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Structural and functional traits predict short term response of tropical dry forests to a high intensity hurricane

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ABSTRACT

Tropical dry forest (TDF) is the most threatened of all tropical forest ecosystems worldwide. In the tropical dry forest of the Pacific Coast of Mexico, in addition to human disturbance, the vegetation has been subjected to natural disturbances such as droughts and hurricanes. The average cyclone intensity and the number of very intense category 4 and 5 storms are predicted to increase in this area and such extreme meteorological events generate further stress to the vegetation. Given that in October 2015 the category 4 hurricane "Patricia" landed on the Chamela-Cuixmala TDF, in this study we: (1) evaluated the effect of a high intensity hurricane on TDF vegetation at two habitat types (secondary forest and old-growth forest); and (2) determined how the vegetation attributes at the species and stand level could be defining the vegetation type of damage, and its recovery capacity. For this purpose, we evaluated species composition, vegetation structure and individuals biomechanical traits in eight vegetation plots, four corresponding to old-growth forests (OGF) and four corresponding to secondary forests (SF), before and after the hurricane. Additionally, after the hurricane we also evaluated the damage, leaf functional traits and resprouting ability at the individual level. In total, we evaluated 3732 individuals of 279 species. Data were analyzed by contrasting the vegetation damage and resprouting ability between SF and OGF. Then, we evaluated for the potential relationship between vegetation composition and structure (stand-level attributes) and vegetation damage and recovery capacity. Finally, we evaluated the association between biomechanical and leaf functional traits and the vegetation damage and recovery at the species level. In general, the most severe types of damage were biased toward taller trees as they could be more vulnerable to mechanical instability. We found that OGF received a greater proportion of severe types of damage than SF, although tall trees in SF could face a higher mortality. Harsh environmental conditions preceding the hurricane could also increase the mortality and limit the resprouting ability in SF. Besides, stems with low height and low wood density were related to a greater resprouting ability. This ability was also associated to leaf functional traits such as the relative chlorophyll content, specific leaf area, leaf fresh mass and leaf density, indicating a greater biomass acquisition in species with higher photosynthetic capacity and resistant tissues. These results suggest that in scenarios of increasing frequency and/or intensity of hurricanes, the TDF of the Pacific Coast of Mexico could change their physiognomy toward a canopy of lower height. The proportion of species combining the capacity to resist damage and harsh environmental conditions with a high resprouting ability (i.e. smaller sizes, productive and resistant tissues, such as the TDF pioneer species), could increase as well.

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1. Introduction

Tropical dry forest is the most threatened of all tropical forest ecosystems worldwide (Miles et al., 2006). Contemporary changes of land use and cover in neotropical dry forests (e.g., fragmentation and deforestation) have lead to complex landscapes in which patches of old-growth forests, secondary forests, cattle ranging areas and agricultural uses co-occur (Chazdon et al., 2009; Sánchez-Azofeifa et al., 2009). More recently, global climatic change is considered as an emerging threat for the persistance and functioning of dry tropical ecosystems (Murray-Tortarolo et al., 2016). Natural and human-induced disturbances shape forest systems by influencing their composition, structure and functional process (Dale et al., 2001). Each disturbance type affects forests differently. Some cause large-scale tree mortality, whereas other affect community structure and organization without causing massive mortality (Dale et al., 2001). Generally, plant community structure, diversity, composition, functional traits and phylogenetic structure differ among secondary forests of different ages and between old-growth and secondary forests (Poorter et al., 2004).

In the tropical dry forest of the Pacific Coast of Mexico, in addition to human disturbance, the vegetation has been subjected to natural disturbances such as droughts and hurricanes. These extreme meteorological events generate further stress to the vegetation (Lugo et al., 2010). The effects of hurricanes on vegetation include sudden and massive tree mortality, complex patterns of tree mortality and altered patterns of forest regeneration (Dale et al. 2001; Lugo et al., 2002). These effects can be increased by past anthropogenic activities that create abrupt changes in stand composition, height and density (DeWalle, 1983; Everham and Brokaw, 1996). Moreover, wind disturbance may render a forest even more susceptible to current anthropogenic disturbances. Unfortunately, most of the studies evaluating the impact of hurricanes until now (i.e. Carrington et al., 2015; Imbert and Portecop, 2008; Lewis and Bannar-Martin, 2012; McGgroddy et al., 2013; Sánchez-Sánchez and Islebe, 1999; Vandecar et al., 2011; Whigham et al., 2003) have focused on the effects on floristic composition and structure and have considered only conserved forests (fragmented and/or continuous); just a few studies consider also secondary forests and rarely these studies try to explain the floristic and functional basis of the vegetation damage and recovery.

Over a four-year period hurricanes have landed twice in the Pacific Coast of Mexico, directly impacting the TDF vegetation and its natural protected areas (i.e. the Chamela-Cuixmala Biosphere Reserve): category 2 Hurricane Jova, in October 2011, and category 4 Hurricane Patricia, in October 2015. This is in agreement with studies indicating an increase in average cyclone intensity and the number of very intense category 4 and 5 storms in the Pacific coast of Mexico (Knutson et al., 2015). These extreme meteorological events produced major changes in several aspects of ecosystem functioning including rainfall and runoff dynamics and primary productivity (M. Maass et al. this issue).

In the present study, we tested whether or not the level and type of damage (in stems and tree crowns) inflicted to the standing vegetation by Hurricane Patricia (strong winds and rainfall), is influenced by the previous anthropogenic disturbance of the dry forest. Specifically, we aimed to answer the following questions: (1) how high intensity hurricanes affect the TDF vegetation, in terms of damage and recovery, at two habitat types (secondary forest and old-growth forest)? (2) How the vegetation structure and composition is related to its damage and recovery capacity? and (3) how plant functional traits explain species damage and recovery?. For this, we first contrasted the vegetation damage and the resprouting ability of the survivors between secondary forests and old-growth forests. Then, we evaluated for the potential relationship between vegetation composition and structure (stand-level attributes) and vegetation damage and recovery capacity. Finally, we evaluated the association between biomechanical and leaf functional traits and the vegetation damage and recovery at the species level.

Since early-successional species tend to dominate in secondary forests, we hypothesized that the magnitude of hurricane damage to the vegetation would differ from old-growth forests as early successional species represent different life histories and regeneration strategies as well as distinct functional traits (e.g., stem density). Besides, the anthropoghenic and natural disturbances interact influencing the severity of the perturbation as well as the rate of recovery in tropical forests (Chazdon, 2003). Secondly, we hypothesized that there is a significant relationship between vegetation structural and functional traits (at the stand level and at the individual level) and their preponderant type of damage and recovery capacity. For example, in TDFs, vegetation damage tend to be biased toward the trees with greater height and basal area because they can show greater mechanical instability during catastrophic winds (Fournier et al., 2006; Van Bloem et al., 2006; Vandecar et al., 2011); the resprouting ability, on the other hand, could be greater in species able to maintain high photosynthetic capacity while maximizing photoprotection and heat dissipation, in order to deal with the harsh environmental conditions of the open canopies in TDF (Alvarez-Añorve et al., 2012). The existence of these relationships would allow us to identify predictors of the impact and response to high intensity hurricanes by TDF vegetation, as well as to understand the floristic and functional basis of damage and recovery. To our knowledge, this is the first study combining different kinds of vegetation traits (floristic, structural, biomechanical and foliar traits) to explain damage and recovery in old growth and secondary tropical forests.

2. Materials and methods

2.1. Study region and sampling sites

This study was carried out in and around the Chamela Cuixmala Biosphere Reserve (CCBR; 19°22′-19°35′N, 104°56′-105°03′W), in the pacific coast of Mexico, where a marked seasonal fluctuation in the precipitation regime occurs (www.ibiologia.unam.mx/ebchamela/www/clima.html). In this area, the average annual precipitation is 915 ± 311 (SD) mm (data for the last two decades), and the dry season lasts approximately seven months, from November to May (García-Oliva et al., 2002, www.ibiologia.unam.mx/ebchamela/www/clima.html). The main vegetation covers in this area include the TDF and the riparian forest (Lott et al., 2002). Nevertheless, the accelerated increase in human activities, mostly due to agriculture and cattle ranching, has caused a significant decrease in these vegetation covers. Currently, the coverage of TDF reaches the 56.1%, whereas the coverage of the riparian forest reaches only the 3.7% (Sanchez-Azofeifa et al., 2009).

The set of permanent plots used for this study was established and sampled before the arrival of the hurricane Patricia. These sites had been used as part of a project related to the study of functionality and diversity of tropical plants communities (CONACyT CB-222202). In total, we used eight sampling sites representing two habitat types (four old-growth forests and four secondary forests), which were selected with the help of Google Earth high-resolution imagery (http://earth.google.com), classified satellite images, and the information provided by landowners and farmers (Avila-Cabadilla et al., 2012, Fraga et al. 2017). Each site was defined by a plot with an area of 1000 m^2 (50 × 20 m) and separated each other by a distance ranging from 1 to 32 km (Fig. 1). At selecting the location of the study plots we corrected for the potential effect of the variation in elevation, slope and aspect, which are tightly related to variation in environmental conditions and resources availability, such as insolation and soil water (Balvanera et al., 2002). All sampling sites were located at an average mean height of 143 m.a.s.l. (range: 200 m.a.s.l), with slopes averaging 10° (range 15°), mostly facing toward the south and the southeast. We avoided north facing slopes because they can show higher heterogeneity in insolation and plant community composition in relation to altitude (Balvanera et al., 2002). Coincidentally, all sampling sites were located in the same area of influence of the hurricane Patricia (area of maximum influence), where the sustained winds averaged 119 km/h and