1 Introduction

The media report almost daily about natural disasters occurring in one part of the world or another. In this respect it is commonly disregarded that earthquakes, volcanic eruptions, tsunamis or hurricanes are primarily natural events, which only due to the proximity to human beings may reach catastrophic effects. Less developed regions are particularly vulnerable, where high population pressure leads to a settlement expansion in successively more risk-exposed areas. If such areas are hit by respective natural events, high number of casualties and physical damage is inevitable.

From an ecological point of view, by contrast, such events have to be treated as disturbances, which may cause massive destruction for the short term, in the long run, however, are essential in controlling rejuvenation of senescent stands and in maintaining natural ecosystems in general (see e.g. White 1979; White a. Jentsch 2001). While – for example – in the Mediterranean Subtropics fire undertakes this task of maintenance of (sub)natural scrub and forest communities, for the Caribbean ecosystems hurricanes are important and rather frequent disturbing agents. The paper at hand tries to portray the destruction and trajectories of recovery for terrestrial, litoral and marine ecosystems on the small Honduran island of Guanaja following the passage of hurricane Mitch. Mitch was as one of the strongest and deadliest tropical Atlantic storms ever (Rappaport a. Fernandez-Partagas 1995; Sandner 1999), with an estimated death toll of more than 11,000 people and another 13,000 hurt. Besides the high number of lives lost, almost all ecosystems of the region suffered great damage. While on the mainland of Central America (especially Honduras and Nicaragua) the high amount of rainfall (estimations of NOAA:
and the subsequent mudflows caused major damage, on the Bay Islands offshore from Honduras – and in particular the island of Guanaja – and higher wave energy were most efficient (Guiney, A. Lawrence 1999). In addition to the already highly destructive power of Mitch, the unusual track and slow velocity of the hurricane had an intensifying effect.

Even if hurricanes are common natural disturbances in the Caribbean, the understanding of mechanisms of damage and trajectories of recovery for areas affected are still poorly understood. In addition, a deeper insight into successional trends and variation of reproductive potential of Caribbean ecosystems after a major hurricane strike is essential in the light of a potential future increase in hurricane frequency and intensity as predicted by some climate change models (Giorgi et al. 2001). This topic is controversially disputed (see Emanuel 2005 and Webster et al. 2005) in contrary to Klotzsch 2006, and our paper is not intended to discuss this issue, however, the record breaking season 2005 seems to support the assumption in some respects.

2 Study area and hurricane Mitch

The Bay Islands consist of three major islands, Útila, Roatán, and Guanaja, situated off the north coast of Honduras and separated from the continental shelf by deep-sea trenches (Harborne et al. 2001). “Mountainous” Guanaja is the north-easternmost island, surrounded by a continuous circle of barrier, fringing and patch reefs (Fig. 1 a. 2).

According to its latitude, the climate of the Bay Islands is tropical, dominated by trade winds from E to NE for most of the year. Temperature averages at 28°C and the mean annual precipitation reaches 2,200 mm (Consultores En Recursos 1996) with an obvious peak in winter, when polar-continental cold fronts (“nortes”) can advance south into the Gulf of Honduras. Between May and October tropical waves regularly move in from the Atlantic (Jaan a. Halas 1983), inducing a potential “hurricane season”.

Controlled mainly by relief and edaphic conditions, several vegetation types occur on Guanaja (Fig. 2). Prior to hurricane Mitch on steep hill slopes a tropical woodland prevailed, dominated by Pinus caribaea var. hondurensis. Lower, less steep or wetter slopes are characterized by an evergreen oak forest with Quercus oleoides associated by Byrsonima crassifolia, while in the deeper incised gullies a rather diverse humid tropical forest occurs. All three forest types are fragmented and altered by former or actual land use. Flat areas along the coast with low tide and regular wave action typically harbour mangrove forest, as well as salt-tolerant beach vegetation.

Hurricane Mitch, originating from a tropical wave offshore from Western Africa on October 8/9th, reached hurricane strength on Oct. 24th. Within 24 hours the pressure dropped to 924 hPa, and the storm system’s diameter at that point extended from Central Nicaragua to South Cuba. Later that day of Oct. 26th the pressure reached the minimum of 905 hPa with winds up to 155 knots, making Mitch the strongest October hurricane ever. On Oct. 27th Mitch passed Guanaja as a category-4-hurricane (Fig. 3). Its centre remained right off the north coast of Honduras between Oct. 27th and Oct. 29th so that Guanaja, despite a weakening of wind speed, was affected by enormous winds for more than 70 hours. Finally, in the night to Oct. 29th Mitch had landfall on mainland Honduras.

3 Materials and methods

In respect of the unequal terrestrial, littoral and marine ecosystems on Guanaja different methods were employed to evaluate the degree of destruction and the present state of regeneration. As no field data on either ecosystem prior to Mitch are available, a comparison between satellite images before (Landsat 5 TM of 1985) and after the hurricane passage (Landsat 7 ETM+ of 2001) was conducted using different change detection techniques for a first classification of the degree of alteration (for details see Mathur 1999; Lillesand et al. 2000), while concepts and methods for change detection are numerous, most of them were developed for terrestrial ecosystems. However, procedures like tasseled cap transformation or change vector analysis can be applied equally to coastal shallow water ecosystems (see Andrefouet et al. 2001), as is done for coral reefs in this study. In addition to satellite images aerial photographs of 1999 were consulted to identify modifications in plant cover.

In the field, terrain inspection and (in case of the coral reefs) numerous dives were realized for a visual qualitative assessment concerning damage and recovery of the different ecosystems in relation to hurricane exposure. Based thereon quantitative data was collected for the three most severely damaged ecosystems, pine forests, mangroves and coral reefs (for location of sample sites see Fig. 1), employing ecosystem-specific sampling procedures. Within the pine forests a total of 52 quadratic 400 m² sample plots were established. Recordings include number and average height of young pine trees, the stem diameter of the tallest living...
tree as well as number, size and stem diameter for the dead pines to assess stand structure prior to hurricane Mitch. In addition, the ground cover of the associated plants (in %) was sampled. Mangroves were surveyed using the “line-intercept-method” (see MUELLER-DOMBOIS a. ELLENBERG 1974) in six littoral swamp forests all around the island (see Fig. 1). Along the transect lines (a total of > 1,700 meters) all taxa present as well as the amount of dead wood were recorded with a resolution of 10 cm, allowing for a recalculation of ground cover values in % for transect segments (here 10 m) afterwards. Coral reef data was collected up to five meters water depth, since this zone suffered the heaviest impact. Special attention was paid to the exposed outer reef zones on the barrier and fringing reefs (Fig. 1).

Despite the variability of impacts and responses caused by the high diversity of reefs and by the reef conditions (MUMBY 1999), it was intended to accomplish a region-wide classification of destruction and regeneration. Random quantitative photo sampling (1x1 m, see Photo 1) was realized in the identified impact ranges, considering amongst others relative dominance of coral and macro-algae species, coral growth forms, conspicuous mechanical destruction and abundance of juvenile colonies.

4 Degree of damage and state of regeneration of the ecosystems on Guanaja half a decade after Mitch

Aside from a few protected sites, all ecosystems on and around Guanaja suffered to some degree by the high wind or wave energy caused by hurricane Mitch. The analyses of aerial photographs of 1999 and the conducted change detection using satellite images of 1985 and 2001, however, reveal that long-term destruction varies greatly between the different plant formations (Fig. 4). The oak and tropical gallery forests were able to regenerate quickly (BAK a. GALLNER 2002; DOYLE et al. 2002; VILLEDa et al. 2000). In figure 5 the sandy beaches appear as still highly damaged. Indeed, these areas suffered strongly due to their exposed location, but during the last years regenerated sufficiently, that no damages are conspicuous anymore, despite an occasional overthrown tree. In contrast, the pine forest and the mangroves, as well as large parts of the coral reefs, show major damage and are in early states of succession, which will be highlighted next.

4.1 Pine forests

Prior to Mitch open pine forests (ground cover ranging between 5 and 75%, tree heights 10 to 25 meters) had an extension of 1,700 ha on Guanaja (CONSULTORES EN RECURSOS 1996). With the exception of three single spots in sheltered locations, these stands suffered almost complete mortality by the hurricane, due to uprooting and defoliation (Photo 2). Today shrub formations represent an early state of regeneration.

Figure 5 illustrates different states of pine regeneration across Guanaja. High recovery is concentrated mainly on the central part of the island south of Michael Rock Peak. Despite strong damage (up to 20 dead pines/plot), a high ground cover and number of young pines occurs. This class also shows the highest increment of young pines (up to 1.6 m) among the natural regeneration. The understory consists of a dense grass cover of more than 80% coverage. In contrast, the mangroves, as well as large parts of the coral reefs, show major damage and are in early states of succession, which will be highlighted next.
“Fortunately” Mitch passed at a time when the seeds reached their ripeness. Due to the complete destruction the hurricane induced the last seed spread. Germination normally starts 12 days after spreading (FRANCIS 1992). It must be assumed that the pines grew constantly during the 5 years between spreading in 1999 and field investigation in 2004. As documented above there are local differences in regeneration depending on the quality of the location. Apart from afforested sites, even the high regeneration sites lead to a 15-year-projection of not more than 5 m height. Keeping the mentioned growth experiments in mind this seems to be low. Most likely, competition among the young pines themselves as well as with the dense grass and shrub vegetation is a growth limiting factor on Guanaja. Growth rates presumably will increase in later successional stages, as soon as the strongest specimen succeeded and pine forests with tree heights of 10–12 m are more likely after the next two decades.

4.2 Mangroves

Prior to Mitch mangrove forests occupied a total of 243.2 ha on Guanaja (CONSULTORES EN RECURSOS 1996). *Rhizophora mangle* was by far the dominant species, commonly associated with *Laguncularia racemosa*. Less frequent but locally present is *Avicennia germinans*. Finally, even if not a mangrove species sensu strictu, *Conocarpus erectus* occurs on higher terrain within mangrove areas and particularly at the transition to the terrestrial plant formations.

According to LEBIGRE et al. (2003) 97% of the original mangrove area was destroyed by the high wind and wave energy. Beside occasional uprooting (in *Laguncularia racemosa*) and breaking of the stilt roots in the case of *Rhizophora mangle*, major damage resulted from complete defoliation of all trees. In general these trees are adapted to occasional disturbance events such as hurricanes (LUGO et al. 2000); in the case of the complete destruction...
destruction on Guanaja, however, it is assumed that a prolonged drought before the hurricane (El Niño in 1998) substantially weakened the trees. Consequently they were unable to re-sprout new leaves, cutting off the capacity for photosynthesis (Bak a. Gallner 2002). This might be the crucial factor for the high destruction (Fig. 4) and low regeneration (Fig. 5) in many parts of the island today.

Seven years after Mitch about two thirds of the sampled transect stretch are still in desolate condition, particularly the mangrove areas of Savannah Bight (Fig. 6a), Mangrove Bight (Fig. 6b), Westend South, Northeast Bight, as well as large parts of the mangrove close to the Airport. These areas are characterized almost exclusively by dead wood (Photo 3), showing virtually no signs of natural regeneration (see Fig. 5). With the exception of Conocarpus erectus, all mangrove taxa present on Guanaja are viviparous or at least crypto-viviparous (see Hutchings a. Saenger 1987). The storm not only removed the leaves but also most of the diaspors. High flood and generally turbulent conditions apparently prevented the settling of the storm-released propagules and without abundant mother-trees in close proximity today, the potential for a swift natural regeneration must be deemed as being low. In contrast to the viviparous mangrove taxa, Conocarpus erectus is able to conduct stump sprouting from drowned trunks and tree branches, essentially accelerating the

Fig. 2: Plant formations and coral reef distribution on Guanaja
Vegetationsdifferenzierung und Riffverbreitung auf Guanaja
The process of revegetation where present, e.g. a large patch in Northeast Bight and in parts of the Airport Mangrove (see Fig. 5).

The loss of mangroves entails several problems. They serve as habitat, important nursery and refuge with ample food for many organisms like birds, fishes and reptiles, creating an extraordinary diverse ecological community (see SAENGER et al. 1983; FARNSWORTH a. ELLISON 1996). Furthermore, mangrove forests play an important role in coastal protection, preventing erosion of the coastline on the one hand and siltation of the reefs by surface runoff from the island on the other. The lack of substitute communities, which are common for many terrestrial ecosystems further intensifies the problem.

To alleviate coastal erosion and the siltation of reefs, the ESNACIFOR started with the plantation of Rhizophora seedlings in 2003. The attempts failed several times as fiddler crabs (Uca spec.) and land crabs (Cardisoma spec.) feed on the seedlings. Even after removing the dead wood providing shelter against predators like birds or iguanas, no sustained success could be achieved and keeping in mind the large area destroyed, a reforestation of the original mangrove area seems to be utopian.
Anyway, even within the most disturbed mangroves a few veteran trees survived in protected sites. Shelter was provided either by the adjoining vegetation or in specific topographic situations as in Savannah Bight, where along steeper terrain some adult *Rhizophora mangle* trees survived (see Fig. 6a). These survivors are the source of diaspors, and might trigger the recovery of the destroyed sites. Given no new devastation, regeneration of the massively destroyed mangrove forests will proceed slowly but steadily, also most likely it will take decades (see OGDEN 1992).

At larger scale, a protective role was provided by the relief of the island, too. Even if classified in figure 4 as highly destroyed, the mangrove areas on the Northwest side of Guanaja (“Westend North”, Fig. 1) are in very vigorous shape today (Fig. 5, Fig. 6c). Tall living trees of *Rhizophora mangle* and *Laguncularia racemosa* are prevalent, indicating a diminished impact of Mitch on the leeward site, protected against the highest gusts by Grant’s and Michael Rock Peak.

### 4.3 Coral reefs

In contrast to the destructive impacts on the plant formations, for the coral reefs negative as well as positive consequences through Mitch can be attributed. It

![Guanaja, destruction classes](image)

*Fig. 4: Destruction of terrestrial, littoral and marine ecosystems on Guanaja*

*Ausmaß der Zerstörung terrestrischer, litoraler und mariner Ökosysteme auf Guanaja*
has to be mentioned that the reefs around Guanaja – as all over the Caribbean – were already weakened by bleaching prior to the arrival of Mitch due to elevated sea surface temperatures in 1998 (WILKINSON 2000), so the coral colonies were stressed twofold by a combination of risen water temperatures and the hurricane impact.

Direct negative impacts from Hurricane Mitch comprise the breaking of branched coral growth forms, tearing out of coral blocks (see Photo 4), rearrangement of rubble and sand, abrasion of coral colonies and an input of considerable amounts of organic and mineral sediments from terrestrial systems. Indirect (i.e. spatially or temporally not directly related to Mitch) impacts consisted in fresh water influence from the mainland (Fig. 7), infestation of the extremely stressed corals with diseases, and as a consequence a change in composition of benthic communities.

However, there are positive aspects, too. Most notably the high wave action resulted in a deep mixing of water layers, effectively lowering the elevated sea surface temperatures and thus terminating the mass bleaching. In addition, abrasion removed algae, thus providing new substrate for coral colonization, and some genera such as Acropora are even favoured by mechanical destruction, as they are able to regenerate

\[ \text{Fig 5: Regeneration classes for terrestrial, littoral and marine ecosystems on Guanaja} \]
Regenerationsklassen der terrestrischen, litoralen und marinen Ökosysteme auf Guanaja
from fragments. Finally the economically disastrous collapse of dive tourism after the cyclone offered some years of relative calm for the sensitive reefs.

The analysis of the wave direction in combination with the collected anecdotal information points to a lee effect of the island itself in the arrangement of the different impact classes along a gradient from NE to SW (see Fig. 4). The less disturbed area encompasses the SW tip and reaches north up to the little peninsula of Michael Rock. Branching corals, sea fans and other reef organisms were intact and, besides a small number of overthrown colonies, no signs of disturbance could be found anymore. In the moderately impacted class the significance of microhabitat and species assemblages in relation to wave exposition is illustrated by the patchy distribution of disturbances. Only where extreme water movement and high waves made direct strikes, destruction signs are evenly distributed over the whole area. On the southern part of the island considerable amount of coral rubble and sediments boosted the effects through abrasion processes, especially in sections near constructions on the reef and spots used for coral mining.

The high variability of habitat characteristics and species distribution is even more important for the regeneration process than for susceptibility (MUMBY 1999). For the reefs of Guanaja, type and intensity of regeneration apparently depends on local coral populations and their different reproductive strategies.

In general most of the scleractinian colonies which died following the severe bleaching event of 1998 and the simultaneous hurricane impact are either covered by algae or got replaced by gorgonians. Nevertheless in a few areas with sufficient hard substrate and high coral cover vivid regeneration is taking place (PORCHER et al. 2001). Why this regrowth (as in Acropora palmata, Acropora cervicornis, Porites divaricata and Favia fragum) is mainly taking place in the first few metres below the surface was not made clear.

Among the main factors driving coral regeneration, the specific reproduction strategy plays a decisive role. Long-living coral species are characterized by effective

Photo 2: Destruction and regeneration within former pine forests on the North side of Guanaja
Zerstörung und einsetzende Regeneration eines Kiefernbestandes auf der Nordseite Guanajas
defensive strategies towards other organisms and a high regeneration capacity releasing less gametes in a few spawning events synchronized at fixed times of the year (GRIFFIN 1998). In contrast, brooders (i.e. species with internal fertilization of eggs; mature sperm swim through the water, find a polyp of the same species that has ripe eggs within it, and then enter the polyp via the mouth to fertilize the eggs internally) are rapidly growing species with a short lifespan, and several reproductive cycles a year, releasing planulae larvae. In addition many brooders are able to reproduce asexually in stress situations adjusting time and type of reproduction, which could explain the high dominance of those species in the high impact sites. As noted by other studies, there exists a correlation between brooding species and unstable habitats with high mortality rates (FITSUM wo.y.).

Figure 5 shows the different types in regeneration for the coral reefs on Guanaja. The southern portion of the island represents a zone repopulated with brooders in shallow parts like *Porites astreoides* and *Favia fragum*. In the NE of the reef complex incrusting growth forms are prevailing. The most divers and species-rich regeneration state including branched and plate growth forms can be found on the moderately disturbed northern side, supporting the “intermediate disturbance hypothesis” for coral reefs as shown by CONNELL (1978), ROGERS (1993) or ARONSON and PRECHT (1995). Regenerative patterns show an impoverished but lively regeneration as a response to major destruction of branched and plate coral species. Apparently currents do not allow larvae transport from intact colonies to the most affected south east side, making local coral populations the only source of reproduction.

Coral reefs can be seen as a mosaic of different regeneration stages, since there are always build-up and degradation processes going on. Hurricanes count for the most effective degradation processes and have always been part of the natural phenomena affecting reefs concerning species abundance and distribution. Today’s reef regeneration, however, proceeds on a much lower level, due to generally less favourable con-
ditions as a consequence of anthropogenic impacts such as overfishing, eutrophication or discharge of toxic substances.

5 Concluding remarks

Ecosystems in general are not static, but are composed of ever-changing coexisting communities. Important triggers for such mosaics are disturbances, which vary strongly in type of agent on the one hand and in magnitude and frequency, and thus in space and time, on the other (see White a. Jentsch 2001). Whereas smaller disturbances (such as single tree falls creating forest gaps) create patchiness within particular communities, macro-scale events like hurricane Mitch may cause rather homogeneous and uniformly disturbed areas. Regeneration patterns, however, are not solely governed by the preceding disturbance, but by the type of the ecosystem disturbed and its underlying ecological configuration (e.g. soils, topography, seed bank, anthropogenic influence, dispersion mechanisms of surviving and/or surrounding organisms, etc.). Hence, rather heterogeneous regeneration patterns might occur even after a more or less uniform destruction. Additionally, the development of successional stages or substitute communities on the disturbed sites (as in the case of the pine forests) or not (in case of the mangroves) are definitely relevant for regeneration processes.

Despite the different types of destruction and specific trajectories of recovery, Caribbean ecosystems appear to be and – keeping the high frequency in mind – also should better be well adapted to occasional hurricane disturbances. The strong destruction in parts of the mangrove forests and the reefs on Guanaja must be attributed to the combination of hurricane impact and drought (mangroves) respective bleaching impairments (corals) prior to the arrival of Mitch. Areas with one of the two stressors reduced (either the hurricane impact or the preceding temperature-influenced deterioration) are less sustained damaged and recover well. Within the pine forests seed spread and germination rate was high and successful, at least at sites not seriously affected by

Fig. 6: Exemplary transects across three mangrove areas (a: Savannah Bight, b: Mangrove Bight, c: Westend North) on Guanaja, showing differences within and between different sites

Ausgewählte Transekte (a: Savannah Bight, b: Mangrove Bight, c: Westend North) auf Guanaja verdeutlichen Unterschiede hinsichtlich des Zerstörungsausmaßes und der Regeneration innerhalb und zwischen den verschiedenen Standorten
clear-cutting and subsequent soil erosion prior to Mitch. However, pine regeneration suffered a serious throwback in 2005, when two human-caused fires, escaped and large parts of the slowly regenerating slopes burned. Although *Pinus caribaea* is a fire climax species in the adult stage, the seedling mortality through fire is high (MUNRO 1966). The consequences for forest recovery are hard to predict. At best a setback for several years must be expected, more likely however is a longer-term impact with increasing soil erosion and retarded recovery as potential future seed sources were destroyed.

The long-term sustainability of the ecosystems on Guanaja – and probably all over the Caribbean – depends to a lesser extent on the occasional disturbance events rather than on the extent and frequency of human-caused disturbing impacts. Anthropogenic effects become more and more important as an increasing number of mainlanders moves to the Bay Islands in search of better living standards compared to mainland Honduras, as well as to participate in the growing tourism (FIELDING 2000; HARBORNE et al. 2001). A larger population on the island leads to a higher pressure on the ecosystems, mainly in terms of reclamation of agricultural areas and uncontrolled settlement expansion. To keep the regenerative capability of the ecosystems on Guanaja after natural disturbances such as hurricane Mitch, a much improved and dedicated environmental education is needed, which must start in primary school. Only if a higher ecological awareness under the upcoming users of Guanaja’s natural resources can be achieved, future natural events will not necessarily be catastrophic.

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**Fig. 7:** On the Satellite image from November 1, 1998 a large plume (yellow) appears, coming from Rio Aquán and reaching out to Guanaja [http://mitchnts1.cr.usgs.gov/projects/coral.html] [15.07.2006].


Photo 4: Overthrown *Montastrea faveolata* (diameter 2 m), the former base now being colonised by macro-algae and *Porites astreoides* specimens

Umgestürzte *Montastrea faveolata* (Durchmesser 2 m); die ursprüngliche Basis wird heute von Makroalgen und Individuen von *Porites astreoides* besiedelt


