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How a hurricane disturbance influences extreme CO$_2$ fluxes and variance in a tropical forest

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Abstract

A current challenge is to understand what are the legacies left by disturbances on ecosystems for predicting response patterns and trajectories. This work focuses on the ecological implications of a major hurricane and analyzes its influence on forest gross primary productivity (GPP; derived from the moderate-resolution imaging spectroradiometer, MODIS) and soil CO$_2$ efflux. Following the hurricane, there was a reduction of nearly 0.5 kg C m$^{-2}$ yr$^{-1}$, equivalent to $\sim$15% of the long-term mean GPP ($\sim$3.0 ± 0.2 kg C m$^{-2}$ yr$^{-1}$; years 2003–8). Annual soil CO$_2$ emissions for the year following the hurricane were $>3.9$ ± 0.5 kg C m$^{-2}$ yr$^{-1}$, whereas for the second year emissions were $1.7$ ± 0.4 kg C m$^{-2}$ yr$^{-1}$. Higher annual emissions were associated with higher probabilities of days with extreme soil CO$_2$ efflux rates ($>9.7$ $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$). The variance of GPP was highly variable across years and was substantially increased following the hurricane. Extreme soil CO$_2$ efflux after the hurricane was associated with deposition of nitrogen-rich fresh organic matter, higher basal soil CO$_2$ efflux rates and changes in variance of the soil temperature. These results show that CO$_2$ dynamics are highly variable following hurricanes, but also demonstrate the strong resilience of tropical forests following these events.

Keywords: carbon starvation, decomposition, diel patterns, ecosystem services, photosynthesis, soil respiration

Online supplementary data available from stacks.iop.org/ERL/7/035704/mmedia

1. Introduction

Large infrequent disturbances (LIDs) are extreme events (i.e., events that exceed the ordinary, usual or expected conditions) that have visible effects on the landscape (e.g., flooding, uprooting of trees or damages to man-made infrastructure) and by definition are unusual in time and space (Turner and Dale 1998). These events could lead to shifts in ecosystems pushing them beyond ecological thresholds that could lead to possible alternative stable states (Scheffer and Carpenter 2003). Hurricanes are disturbances that could affect large areas and result in evident visible effects on ecosystems and urban infrastructure. Thus, a current challenge is to understand which are the legacies left by hurricanes (and other disturbances) on urban and natural ecosystems to predict the
response patterns and trajectories and evaluate their ecological (Bengtsson et al. 2003) and economic implications (Turner et al. 2003).

Initially, most research after hurricane disturbances was done on the visible effects on ecosystems as a way to evaluate the impact and response to these events (Lugo 2008). Furthermore, the abundance of studies on visible effects suggest that these are arguably easier to quantify (e.g., timber or crop losses) than invisible effects (i.e., change in nutrient dynamics, belowground processes, or CO₂ emission rates), or that there was simply less interest in evaluating the latter (Magnuson 1990). Recently, several studies have focused on the legacy of invisible effects after hurricanes. These effects include shifts in ecosystems processes such as the reduction of primary productivity (Barr et al. 2012, Chambers et al. 2007), nutrient dynamics (Lugo 2008, Ostertag et al. 2003), root mortality and production (Beard et al. 2005, Vargas et al. 2009), and trace gas fluxes from soils (Steudler et al. 1991, Vargas and Allen 2008).

The response patterns and trajectories of the effect of disturbances in ecological processes could be evaluated and characterized by analyzing the extremes of the magnitudes in the measured variables. These statistical extremities can exceed a threshold with respect to a previous period or a long-term record, say \( X_{t+n} \gg X_{\text{mean}} \), and therefore the return towards \( X_{\text{mean}} \) could be interpreted as a response towards mean long-term dynamics. This could be evaluated by studying extreme statistical events (e.g., using extreme-value distribution, Katz et al. 2005) as a result of the legacy of a disturbance on ecosystems processes. Evaluation of thresholds and ecosystem recovery after disturbances have been done largely from a theoretical approach (Carpenter and Brock 2006) because it is difficult to generate large amounts of information and in most cases disturbances arrive as a surprise at study sites. With the growth of environmental monitoring networks (e.g., NEON, ICOS, FLUXNET) it may be possible to generate better and larger spatial and temporal information on how different disturbances influence ecosystem processes (Vargas et al. 2012).

The objective of this work is to study the response of forest CO₂ fluxes by analyzing their responses in magnitudes and trends following a major hurricane. First, the value-added product (i.e., MOD17A2) derived from moderate-resolution imaging spectroradiometer (MODIS) was used to evaluate the long-term (years 2003–8) impact and response of forest gross primary productivity (GPP). Second, the soil CO₂ efflux, the flux of microbial and plant-respired CO₂ from the soil to the atmosphere, was analyzed for over two years following the disturbance to evaluate the short-term effect of the hurricane on soil processes.

Much attention has been drawn to the study of extreme events, but these events are determined by statistical extremity with respect to a historical reference period (e.g., extraordinary deviation from the median of probability distributions Reiss and Thomas 2007). For this study, the passing of a hurricane could be seen as an extreme weather event that caused evident changes in the structure of the ecosystem such as plant defoliation and biomass loss (Vargas et al. 2010b). The scientific questions asked in this study are: (a) How does a hurricane disturbance influence forest long-term GPP? (b) How fast does the litter deposited from plant defoliation stay on the forest floor and how does this influence the soil CO₂ efflux rates? (c) How does a hurricane affect the variance and statistical extremities of these fluxes, and how do these extreme rates influence the annual carbon budgets?

2. Methods

2.1. Study site

The study was conducted at El Eden Ecological Reserve (latitude 21°12.6′N, longitude 87°10.93′W) in the northeast portion of the Yucatan Peninsula, Mexico. This site has a mean annual temperature of 24.2 °C and annual precipitation of 1650 mm. The climate is typical of seasonally dry tropical forests, with a pronounced dry season (<100 mm/month) from January to April. The forest was naturally regenerated after a severe fire in 1989 resulting in a dense, even-aged stand with total aboveground carbon of nearly 31 mgC ha⁻¹ and total belowground carbon of 66.7 mgC ha⁻¹ (Vargas et al. 2008). Soils are composed of approximately 30% soil organic matter, are shallow with a depth of nearly 20 cm, and are underlain by limestone bedrock. Soils have a bulk density of 0.61 g cm⁻³, pH of 7.6 and porosity of 0.77. The soil texture was 63% sand, 22% silt and 15% clay.

Hurricanes are distinct disturbances for tropical ecosystems within the Atlantic basin. Between 1857 and 2007, thirty-five hurricanes made landfall within a 200 km radius around the study site, but only twelve hurricanes hit within a 50 km radius in that timeframe (www.csc.noaa.gov). On 21 October 2005, hurricane Wilma made landfall over the island of Cozumel, Mexico, and emerged over the Gulf of Mexico on 23 October. The immediate effect of the hurricane was the reduction in leaf area index (Vargas et al. 2009). Hurricane Wilma was the most intense hurricane on record in the Atlantic basin with maximum winds over 295 km h⁻¹ and a record low barometric pressure of 882 mbar (www.nhc.noaa.gov). Before hurricane Wilma, the last hurricane that made landfall within a 50 km radius of the study site was in September 1944 (www.csc.noaa.gov).

2.2. Instrumentation

During September of 2005, two soil sensor nodes were installed at the study site (Vargas and Allen 2008). Measurements stopped when the hurricane passed in October and were resumed starting on 1 January 2006 and continued through April 2008. Each sensor node consisted of soil temperature, soil moisture and soil CO₂ sensors at three depths (2, 8 and 16 cm) as previously described (Vargas and Allen 2008). Soil temperature and soil water content were also measured at 15 min intervals with EC-H₂O soil sensors (EC-TM Decagon Devices, Inc. Pullman, WA). Soil CO₂ concentration was continuously measured at 15 min intervals with Vaisala CARBOCAP CO₂ sensors (GMM222, Vaisala,
Figure 1. Mean daily average of MODIS-GPP (i.e., gross primary productivity [GPP] derived from NASA’s moderate-resolution imaging spectroradiometer [MODIS]) for years 2003–8 (a); and 30 day variance of MODIS-GPP for that same period (b). The gray area in (a) represents ±1 standard deviation, and the horizontal dashed line in (b) represents the long-term mean value of the 30 day variance. The arrow indicates the approximate time when hurricane Wilma hit the study site.

Helsinki, Finland). Soil CO$_2$ concentrations were corrected for temperature and pressure using the ideal gas law according to the manufacturer. Soil CO$_2$ efflux was calculated using the flux-gradient method as described by Vargas et al. (2010a), which included corrections for temperature, pressure and used the (Moldrup et al. 1999) model for soil CO$_2$ diffusion.

2.3. Gross primary production

To provide information about the influence of hurricane Wilma on longer-term ecosystem CO$_2$ fluxes, the value-added product MOD17A2 was used to report gross primary production (MOIDS-GPP; Zhao and Running 2010). Thus, a 3 km $\times$ 3 km grid, centered at the study site, was selected to acquire the MOD17A2 product from Collection 5 from the ORNL DAAC (2011). Details about preparation of subsets including data MODIS reprocessing, methods and formats can be found at ORNL DAAC (www.daac.ornl.gov/MODIS/modis.html). Temporal linear interpolation was used to replace pixels with poor quality control flags. The 8 day MODIS-GPP values were extrapolated to daily values (gC m$^{-2}$ d$^{-1}$) using a simple linear interpolation. MODIS-GPP was calculated from year 2003 to 2008.

2.4. Soil litter pools

During September 2005 twelve 0.25 m$^2$ plots were established within a 2400 m$^2$ plot at the forest stand where the soil CO$_2$ measurements were done. Soil litter was collected from each 0.25 m$^2$ plot and divided by different pools: O$_1$-horizon (slightly decomposed litter with debris <5 cm in diameter) and O$_2$-horizon (decomposed litter layer). The O$_2$-horizon was subdivided into O$_e$ $>$ 2 mm (material larger than 2 mm; partially decomposed litter) and O$_e$ < 2 mm (material smaller than 2 mm; highly decomposed litter) as reported previously at the study site (Vargas et al. 2008). All samples were dried at 65 °C for 72 h to determine dry weight and then ground for total carbon and nitrogen analysis determined by dry combustion using a Thermo Finnigan Flash EA1112N/C analyzer (Milan, Italy). Values of all samples are expressed in nitrogen percentage (%N) and mgC ha$^{-1}$ by multiplying the dry weight times the carbon percentage. The same protocol was repeated during December 2005 to evaluate the immediate impact of the hurricane on soil litter pools.

2.5. Data analysis

Extreme statistical events were determined by assessing extraordinary deviations from the median of a probability distribution (Jentsch et al. 2007). Soil CO$_2$ efflux representing a statistically extreme event was determined by analyzing data between January 2006 and April 2008 (i.e., 2.3 yr). The minimum threshold of an extreme value of CO$_2$ efflux was determined by calculating the upper 95th percentile of CO$_2$ efflux using extreme-value distribution (Katz et al. 2005). These data were used to determine how the probability of extreme CO$_2$ efflux events changed following a LID (i.e. hurricane). First, the cumulative distribution function that corresponded to extreme CO$_2$ efflux events was calculated with a moving-average analysis and a 30 day window. Second, the ratio of an extreme CO$_2$ efflux event by the 30 day average window was evaluated to track the relative contributions of these extreme fluxes in time. Third, the moving-variance on a 30 day window was calculated for MODIS-GPP, soil CO$_2$ efflux, soil temperature (at 8 cm depth) and soil water content to investigate the influence of the hurricane on the spread or moments of the distribution using a 30 day window.
Finally, to investigate the influence of the hurricane (e.g., input of fresh litter, root mortality) on soil CO$_2$ efflux, the basal soil CO$_2$ efflux as calculated using the following empirical formula:

$$\text{CO}_2\text{ efflux} = SR_B * \exp(B_1 * (20 - T_s))$$ (1)

where basal soil CO$_2$ efflux (SR$_B$) was defined as the rate of soil CO$_2$ efflux at 20°C. This temperature was the mean soil temperature at 8 cm depth for the measured period. Basal soil CO$_2$ efflux was calculated first for the year 2006 (i.e., first year following hurricane Wilma) and then for the measurements from 2007-onwards to investigate potential differences.

3. Results

The average annual sum of MODIS-GPP between years 2003 and 2005 was 3540 ± 181 gC m$^{-2}$ yr$^{-1}$ and between 2006 and 2008 was 3313 ± 252 gC m$^{-2}$ yr$^{-1}$ (figure 1(a)). Importantly, MODIS-GPP was reduced substantially for 2006 to an annual sum of 3039 ± 460 gC m$^{-2}$ yr$^{-1}$; equivalent to a reduction of nearly ~15% of the long-term mean MODIS-GPP. The mean value of the variance between 2003 and 2008 was 0.5, and the largest values were observed for the year 2006 following hurricane Wilma; these values correspond to the drastic reduction of MODIS-GPP for that year (figure 1(b)).

The immediate effect of the pass of the hurricane was the increase of canopy openness (Vargas et al. 2009) and therefore an input of fresh organic matter into the soil. Two months following the hurricane there was significantly (Kruskal–Wallis test; $P < 0.05$) higher nitrogen percentage in the $O_i$ and $O_e > 2$ mm litter pools, but only significantly higher (Kruskal–Wallis test; $P < 0.05$) carbon stored in the $O_e < 2$ mm litter pool in comparison with pre-hurricane values (figure 2).
Figure 3. Mean daily average of soil CO$_2$ efflux (a), soil temperature (b) and soil water content (c) from 1 January 2006 to 20 April 2008. Soil volumetric water content and soil temperature values represent mean daily average between 2 and 16 cm depth. The 95th percentile threshold to identify an extreme CO$_2$ efflux using extreme-value distribution is represented by a dashed line in (a). Gray areas represent ±1 standard deviation.

Annual soil CO$_2$ emissions for the first year following the hurricane disturbance (January–December 2006) were 3933 ± 469 g C m$^{-2}$ yr$^{-1}$ whereas for the second year (January–December 2007) emissions were 1656 ± 383 g C m$^{-2}$ yr$^{-1}$; representing a reduction of nearly 58% (figure 3(a)). Overall, there were significantly higher (t-test $t = 24.36; \ P < 0.001$) mean CO$_2$ efflux rates for 2006 (10.8 µmol CO$_2$ m$^{-2}$ s$^{-1}$) than for 2007 (4.5 µmol CO$_2$ m$^{-2}$ s$^{-1}$). Soil CO$_2$ efflux rates >10 µmol CO$_2$ m$^{-2}$ s$^{-1}$ were common during 2006 (figures 3(a), 4(a)), and these high rates were present during both the day and night showing no substantial diel differences in these extreme fluxes (figure 4(a)). Mean soil temperature at 8 cm was 25°C (figure 3(b)) and mean soil water content was 0.14 m$^3$ m$^{-3}$ (figure 3(c)) for both years indicating similar weather conditions.

The 95th upper percentile threshold to identify an extreme CO$_2$ efflux was 9.7 µmol CO$_2$ m$^{-2}$ s$^{-1}$ (dashed line in figure 3(a)). For the first 150 days of 2006 the probability of extreme CO$_2$ efflux was >60%, and between days 150 and 365 was <40% (figure 4(b)). For the second year following the hurricane the probability to observe extreme CO$_2$ efflux dropped to <5%. The 30 day ratio (i.e., relative contribution) of an extreme CO$_2$ efflux event ranged between 0.7 and 1.7 with a mean of 1.12 (figure 4(c)). Extreme CO$_2$ efflux rates had a mean of 14 µmol CO$_2$ m$^{-2}$ s$^{-1}$, and the magnitude of these extreme fluxes decrease with time (figure 4(d)).

The 30 day variance window of soil CO$_2$ efflux had a mean of 3.3 taking into account all the measurements (i.e., >2 years of measurements). During most of the first 300 days of measurements the 30 day variance window was higher than the value of 3.3 (figure 5(a)). In contrast the 30 day variance window of soil temperature was highly variable and did not follow a distinct pattern following the hurricane event (figure 5(b)). The highest variance for soil temperature was associated with sharp decreases in temperature during the months of November (figure 3(b)). Soil water content 30 day variance window followed patterns of drying and wetting of soil due to water pulses (figures 5(c) and 3(c)).
The ecological implications of a major hurricane were studied by analyzing the change in variance and extremeness of forest CO$_2$ fluxes in a tropical forest. It is suggested that the temporal patterns and trends of variance and extremeness represent ecological implications and provide information about ecosystem response trajectories following this extreme event.

Following the hurricane MODIS-GPP reached maximum values of nearly 12 gC m$^{-2}$ day$^{-1}$ for the year 2006, which were similar to the maximum values for years 2003–5 (figure 1(a)). Noteworthy, by April 2006 there was a sharp reduction on MODIS-GPP, which coincided with a sharp decrease in soil moisture (figure 3(c)). A previous study has shown that trees in tropical forests can vary the concentration of non-structural carbon compounds and these concentrations are associated with climatic conditions (Wurth et al 2005). Furthermore, following hurricane Wilma the trees at the study sites were able to rapidly produce new fine roots, but these new structures were built from stored carbon of up to 11 years old (Vargas et al 2009). Therefore, one possible explanation is that these plants rapidly invest in the production of new structures but with a cost of non-structural carbon reserves that could make them vulnerable to stressful conditions (i.e., drought events) in the following year.

The sharp reduction of MODIS-GPP in the year of 2006 resulted in nearly 15% decrease in annual MODIS-GPP. This reduction was associated with large variability (i.e., large standard deviation and variance in figure 1) of MODIS-GPP following the sharp reduction and the drought event. This implies that some pixels within the 3 m $\times$ 3 km area where MODIS-GPP was calculated had very high values and others very low values. Thus, the potential carbon starvation explanation given in the previous paragraph could not apply for all the trees within the study area. This suggests that some trees must have responded differently to the drought event following the hurricane and open new research questions: (a) How and when plants allocate non-structural carbon reserves following stressful conditions? (b) Does investment of non-structural carbon reduces resiliency to future stressful conditions? Importantly, forest MODIS-GPP returned to long-term dynamics of variance, magnitudes and patterns for the years of 2007 and 2008. This suggests that although a hurricane disturbance has large implications in forest photosynthesis these forests can recover pre-hurricane dynamics, patterns, and magnitudes within 2 years.

The effect of the hurricane disturbance on soil CO$_2$ efflux was an increase in the probability of extreme CO$_2$ efflux (i.e., a flux $>9.7$ µmol CO$_2$ m$^{-2}$ s$^{-1}$), and their relative importance increased with time as the probability and

![Figure 4](image-url)
Figure 5. Time series of a 30 day variance for soil CO$_2$ efflux (a), soil temperature (b) and soil water content (c) derived from data presented in figure 3. The horizontal dashed line in all figures represents the long-term mean value of the 30 day variance. Measurements were taken between 1 January 2006 and 20 April 2008.

magnitude of these fluxes decreased (figure 4). Importantly, there was no distinct diel pattern of soil CO$_2$ efflux trends, nor were extreme efflux rates associated with daytime temperatures (figure 4(a)). This contrasts with what is commonly seen in temperate ecosystems characterized by a strong CO$_2$ efflux diel pattern with higher efflux located during the daytime and driven by diel fluctuations of soil temperature (Gaumont-Guay et al. 2006).

Following the hurricane the variance of soil CO$_2$ efflux showed a constant reduction suggesting a potential recovery of the rates for year 2007. Although no long-term records exist to compare this trend it is possible that soil CO$_2$ efflux followed the trend of MODIS-GPP variance and therefore implying also a rapid recovery of this ecosystem process following the hurricane. For instance, the variance of soil CO$_2$ efflux was negatively correlated with the variance of soil temperature for the first 300 days of measurements suggesting that constant extreme soil CO$_2$ efflux rates could be driven by large variations (i.e., high variance) in soil temperature. In contrast, the soil CO$_2$ efflux variance following the first 300 days was correlated with MODIS-GPP variance suggesting a recovery of the link between these two variables (Vargas et al. 2010a).

The trend of reduction in extreme CO$_2$ efflux events following the hurricane could be explained by a depletion of available substrate for heterotrophic respiration (Harmon et al. 2011). It is well known that following wind disturbances there is a large accumulation of easily decomposable organic matter due to deposition of nutrient-rich litter as seen in our study site (figure 2). Our results support previous observations showing that newly deposited nutrient-rich biomass following wind disturbances are rapidly decomposed in tropical forests (Harmon et al. 2011, Ostertag et al. 2003, Vargas et al. 2010b), but our results show that a large portion of the litter biomass is transferred to the highly decomposed litter pool (i.e., O$_{e}$ < 2 mm). This increase in biomass to the O$_{e}$ < 2 mm pool could have served as substrate for higher soil basal CO$_2$ efflux observed during 2006 in comparison with the lower soil basal CO$_2$ efflux for the following year associated with lower annual fluxes. These results show that forest soil CO$_2$
dynamics are highly variable following hurricanes but also demonstrate the strong resilience of tropical forests following these events.

5. Conclusions

This study shows that patterns and trends of extremeness and variance of forest CO₂ fluxes provide information about ecological implications after disturbances, and could be used to identify ecological transitions and potential recovery trajectories. The long-term annual sum of MODIS-GPP was nearly 3.0 kgC m⁻² yr⁻¹ and was reduced by 0.5 kgC m⁻² yr⁻¹ for the year following a hurricane disturbance. The reduction on MODIS-GPP was associated with a drought episode, which could have caused strong stress on some plants already affected by the hurricane. The annual sum of soil C emissions (>3.9 kgC m⁻² yr⁻¹) following the hurricane were the largest reported in the literature (Bond-Lamberty and Thomson 2010b). One year following the disturbance the annual sum of soil C emissions were only 1.7 kg C m⁻² yr⁻¹ representing a reduction of nearly 58%, and are within the range of rates from other tropical forests (Bond-Lamberty and Thomson 2010a).

The difference in soil C emissions between years was equivalent to 22 ton C ha⁻¹. If we assume a mean value of US$43 per ton of C (Yohe et al 2007) the excess in soil C emissions for the first year following the hurricane results in a potential cost of US$946 ha⁻¹. The reduction of forest photosynthesis following the hurricane was equivalent to 5 ton C ha⁻¹. This reduction in forest C sequestration represents an additional potential cost of US$215 ha⁻¹. These costs associated with an invisible effect (i.e., increase in soil CO₂ efflux and reduction in photosynthesis) of a disturbance is generally not included when evaluating economic assessments of extreme weather events, and should be taken into account for policy and ecological discussions on the influence of disturbances on terrestrial ecosystems.

The study of disturbances and their consequences on ecosystem processes still represents a challenge for experimental and modeling research (Ciais et al 2005, Liu et al 2011). Importantly, the definition of ‘extreme events’ needs to be revisited because in most cases an extreme event is determined by statistical extremity with respect to a historical reference period (Reiss and Thomas 2007). Thus, historical and multiple long-term records are critical to properly evaluate the statistical extremity of a response variable and the full ecological implications and recovery pathways for different ecosystem processes.

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