Immediate impact of a hurricane on the structure of a tropical butterfly community.

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Abstract

More intense and frequent hurricanes may lead to long-lasting effects to tropical ecosystems. Here we describe the immediate impact on the butterfly community of a lowland forest in Belize, following Hurricane Earl. Species richness and abundance increased post-hurricane, likely driven by convergence of the organisation between the canopy and understory communities.

Key words:

disturbance; Lepidoptera; tropical forest; wind-storm

FORESTS ARE SHAPED BY THEIR DISTURBANCE HISTORIES, with the occurrence of hurricanes and other natural events influencing their composition, structure, and functional processes. It is arguable that the frequency and magnitude of natural disturbance events are increasing in the tropics due to the onset of climate change (Seidl et al. 2017). Whilst being a natural part of forest dynamics, when disturbances exceed their natural range of variation, the change in forest structure and function may be extreme (Lugo 2000). Increasing sea surface temperatures of the Atlantic ocean are potentially leading to twice as many hurricanes in Central America per year, having profound influences in shaping plant and animal communities, soils, and even landforms in Caribbean forests (Bender et al. 2010; O'Brien et al. 1992). Impacts of hurricanes invariably involve high levels of vegetation damage, leading to immediate and delayed patterns of tree mortality, alteration of forest structure with the opening of gaps, increased litterfall, and changes in nutrient cycling (Lugo 2000; Brokaw & Walker 1991; Lodge & McDowell 1991). As such, animal communities are subject not only to the direct physical damage and mortality incurred during and immediately after the storm, but also to the indirect impacts of changes in microenvironments and thus available niches, and reduction in resource availability in terms of both food and refugia (Waide 1991; Willig et al. 2011; Schowalter et al. 2017).

Impacts of disturbance on butterfly communities have been found to involve convergence of community organisation due to loss of canopy habitat, driving canopy specialists to the understory level (Fermon et al. 2005). Furthermore, disturbance and opening of forest gaps can result in selective filtering on the functional composition of the butterfly community, in terms of geographic range size and flight morphologies (Dumbrell & Hill 2005; Hill et al. 2001). Disturbed forests are thought to be characterized by more generalist, wide ranging butterfly species with wing morphologies that enable them to be highly mobile with widespread distributions. Fruit-feeding butterflies, with the larval stages being dependent on particular host plants and the adults being closely linked to their habitat through food availability, are found to respond quickly and consistently to changes in their microenvironments, reflecting damage caused by disturbance events (Fleishman & Murphy 2009; Bossart et al. 2006). In addition to their well described ecology and relatively resolved systematics, this makes fruit-feeding butterflies valuable as environmental indicators (Bonebrake et al. 2010).

Despite the importance of Belizean rainforests as an integral part of the globally significant Mesoamerican Biological Corridor and their vulnerability to disturbance, including hurricanes forming over the warming Atlantic waters, there is very little research addressing Belizean terrestrial ecosystems (Villarini & Vecchi 2013; Cherrington et al. 2012). As such, this study describes the immediate impact of Hurricane Earl on the fruit-feeding butterfly community in a lowland forest in Belize, by investigating the change in the community in terms of diversity and composition before and after the hurricane.

The study was conducted at Pook's Hill, a 300-acre private reserve located in the Cayo District of Belize (17°09'12.0" N, 88°51'06.0" W). The site consists largely of primary lowland broadleaf forest, connected in the south to the Tapir Mountain Nature Reserve, and bordered by the Roaring River and agricultural landscape to the east. Thirty-two static fruit-baited traps (Fig. S1) were set up in a grid-like formation approximately 150m apart (Fig. S2). Each trap was hung 1m from the ground at the understory level and baited with 1tbsp of mashed banana, rebaited daily.

Trapping was conducted from 14th July to 25th August 2016. Half-way through data collection, on 4th August, Hurricane Earl passed directly through the study site as a Category 1 hurricane, with wind speeds of 65-75kt (120.38-138.9 km/h) and storm rainfall of 9-12 inches

(228.6-304.8 mm) (Steward 2017). Data were collected and analysed from all 32 trapping sites, over 12 days pre- and, for 28 of the sites, over 10 days post-hurricane, giving a total of 664 trapping days. Any butterflies caught were identified to species, sexed, and measured. Biometric measurements consisted of forewing length, body length, and body width. Condition was scored as 4 ranks with a score of '1' denoting perfect body condition and '4' indicating a very faded and brittle individual. Additionally, records pertaining to number of host plants, representing niche breadth, and geographic range size for each butterfly species were gathered from Devries (1987), Natural History Museum "HOSTS Database" (2010), and "Caterpillar Database" (Janzen & Hallwachs 2009). Furthermore, percentage canopy cover, canopy height, tree species richness, stem density, and diameter at breast height (dbh) were measured within a 5m radius of each trapping site before and after the hurricane. Damage to forest structure was estimated for the area along six 100m transects (at least 200m apart), where the proportion of damaged trees (trees with dbh >5cm which had at least the loss of one major limb) were recorded.

Principal Components Analysis was conducted in order to simplify the 5 habitat variables, with a parallel analysis indicating that PC1 and PC2 ought to be retained in further analysis. PC1, accounting for 54 percent of variation, corresponded to the understorey structure while PC2 accounted for 20 percent of the variation and represented canopy attributes (Table S1). Both PC1 and PC2 scores declined following the hurricane, indicating the forest structure becoming more open, with less canopy cover and reduced vegetation complexity in the understory (Fig. S3). The transect data showed that the field site experienced substantial impact from the storm with c.60 percent of the trees (>5cm dbh) showing a considerable level of damage. Changes in butterfly species richness and abundance were assessed at trap level using general linear models, with a negative binomial error distribution to control for overdispersion.

For these models, habitat variables (PC1 and PC2) were nested within ‘Hurricane’, a categorical factor with two levels, before and after. Abundance of individual genera and of forest guilds (canopy, understory, and generalist butterflies, as specified by Devries & Walla 2001 and DeVries 1988) before and after the hurricane was compared using chi-square tests, adjusting for multiple comparisons using a sequential Bonferonni correction. Additionally, similarity between the communities before and after the hurricane was estimated using the Bray-Curtis index (Colwell 2013). Changes in traits (biometric measurements, condition, range size, and niche breadth) were assessed at the trap level, using general linear models, with a gamma error distribution. For these models, habitat variables (PC1 and PC2) were nested within ‘Hurricane’, a categorical factor with two levels, before and after.

A total of 486 individuals of 64 species were recorded, 173 individuals of 50 species pre- and 313 individuals of 50 species post-hurricane (Table S2). Both species richness and abundance per trap increased following the hurricane, although were not influenced by habitat variables (Fig. 1; $F_{1,53}$=10.925, P=0.002; $F_{1,53}$=11.840, P=0.001, respectively). Furthermore, overall abundance of canopy and generalist butterflies also increased following the hurricane (Table 1). This is likely an indication of the stratification of the canopy and understorey butterfly communities becoming less distinct, leading to convergence of community organisation (Dumbrell & Hill 2005). This is further supported by 4 of the 10 genera with sufficient sample sizes (total individuals trapped >10) showing significant increases in abundance post-hurricane, following sequential Bonferroni correction, all of which were generalist or canopy specialist taxa (Table S3). Due to the heterogeneity of forest structure, canopy butterflies are recorded at the understorey level pre-hurricane, particularly in or near forest gaps that may support a more even butterfly assemblage (Houlihan et al. 2013; Hill et al. 2001). As such, turnover in the butterfly community pre- and post- the hurricane was low (Bray-Curtis=0.485). However, at this inter-site scale the species richness and abundance of the community did not show changes in relation to the forest structure, a relationship that is likely only evident at a larger, forest-wide scale (Hill & Hamer 2004).

Forewing length and body length both increased with understorey vegetation complexity (PC1) ($F_{2,51}$=8.280, P=0.001; $F_{2,51}$= 11.980, P<0.001, Table S4, Fig. S4), however did not change following the hurricane and were not influenced by canopy attributes (PC2) (Table S4). This indicates that bigger butterflies were found in denser, less disturbed forest. The other traits (body width, condition, range, and niche breadth) did not show any change following the hurricane, nor were influenced by habitat variables (Table S4). This suggests there was no demonstrable selective filtering imposed by the hurricane on these functional traits within the butterfly assemblage. Previous studies have found mobile and generalist species to be favoured in disturbed conditions (Dumbrell & Hill 2005). This is likely due to the community already being adapted to persisting in a naturally disturbed habitat, owing to a history of frequent and destructive disturbance events in Belize (Lewis 2001). Long-term sedimentary records indicate the mean recurrence of major hurricanes in Belize is once a decade (McCloskey & Keller 2008; Denommee et al. 2014). While records over the past 100 years report 26 hurricanes, resulting in 2.6 disturbance events per decade (Friesner 1993; National Hurricane Center 2017). Previously to hurricane Earl, the field site in central Belize was impacted by hurricanes Richard (25 October 2010) and Iris (9 October 2001).

The butterfly community was found to be relatively resistant to the immediate impact of the hurricane. However, the longer-term shifts in the interactions between the butterflies and the forest flora once the impact of the hurricane has taken effect in the plant community are unknown. Long-term studies, over 19-year period, on general canopy arthropod communities have shown dynamic responses to hurricane disturbance for different taxa, with important effects of host tree species and initial local conditions (Schowalter et al. 2017). It is recognised that within populations faced with frequent disturbance, or stresses such as imposed by climate change, while behavioural mitigation strategies are favoured on short time scales, adaptive responses to the disturbed environment is favoured on longer timescales (Cole et al. 2014; Aguilée et al. 2016). This study indicated an immediate behavioural response in the butterfly community, contributing to the body of work detailing impacts of hurricanes. However, longer-term research into hurricane impacts is limited (Schowalter et al. 2017), despite a wealth of research addressing the long-term nature of other types of disturbance, such as logging and land-use change (Dumbrell & Hill 2005; Hamer et al. 2003; Cleary & Genner 2004). With the magnitude and frequency of hurricanes set to increase with the onset of climate change (Knutson et al. 2010), it is important to understand the level of tolerance of animal communities to such wind-storm events.

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DATA AVAILABILITY STATEMENT

The data used in this study will be archived at the Dryad Digital Repository upon acceptance of the manuscript.

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TABLES

TABLE 1. Recorded number of individual butterflies within each forest guild (canopy, understory, and generalist) before and after Hurricane Earl trapped in a lowland forest, Belize, with chi-square tests to assess change in abundance where * = significant following Bonferroni correction of the critical value.

Guild	Pre	Post	Total	P-value
Canopy	54	152	206	*<0.001
Understory	93	112	205	0.185
Generalist	26	49	75	*0.008

FIGURE LEGENDS

FIGURE 1. Change in (A) species richness and (B) abundance of the butterfly community in a lowland forest in Belize following Hurricane Earl, with the global mean (dashed line).

A. FIGURES