind protection by micro- and/or macro-topography existed at the mangrove localities of Airport and El Pelican, where at least some segments with living mangroves were present in 2005. On the highly wind-exposed side of the island (Mangrove Bight, Savannah Bight and West End South), however, mangroves showed almost no signs of regeneration at the first survey in 2005.

As chances for natural regeneration in the severely hit mangrove sites were assumed to be low [46], the Honduran forestry agency ESCNACIFOR (Escuela Nacional de Ciencias Forestales) started a reforestation campaign in 2003 in some localities (Airport south of the canal, as well as Mangrove Bight and Savannah Bight at the seaward margin). Some years later, an American voluntary initiative started the planting of *Rhizophora mangle* propagules, again in the severely hit northeastern part of the island (mainly Mangrove Bight and Savannah Bight). However, mortality rates of the planted seedlings were very high (locally up to more than 90%). Peat collapse, modified site conditions (e.g., salinity, high radiation, excessive heat, etc.), and/or the feeding behavior of crabs might have been responsible for the low success. Planting of seedlings grown up in nurseries slightly enhanced the success of the establishment. As planting efforts were very local, most mangroves on Guanaja recover by natural regeneration, locally, however, some progress might result from planted seedlings that became established successfully. For instance, the increase of mangrove tree cover up to >10% in Savannah Bight in 2009 may partly go back to some of the planting done by the ESNACIFOR a couple of years earlier. In Mangrove Bight, where planting efforts were conducted as well, no substantial increase in mangrove cover happened due to widespread die-back of seedlings. Rather, this area was characterized by a strong increase of herbaceous and graminoid taxa. In 2009 it was hypothesized that the low success of mangrove seedling (planted and natural) might be related to the presence of competitors and that a long-term transformation of former mangrove to saltmarsh is taking place, as reported by the authors of [22]. As mangrove cover tremendously increased in all severely disturbed sites between 2009 and 2016 (see Figure 5), regardless of whether there were no planting efforts (as in the West End South), there was some successful planting (as in Savannah Bight), or there was an interim herbaceous phase (as in Mangrove Bight), a high resilience of mangroves is indicated even though the tree species (in particular, *Rhizophora mangle*) are not very resistant to severe storm impacts.

Two decades are for sure not a sufficiently long period of time to evaluate the entire successional cycle of regeneration, for which, according to the authors of [11], a minimum of three to four decades have to be assumed. Therefore, concluding remarks on the course of regeneration of hurricane disturbed mangroves on Guanaja cannot yet be made. However, based on the six mangrove sites studied, different successional trajectories during the first two decades after the disturbance can be identified, which might be valid for Caribbean mangroves in general (Figure 7). Mangroves protected from the most severe winds, where trees shed leaves but remained unharmed otherwise, experience a swift return to vital forests comparable to those present prior to Mitch by trees simply re-sprouting leaves from intact leaf buds (Cycle A in Figure 7). This trajectory is represented by West End North, where the mangroves were obviously protected from the most severe winds by the mountainous backbone of the island. Within a few years, the final state of succession is accomplished and forest structure is driven again by internal dynamics, as indicated by shifting ground cover values between 2009 and 2016 for mangrove trees in West End North (Figure 5, see also the shifts of one singular transect segment in Figure 4 due to a treefall gap).

Besides large-scale protecting effects, local small-scale protection must have been effective as singular individuals of all three mangrove species survived Mitch even in the most severely affected sites. Protection was provided by natural and/or artificial scarps surrounding the mangroves. In addition, the forest stands themselves might have provided protection to young trees established within former canopy gaps [47]. These low-growing trees were effectively protected from the most severe winds by tall, heavily affected old-growth trees and are potentially a crucial source of diaspores driving regeneration. This highlights the significance of the stand structure prior to disturbance for post-disturbance developments. Homogeneous, one-layered, even-aged, and monospecific stands most likely will regenerate more slowly than forests with a more heterogeneous structure of canopy gaps favoring young trees and tall, emergent trees acting as wind breaks at the canopy level. In such a forest, only the exposed trees are affected by winds, sparing many diaspore-bearing young individuals, which allows for a swift regeneration after the disturbance [11]. In contrast, if most diaspore-producing individuals within homogeneous stands are lost to the storm, regeneration takes considerably longer, as the influx of diaspores is delayed due to a poor diaspore availability in the immediate surrounding. In extreme cases—if no survivors are present—such influx must occur completely from abroad, which involves a high degree of randomness.

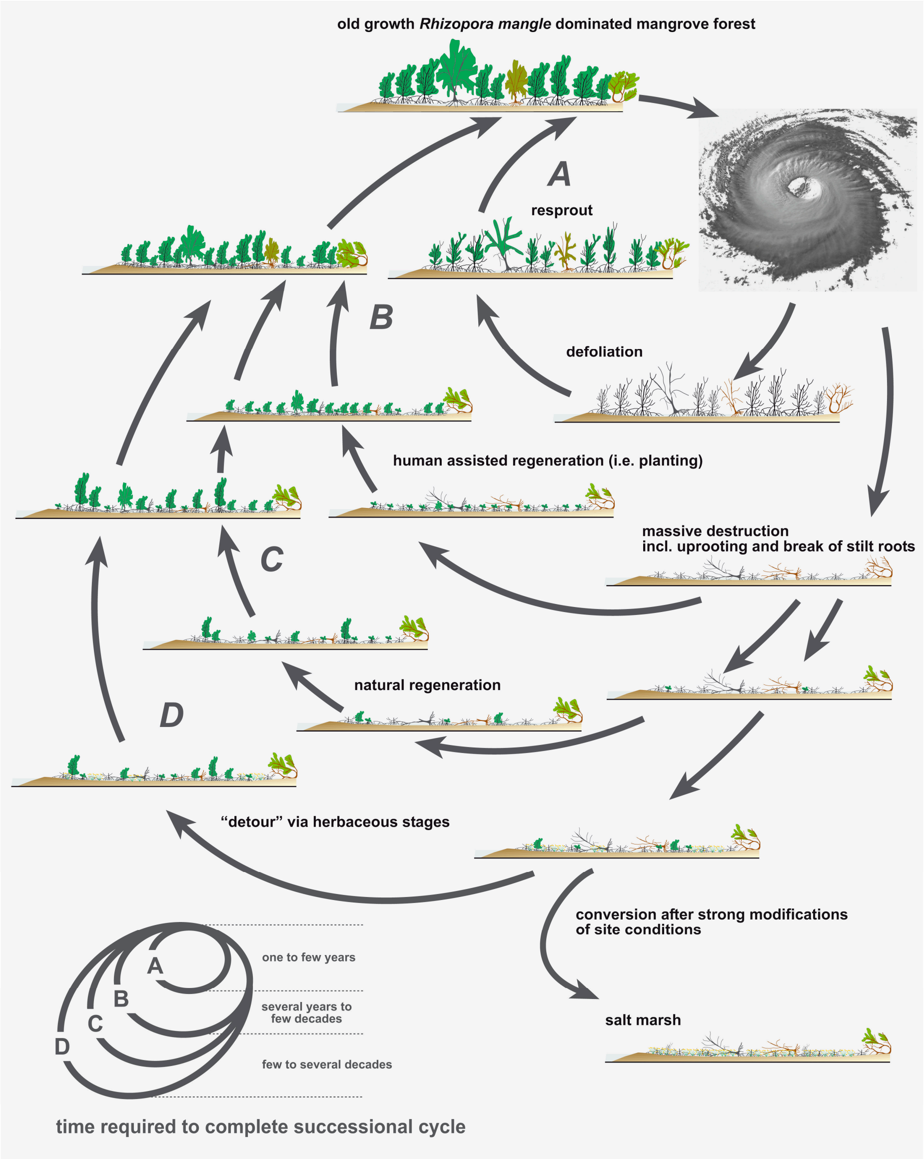


Figure 7. Schematic representation of different successional trajectories and the time frame required as portrayed within the mangrove sites studied on Guanaja within the first two decades after the hurricane disturbance.

Disturbance intensity, however, is not the sole variable controlling regeneration, as different trajectories of the severely disturbed mangrove sites of Mangrove Bight, Savannah Bight, and the West End South reveal. While the latter with few survivors in the immediate surrounding and no afforestation measures conducted is characterized by a slow natural regeneration (Cycle C in Figure 7), Savannah Bight shows some acceleration in regeneration with an increase in mangrove cover from 1.5% in 2005 to 11% in 2009 (Figure 5). Whether this is a consequence of planting efforts conducted by the ESNACIFOR in 2003 and 2004 cannot be said with certainty, as these efforts in general were not very successful. However, it cannot be ruled out that some of the diaspore-bearing individuals on the seaward side of the Savannah Bight transect in 2009 date back to these efforts and are responsible for the enhanced regeneration (Cycle B in Figure 7). The larger part of (sub)adult individuals, however, originate from a few survivors in topographically protected locations at the edge of the mangrove area.

Mangrove Bight, finally, differs from all other mangrove sites studied on Guanaja in its high amount of halophilous herbs and grasses. Modified site conditions and high radiation input increasing substrate salinity, at least seasonally (in the dry season), might be responsible for that. The hypothesis based on observations in 2009 that this could be an initial stage of a long-term transformation of former mangroves towards a treeless saltmarsh (see Figure 7), as described by the authors of [22] regarding strongly altered mangroves in the Florida Everglades, has to be abandoned after the survey in 2016. The significant increase in mangrove cover—partly natural, partly human supported—between 2009 and 2016, going hand in hand with an increase of grasses and herbs, indicates that a herbaceous phase might just be a detour with temporary shifts in the species composition on the way back to mangroves (Cycle D in Figure 7, see also [11]). This trajectory contradicts the assumption of strict auto-successional pathways within mangroves following severe disturbances. In fact, a herb and grass layer might even facilitate mangrove seedling establishment after sever disturbances, as reported from Caribbean mangroves [19].

5. Conclusions

While obviously not being resistant to storm impacts, mangroves show a high degree of resilience and are able to regenerate within relatively short periods of time even after severe disturbances via different successional pathways. The fact that there is not much difference in the regeneration progress of sites with anthropogenic support due to reforestation (parts of Savannah Bight and Mangrove Bight) and those without (West End South, El Pelican) proves the high resilience of mangrove forests as hurricane-prone Caribbean ecosystems. If mangroves would not have this ability, they surely would have been replaced by other systems, considering the high frequency of tropical storms within the Caribbean basin. How this ability will be stressed by climate change in the future remains to be seen. Climate models assume both an increase in intensity of tropical storms as well as an increase of strong hurricanes (>SS3) during the 21st century under global warming [31]. How this might lead to cumulative and probably irreversible effects on Caribbean mangroves and whether this will reduce the resilience of these systems is one of the central topics related to the fundamental ecosystem services mangroves provide [23,48]. While mangroves are already at high risk by deforestation and anthropogenic modifications, these "quasi-natural" (in the sense of anthropogenic enforced natural influences) atmospheric processes linked to climate change make their future more uncertain than ever.

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