Vulnerability of a tropical ecosystem to hurricane disturbance: simultaneous responses of complex biostructure

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Understanding and predicting responses of ecosystems to large, infrequent, severe perturbations remains one of the most challenging tasks for ecologists. Hurricanes represent one type of severe perturbation that may be increasing with the changing global environment. Hurricane Wilma, a category 5 storm, demonstrated vulnerability of complex mature tropical forests to severe wind disturbance. During the past century, mature forests have declined drastically, often with only small remnant patches remaining. Using multiple structural, functional and taxonomic groups, our data indicate that many of the complex processes characteristic of mature forests may be more dramatically affected than those of early- to mid-successional stages (Fig 1). Specifically, there was greater mortality of the larger trees, characteristic of the mature forest. Insects, canopy birds and epiphytes all declined in the mature forest, but they either did not change, or rapidly recovered in the early seral stands. Recovery and retention of complex mature ecosystems may be difficult if large-scale wind disturbances increase in frequency and intensity with climate change.

Large, infrequent disturbances (LIDs) have fundamentally different properties from most perturbations studied in ecological research. LIDs have been differentiated from "typical" disturbances in that they have larger spatial extent, greater intensity and longer duration, are infrequent with respect to human scales or the life span of organisms in the environment, and because of this scaling property, their impacts may persist well-beyond those of more "normal" successional processes by overlay numerous patches of existing wildlands, successional seres, and human-dominated[1]. Thus, differing legacies remaining from the prior state could result in a mosaic of recovering landscapes within the LID footprint.

Hurricanes and other large windfalls leave a distinct signal resulting in a vastly different form of disturbance than others[2, 3, 4]. Most disturbances disrupt the soil and denude the existing vegetation removing vegetation, litter and soil carbon. Hurricanes alter the architecture, but can largely leave intact most of the tree trunks, the soil (except where severe erosion/landslides occur), and lower structure of the canopy. There is a massive enrichment of organic matter[5], and in hurricane-prone ecosystems, such as the Yucatan Peninsula, re-growth from the surviving plants can be expected to occur rapidly[6, 7, 8]. Recovery is slower from disturbances disrupting soils than if only aboveground structure (e.g., wind damage), but the parameters measured focus on soil fertility, but not subtle shifts in soil biota[9]. The landscape matrix will have important consequences to recovery[9]. As hurricanes, such as Wilma, cross a large area with many different vegetation conditions, we wanted to determine if the impact is similar across seral stands due to the severe disturbance, or if some stages are more susceptible to disturbance than others (Fig 1).

Understanding patterns of impact and differential recovery across pre-existing landscape elements and seral stages following a widespread severe disturbance becomes especially critical as changes in the intensity and frequencies of the forcing LIDs are subject to global environmental change. Ecological succession is a slow process, and developing mature forests that support a number of species may take a century or more[9]. Clearing forests for agriculture, and escape of wildfires has resulted in a large-scale conversion of mature to early seral forests across the Yucatan Peninsula[10, 11]. Hurricane frequency and intensity appears to have increased since 1995 in the North Atlantic[12, 13].

In October of 2005, hurricane Wilma passed directly over the El Eden Ecological Reserve, Quintana Roo, Mexico (lat 21°12’N, long 87°11’W). As this hurricane approached the island of Cozumel, it was the most intense hurricane ever formed in the Atlantic Basin (882mbar). It came ashore slowly, and drifted northwesterly, making a short diversion to pass directly over the reserve. The barometric pressure at the reserve dropped to 970mbars, and because of the slow movement rates, the rainfall exceeded 1.5m over a two-day period. Winds were estimated in excess of 200km/h.

Over the past decade, we have completed a large array of studies on a seasonal tropical forest at the El Eden Ecological Reserve, in the Yucatan Peninsula, Mexico, to understand the carbon accumulation, restoration ecology, and biodiversity[6, 14, 15]. This includes a carbon inventory[16] and installed an embedded sensing network to study C, energy and water fluxes[17]. Here we report the immediate impacts of the hurricane on this seasonal tropical forest.

The El Eden Ecological Reserve is especially conducive for studying the impacts of the hurricane for a variety of reasons. The topography is flat and it is underlain with a uniform limestone bedrock base. The soil overlaying the bedrock is comprised of a highly organic layer of humic materials and decomposing litter. The region has experienced frequent fires that burned into the reserve at various times. Thus, the site has forest patches ranging from mature forest (with no known burn, and trees greater than 100 years old), to seral stands that were burned in 1976, 1989, 1995, and 2001. There is evidence that the Maya used the mature forest in Preclassical times. Some selective harvest of the forest was undertaken in the 1920s, and large, mature *Manikara zapota* trees were slashed for resin extraction, but those trees and other large *Brosimum alicastra* and *Ceiba pentandra* trees indicate that the site was not subjected to major disturbance[18].

The most dramatic and evident impacts of hurricane Wilma on the forest itself was on the forest vegetation. The rapid pressure change and high winds stripped virtually all leaves and small branches resulting in an upright architecture comprised of poles, whose size depended upon the species composition and seral stage. Prior to the hurricane, net radiation at the forest floor was less than 200 $\mu E \cdot m^{-2}s^{-1}$. Upon the arrival of the hurricane eye, the barometric pressure dropped to approximately 970 mbars and, immediately after the hurricane passage, the net radiation of the forest floor increased to 1000 to 1200 $\mu E \cdot m^{-2}s^{-1}$. The $200 km \cdot h^{-1}$ peak winds resulted in a large number of downed trees. Despite the intense damage the vegetation recovered within two months of the hurricane. Before the disturbance, the canopy coverage exceeded 90% and within two months after the hurricane, it recovered to nearly 80% in the mature forest, with similar results for the secondary forests. The leaf area index was 2.8 before the hurricane and 2.1 two months after the hurricane in the mature forest, but 2.5 and 1.8 in the early successional forest, respectively. These results show the rapid response of remaining trees to recover leaf area after wind disturbances.

We estimate an average litter input of 743 g m^{-2} (ranging from 640 at the 1999 burn site to 870 in the mature forest), but two months after the hurricane most of the litter was decomposed. Pre-hurricane litter biomass in the mature forest and in the 4 four yr forest was nearly 15 and 2.6 Mg/ha, respectively, whereas two months after the hurricane litter biomass was 9.9 and 7 Mg/ha. Mean daily soil respiration after the hurricane was nearly 23% higher than before the hurricane (the mean daily value was 8.4 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ before the hurricane and 10.3 $\mu mol\ CO_2 m^{-2}s^{-1}$ after). Annual soil respiration of one year before the hurricane was estimated to be 9 Mg C $ha^{-1}\ yr^{-1}$, while soil respiration for the year following the hurricane ranged from 10.4 to13.7 Mg C $ha^{-1}\ yr^{-1}$. These results show the rapid litter turnover rates and recovery of soil biomass in mature forests as seen in other tropical forests[19].

Surprisingly, there were no measurable differences among tree species in any of the plots evaluated. There was a significant difference in tree size among those killed by the hurricane between the mature forest and the seral stages, but this was probably simply a function of pre-existing differences in the overall size of the trees among stages (Fig 2). There was a strong correlation between the stand age and the size of the trees (r=0.86). Both the percent of damaged (r=0.95) and dead (r=0.74) trees correlated with the size of the trees, and thus the age of the stand. Few of the trees in the early seral stands were dead or damaged, but 38% of the trees in the mature forest were either dead (25%) or damaged (13%).

Canopy epiphytes were heavily damaged by the hurricane. In the mature forest, there were 14.5 epiphytes per $100m^2$. Following the hurricane, 20% were on trees that were blown down. The epiphytes remaining on the standing trees also declined to 10.5 per $100m^2$. There was no evidence of seedling re-establishment or recruitment for the year following the hurricane. Less than 3% of the epiphytes were found in the younger forests, or a density of 0.4 per $100m^2$. The density did not change in these forests following the hurricane.

Root length, mycorrhizal hyphal infection, and numbers of arbuscular mycorrhizal fungal spores all declined (p=0.085) in the mature forest. Alternatively, roots and mycorrhizal fungi showed either increased activity or rapid recovery in early seral forest stands. Vesicles initially increased, indicating more C stored by the fungi, but the functional groups of AM fungi were highly variable.

Re-growth of both leaves and roots was already evident by December 2005. We expected that we would initially see re-growth of leaves, and utilization of the new carbon for producing new roots and arbuscular mycorrhizal roots. However, ^{14}C of new fine roots (<3 mm diameter), produced 1-2 months following the hurricane event, showed that stored non-structural C was initially used to re-grow the new roots in forests older than 16 yrs. The mean radiocarbon (^{14}C) values for new fine roots of forests aged six to ten years was 70‰**,** while for forests older than 16 years was between

90 and 105 ‰. This carbon did not come from newly fixed C, which would have a ^{14}C value of less than 70 ‰.

Before the hurricane, the mature forest had an extraordinarily high diversity and density of insects compared with the secondary forest[20]. However, after the hurricane, both the density (relative abundance of 1000 per trap in the secondary forest versus 200 in the mature forest) and diversity (a Shannon Diversity index of 4.05 in the secondary forest versus 3.31 in the mature forest) were lower in the mature forest than the secondary forest. Three groups in particular, showed some important differences (Fig 3). Numbers of both Chironomidae (midges) and Hymenoptera (bees) in the mature forest were lower than in the secondary forest. Midges were present only in the first sampling in the mature and secondary forests a few individuals were found in the secondary vegetation for the second sampling period and in mature forest appear again in the fourth sampling date. Hymenoptera increased through the year in the secondary forest. But, in the mature forest, the numbers increased in June, but then numbers declined and were almost undetectable. Both of these groups represent important food sources for birds, and are important pollinators.

The Formicidae (ants) represent a critical group of organisms. They regulate soil food webs and affect plant interactions[21]. Prior to the hurricane, the numbers of ants in the mature forest was four to eight times the numbers in the secondary forest, with up to 30% more species[20]. However, following the hurricane, the numbers of ants in the mature forest were was dramatically lower than in the secondary forest, and showed no significant increase throughout the year following the hurricane. In the secondary forest, the numbers of Formicidae increased rapidly throughout the sample period (Fig 3).

Birds occupying mature forest were more strongly impacted than those in secondary forest. There was no evidence that the overall species composition of birds changed from before versus after the hurricane and all species recorded before the storm were found within six months afterwards. The abundances of canopy dwelling birds and frugivorous and nectarivorous birds combined were significantly lower in the winter immediately following the hurricane than in the winter two years prior to the storm; these reductions were greater in mature than secondary forest (Fig. 4). Carnivores were significantly more abundant after the storm, but this increase was only evident in the mature forest. Insectivorous birds demonstrated a non-significant increase in abundance after the storm, whereas they increased equally in both seral stages. The pre-hurricane abundance of ground-dwelling birds varied between 2.3 (± 0.4) to 4.1 (± 0.5) bird sightings per 5 min observation. In January 2006, the numbers of ground-dwelling birds was low, but by the dry season had recovered to 7.1 (± 0.5) in the spring and 7.3 (± 0.5).

The disproportionate reduction in the abundance of canopy dwellers and frugivores/nectarivores in the winter immediately after the hurricane may be due to disproportionate reductions in canopy cover, vegetation height, and fruit abundance in this seral stage[22]. Frugivores and nectarivores collectively appeared to increase seven to nine months following the storm, possibly as their preferred resources became more abundant. The increase in carnivores and insectivores (in the secondary forest) after the hurricane may be due to temporary increases in the availability of their prey. Initial reductions in cover may have increased visibility of prey for carnivores, whereas the mobility and high population growth rates of insects combined with humid conditions may have allowed them to quickly re-establish populations in the impacted area after the storm, providing ample food for insectivorous birds. Short-lived responses of insectivorous, frugivorous, and nectarivorous birds to hurricanes have been observed in other areas of the Caribbean[23, 24]. No differences in mammals have been observed. Both *Artibeus jamaicensis* (frugivorous bat) and *Myotis* sp. (insectivorous bat) were observed, and jaguars (*Felis once*), pumas (*F. concolor*), and margays (*Leopardus wiedi*) have been observed since the hurricane.

The hurricane damage was not uniform among successional seres. The most severe impact appears to be found in the mature forest. The larger trees tended to be downed or damaged compared with younger, smaller trees. There was a greater amount of downed coarse wood in the mature forest, potentially increasing the fuel load, but litter deposited by the hurricane was rapidly decomposed. In contrast, the four-year old forest had lower amount of coarse wood but higher amount of litter two months after the disturbance. Epiphytes were damaged across the site, but few were found in the early seral forests before the hurricane. The insects, and the birds that feed in the canopies, were subject to greater loss in the mature forest than in the early seral stands. Formicidae, and Hymenoptera were especially reduced in the mature forest, but rapidly recovered in the secondary successional areas.

In summary, most animals, litter biomass, and plant coverage rapidly recovered to pre-disturbance levels. However, the greatest damage was to the mature forest. Under scenarios of increasing hurricane severity and frequency, the preferential damage to mature forests raises concern for the future of these critical ecosystems. Many of the bird and mammal communities, showed a minimal response. Others, such as the epiphyte community and canopy birds, were dramatically affected. Soil processes, from mycorrhizae to root carbon dynamics, to ant communities, were subtly altered, especially in the mature forest.

The Yucatan Peninsula experienced a dramatic increase in intense hurricanes during the past decade compared with the past hundred years[25]. During 2005 alone, three large hurricanes (Emily, Stan, and Wilma) crossed the northern part of the peninsula among the record 27 named storms. As it is, much of the mature forests of the Yucatan Peninsula as well as seasonal tropical forests globally have been lost due directly to land use change and to escaped fires resulting from land clearing[10, 26]. Following a hurricane, the downed limbs and trees provided a high fuel load. Both invading plants (in the gaps created by loss of large trees in mature forests) and the ladder fuels provide a greater opportunity for fire[4, 27]. Mature forests support species that do not persist in successional stands. This includes a high diversity of understory plants, and insects, most of which have not yet been described. We do not have good data for small mammals, amphibians and reptiles, but those that are associated with mature forests may also be susceptible. If the trend toward increasing catastrophic disturbance continues, care to retain existing forests and management to restore mature forests from secondary forests may become a crucial step in sustaining global biodiversity and ecosystem services.

Methods and Materials

The research was focused at the El Eden Ecological Reserve, Quintana Roo, Mexico (lat 21°12'N, long 87°11'W). This Reserve is comprised of about 2000ha of seasonal tropical forest, with a mix of seral vegetation resulting from fires that burned into the reserve from different areas and angles. The site is virtually flat, with a thin layer of uniform highly organic soil, and a limestone karst bedrock. The biodiversity, land-use history, and characteristics of the site are described in detail elsewhere[14].

Measurements

Plants- Litter biomass- During September 2005 , at each forest stand, we established three litter baskets to capture litterfall. We sample litter on the forest floor by sampling three locations of 0.5 x 0.5 m in the vicinity of each litter basket during September 2005 (1 month before the hurricane). Litter samples were oven dried at 80°C for 48 hours and then weighted. All measurements were repeated during December 2005 (2 months after the hurricane). We could not gain immediately access to the litterfall baskets and litter on the forest floor due to hurricane damage.

Sensors- At the 16 yr old forest, we measured barometric pressure and photosynthetically active radiation (PAR) at 1.5 meters above the forest floor as a measure of light availability under the canopy. At each one of the forest stands we installed soil temperature sensors and soil volumetric water content (VWC) sensors (ECHO, Decagon Inc.) inserted horizontally at 0.08 and 0.16 m depth. All measurements were recorded at 15 minutes intervals. We measured the concentration of soil CO_2 using solid-stte CO_2 sensors (GMT 222, Vaisala, Finland) at three soil depths 0.02, 0.08 and 0.16 m. We modeled soil respiration based in soil CO_2 concentration using the gradient flux method[28].

Soil characteristics- In September 2005, three 60 m transects were established within three successional stages: 1999 burn, 1989 burn, and mature forest. Along each transect two soil samples were randomly collected using a 11.5 cm diameter soil core. Soil samples were collected in September 2005 (one month before Hurricane Wilma), December 2005 (two months after Hurricane Wilma), and September 2006 (one year after Hurricane Wilma). Fine roots, < 3 mm diameter, were collected from individual soil cores by passing them through a series of sieves, and fine root length was determined using Newman's line intersection method[29]. Fine root length bulk density is defined as the length of fine roots divided by the volume of the soil sample (cm/cm^3). Soil organic matter was determined by mass loss on ignition[30]. Five replicates per site were heated at 360 C for two hours in a muffle furnace, where soil organic matter was calculated as the difference between pre- and post-ignition mass. Soil pH and soil electric conductivity (EC) was also determine in a 1:1 (soil: water) solution.

Mycorrhizal fungi- The percent of root length infected by arbuscular mycorrhizal fungi (AMF) was determined on fine roots collected before and immediately after Hurricane Wilma. A sub set of roots from individual soil cores were cleared in 10% (w/w) KOH and stained with trypan blue, mounted on slides and microscopically assessed for the presences of AMF hyphae, vesicles, and arbuscules. Spores were extracted by sucrose floatation[31].

Epiphytes- Vascular epiphytes were quantified before (August 2005) and after (December 2005) Hurricane Wilma in the different habitats within El Eden Ecological Reserve: mature forest, site of 1989 fire (16 years old), site of 1995 fire (10 years old), and site of 1999 fire (6 years old). Two investigators slowly walked for 1km surveying and counting all epiphytes within a 6m corridor (3m to either side of the walked transect) and up to a height of 4m. The same protocol was used at both sampling dates, resulting in quantification and identification of all vascular epiphytes from the ground to 4m height in 6000m^2 of each habitat type.

Insects- Samples were taken 100 meters inside and parallel to the main road of El Eden, 9 km length. The transect covered three vegetation types: secondary vegetation, savannah and mature forest. Ten yellow traps (20 cm diameter) with soap and water were put every 300 meters for 24 hrs for a total of 37 sampling points: 29 points in areas of secondary forest and 6 in mature forest. Sampling dates were: February, June, August and November. Individuals collected were conserved in alcohol (70%). Samples were by family and morphospecies in the laboratory of the Facultad de Medicina Veterinaria y Zootecnia de la Universidad Autónoma de Yucatán. Insect collection was deposited in the Entomological Collection of UADY. Insect diversity analysis was done for each vegetation type through the year of study, since number of sampling sites were different in each vegetation type, direct comparisons of richness between them was not possible

Birds- We evaluated the impacts of Hurricane Wilma on birds in mature and secondary forest by (1) comparing bird abundance and richness before and immediately after the storm and (2) quantifying the recovery, or temporal trends, in bird abundance and richness during the year following the hurricane. Prior to Wilma (March 4-6, 2003) J.

Rotenberg (unpubl. data) surveyed the winter bird community in El Eden using unlimited radius, 5-min point counts conducted within four hours after sunrise. In winter 2006 (Jan 25 – Feb 9), three months following Hurricane Wilma, we used the same methodology to survey birds at 12 of the same locations previously visited in winter 2003. We used Mixed Model ANOVAs to evaluate differences in bird abundance and richness before and after the storm, i.e., immediate storm impacts, where time relative to the storm (pre- and post) represented the within subject treatment and seral stage (mature and secondary) was included as a between subject treatment. We included interaction effects in our models to determine whether mature and secondary forest birds experienced different impacts. We used 5-min acoustic recordings to survey birds four times over a one-year period following Hurricane Wilma in order to evaluate longer-term temporal responses of the bird community; we surveyed birds in winter (Jan 25 – Feb 9), spring (May 30 – June 5), summer (Aug 16 - 20), and fall (Nov 7 - 11) 2006. Acoustic surveys were performed in the field using the Soundscape Recording System (SRS; Celis et al. unpubl data) consisting of four Sennheiser © ME62/K6 omni-directional microphones and an Edirol © 4-channel recorder (Roland). Acoustic recordings were interpreted by a single individual (ACM) in a soundscape recreation room with four speakers. We used Repeated Measures ANOVAs to quantify temporal trends in bird abundances and species richness in the two seral stages following the storm, where time after storm was the within subject treatment of interest.

Mammals- A motion sensitive Wildlife Pro Camera System was used to capture mammal species at the HabitatNet biological diversity plot. The incident delay was set to 20 seconds to maximize photographic opportunity for mammals utilizing the trail bordering the plot. Scatological as well as tracks from various mammal species were in evidence indicating trail use by them. The camera set-up included 35 mm film (ISO 400) and was set 1.0 meter above the ground, strapped to a tree. Additionally, the camera was angled to the trail so that any movement within 2.5 meters of the lens and motion detector would trigger the camera. Miscellaneous branches from understory plants were removed so that shrub branch movement, due to wind, would not activate the camera. Moist cat food was deployed within the camera range to attract carnivores.

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Acknowledgements: This research is supported by grants from NSF (DEB9981607, DEB0615427, EF0410408), UCR, and UC MEXUS-CONACYT. We thank El Eden Ecological Reserve for their continued support and access to their research facilities.

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Figure 1. Possible recovery outcomes might depend on a combination of prior disturbance site history, the damage suffered by the disturbance, and post hurricane conditions Are the outcomes related to previous site history (e.g. 6∏A, 10∏B…) or are they disconnected? Our data suggest that the early seral stages have minimal change, other than the loss of a few large trees. The mature forest lost many large trees and showed a reduction in canopy organisms. As mature forests are reduced in scale with human pressures, the ability of the remaining forests to serve as sources for re-colonizing organisms and to retain their previous functioning may diminish.

Figure 2. Dead and damaged trees in the different seral stages. There was a significant relationship between the stand age and size class (r= 0.86), and between the size classes and damaged trees (r=0.95) and dead trees (r-0.74).

Figure 3. Insect data per trap, all decline in the mature forest, and increase in the secondary vegetation.

Figure 4. Difference in abundance of canopy dwelling birds (A), frugivores and nectarivores combined (B), carnivores (C), and insectivores (D) between winter 2003 (Pre-Wilma) and winter 2006 (Post-Wilma). Mixed Model ANOVAS performed using SPSS Version 11.0.1 (SPSS 2002).