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Hurricane impacts on plant-herbivore networks along a successional chronosequence in a tropical dry forest☆

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ABSTRACT

Hurricanes are one of the major natural forces affecting plant and animal dynamics in areas where tropical dry forests (TDF) are located. Most studies of hurricane impacts have evaluated the effects on plants, but few have addressed how interactions between plants and animals are affected. We investigated the effect of hurricane Jova on plant-lepidopteran interaction networks along a TDF successional gradient in the Chamela region on the Mexican Pacific coast. We surveyed plant-lepidopteran larvae trophic interactions during 2007–2010 and re-surveyed this association in 2012 and 2013, following the landfall of a category 2 hurricane. The parameters of plant-lepidopteran interaction networks changed after the hurricane. Network size, number of compartments and specificity (H2) diminished, while connectance and robustness increased. Network differences throughout the chronosequence remained similar to the patterns observed in previous studies showing larger networks and higher levels of robustness but lower connectance in late successional stages than in recently abandoned pastures. It is interesting that even though the hurricane affected plant-lepidopteran interaction networks, the topology related to forest succession remained unaltered after the passage of the hurricane, demonstrating the long legacy of the human footprint on ecosystems.

1. Introduction

Tropical dry forests (TDF) are located in tropical and subtropical regions of the world, where hurricanes are one of the major natural forces affecting plant and animal communities. Hurricanes are an example of large and infrequent disturbances that have profound effects on ecosystems (Lugo, 2008). Post-hurricane plant dynamics involve the growth of secondary succession species replacing large trees with slow growth rates (Denslow, 1980; Zimmerman et al., 1994; Denslow, 1995). However, while TDF species have evolved with these occasional large disturbances over a long time period, we are unsure how they will react to the increasing hurricane magnitude, frequency and intensity predicted by recent climatic models. Particularly, hurricanes are already becoming more severe and frequent on the Pacific coast of Mexico than they were previously recorded (Knutson et al., 2015).

Most investigations studying hurricane impacts have addressed the effects on vegetation, including changes in animal communities (Lugo, 2008) and plant animal interactions (Ferguson, 1995; Pascarella, 1998; Rathcke, 2001; Angulo-Sandoval et al., 2004; Horvitz et al., 2005). However few studies have documented the impact in plant-animal networks (Sánchez-Galván et al., 2012). Following the passage of a hurricane, the most evident damage is the loss of canopy foliage, which translates into increased light intensities and temperatures within the forest and a decrease in relative humidity (Lugo, 2008), and therefore modifying the microhabitat for animal species. Lugo (2008) proposed that the main post-hurricane impacts on animals are mediated through changes in the ecological space available to organisms, habitat modification, as well as to increased landscape heterogeneity and variability in ecosystem processes. Depending on the life histories of the species involved, the hurricane impact can thus present wide variation. For example, while bird communities, particularly nectarivores and fruit/seed eaters, showed a general decline following Hurricane Hugo in the US Virgin Islands (Askins and Ewert, 1991; Wauer and Wunderle, 1992), whereas bats showed decreased abundance and boas increased

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their home range in Puerto Rico (Wunderle et al., 2004).

In the case of invertebrates, the impacts of a hurricane are strikingly noticeable. Population counts on invertebrates after Hurricane Hugo in Puerto Rico showed dramatic reductions for three species of snails and two walking-sticks (Willing and Camilo, 1991). For lepidopterans, Torres (1992) documented an outbreak of 15 generalist species probably due to a flush of new foliage that occurred after the hurricane and the ability of these species to include novel host plants in their diet. This outbreak was subsequently controlled by Dipteran and Hymenopteran parasitoids. However, changes in plant-animal interaction networks following a hurricane strike have never been fully investigated.

Lepidopteran communities studied along a successional gradient following anthropogenic disturbances in a TDF of the Mexican Pacific coast have revealed marked changes in richness, diversity and species composition (López-Carretero, 2010). Moreover, lepidopteran–plant interaction network in the same locality has been shown to differ among successional stages (Villa-Galaviz et al., 2012). Lepidopterans are a key group of animals that are highly relevant for pollination, and therefore their conservation is crucial to maintain ecosystem functions and services (Bawa et al., 1985; Haber and Frankie, 1989). Because hurricanes on the Mexican Pacific coast have been predicted to increase in frequency and magnitude, it is important to investigate the effect that these extreme events have on biodiversity and ecosystem functioning, including plant-animal interactions, in order to determine and document resilience of this ecosystem. Here we investigated the effect of category 2 Hurricane Jova on lepidopteran diversity and on the plant-lepidopteran interaction network across a TDF successional gradient. In particular, we addressed the following questions: (*i*) are mature forest plant-herbivore networks more resilient to hurricane disturbance than early successional forests? and (*ii*) is the footprint of the successional gradient on plant-herbivore networks maintained after the hurricane?

2. Materials and methods

2.1. Study site

This study was carried out in the Chamela-Cuixmala region of Jalisco, Mexico (CCBR, 19 °22′–19 °39′ N, 104 °56′–105 °10′ W), comprising the Biosphere Reserve (13,142 ha of conserved land) and its surroundings. The average annual rainfall is 795.3 mm but varies greatly from year to year (from 366 to 1329 mm) and is mainly concentrated (87%) within the rainy season from June to October (Maass et al., this issue). The vegetation within the reserve primarily consists of TDF (1149 plant species with an average canopy height of 6 m) and semi-deciduous forest established along larger streams (average canopy height of 10 m) (Lott et al., 1987). The surrounding area consists of a mosaic of secondary succession forests, agricultural fields and cattle grazing pastures (Sánchez-Azofeifa et al., 2009). The TDF found at the Chamela-Cuixmala region is considered one of the most diverse of its kind, with 1200 plant species and a high levels of endemism (Lott et al., 1987; Trejo and Dirzo, 2000). The invertebrate inventory is still very limited; 1877 arthropod species have been described in the reserve, 583 of which are lepidopterans (Pescador-Rubio et al., 2002).

2.2. Hurricane Jova

Hurricane Jova struck the coasts of Colima and Jalisco, Mexico on October 10th 2011 as category 2 in the Saffir Simpson scale. During the hurricane, maximum wind intensities reached 205 km/h with gusts of up to 250 km/h. By October 13th, it lost strength and was reduced to a tropical storm category. Jova lasted 168 h, advancing 2000 km at an average speed of 12 km/h (Brennan, 2012) and producing 187.9 mm of precipitation in two days at the Chamela biological station.

2.3. Sampling protocol

From 2007 to 2010, we sampled lepidopteran larvae every year in 11 plots corresponding to the experimental design of the CIECO-UNAM Tropical Forest Management project (MABOTRO). This project features a successional chronosequence of abandoned agricultural fields and cattle ranching pastures (Avila-Cabadilla et al., 2009). This chronosequence consists in plots of four stages of secondary succession: initial (fields abandoned for four years), early secondary forest (6–9 years of abandonment), late secondary forest (13–16 years of abandonment) and mature forest. There were three replicates for each successional stage, with the exception of the initial stage, which only had two due to a fire in the third replicate. Plot size was at least 1 ha (the mature forest plots are immersed in the biosphere reserve and are larger) and the distance between plots of the same successional stage was 3 km. Within each plot, in a defined area of 20 × 50 m, we established four parallel 2 × 20 m transects separated by 10 m. With the exception of lianas, all woody plants with stems ≥1 cm in diameter and ≥50 cm in height within these transects were labeled.

During the rainy season of each year during the period 2007–2010, we surveyed caterpillars on all leaves and stems of all marked plants within transects up to 3 m in height. In adult trees, which represented only 10% of all marked individuals, a subsample of three branches – consisting of approximately 100 leaves - was taken for each tree. Caterpillars were recorded and reared in the laboratory for subsequent taxonomic identification of adults (see Villa-Galaviz et al., 2012 for details).

We also generate DNA Barcoding sequences (~650 bp of the cytochrome oxidase I mitochondrial DNA gen; Hebert et al., 2003) to molecularly characterize presumptive species using the Barcode Index Number (BIN) system (Rhatnasingham and Hebert, 2013). For this, one leg of each adult specimen, or the head capsule, if the caterpillar died was removed for DNA extraction using the EZ-10 Spin Kit minipreps DNA Genomic Column kit (BIO Basic, Toronto, Ontario, Canada). The amplification protocol and primers employed followed Ceccarelli and Zaldívar-Riverón (2013). Sequences were edited with the program Sequencher version 4.0.5 (Gene Codes) and manually aligned based on their translated amino acids. The Barcoding sequences, locality details and GenBank accession numbers can be retrieved from the project file 'Lepidoptera from Chamela, Mexico' (MXBLP), which is found in the projects section of the Barcode of Life Data Systems (www.boldsystems.org).

In a previous study of this system, we reported plant-herbivore networks to be highly resilient during forest succession (Villa-Galaviz et al., 2012). For each successional stage replicate, we constructed a bipartite network and calculated the following network structure descriptors: network size (number of lepidopteran and plant species interacting), connectance (fraction of realized interactions from the possible total) (Dunne et al., 2002), robustness (based on the species fraction that survives after removing one species, the value is obtained after calculating the area below the extinction curve) (Memmott et al., 2004; Burgos et al., 2007), number of compartments (network subgroups not connected with other subgroup) (Tylianakis et al., 2007), and network specialization (H2, measures the deviance between the realized interactions for one species and the expected for each species with respect to the total possible interactions in the network) (Blüthgen, 2006). When comparing these network parameters among successional stages, we did not find differences between secondary and mature forest and only the recently abandoned fields showed significant differences (Villa-Galaviz et al. 2012).

To evaluate whether this resilience in plant-herbivore networks across succession remained after the occurrence of an extreme event such as Hurricane Jova, we sampled the same plots during 2012 and 2013 and compared plant-herbivore network structure metrics before and after the hurricane.

Linear mixed effect models (R nlme package) were used to