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# Special Issue: Resilience of tropical dry forests to extreme disturbance events

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ABSTRACT

Extreme climatic and anthropogenic disturbance events are driving forces of regional and global forest change. This special issue is dedicated towards evaluating tropical dry forest resilience to such events in Mexico at the landscape, ecosystem, community and population levels. Collectively, the articles herein suggest that tropical dry forests are highly resilient to these extreme disturbances, at least in the short-term, because different patterns and processes across ecological levels can recover relatively quickly to pre-disturbance conditions. However, because forest recovery is strongly controlled by water availability, extreme dry years after disturbance may limit its resilience capacity. Understanding the precipitation regime in these seasonally dry forests will be crucial for improving their management as the frequency of extreme events increases. A common theme of several articles in this special issue is that resilience of tropical dry forests to the interacting effects of climatic and anthropogenic disturbances seems so far idiosyncratic and unpredictable and merits further research in the long-term.

## 1. Introduction

Ecological disturbance theory is well-established in the scientific literature due to several decades of intensive scientific research on the importance of small and infrequent natural and anthropogenic disturbances on population, community and ecosystem dynamics. However, there is also recognition of the importance of the recent increase of extreme disturbances directly or indirectly linked to global climate change. White and Pickett (1985) defined disturbance as “any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment”, and this is probably the most widely accepted definition of ecological disturbance.

As disturbance theory has matured, other ecologists recognized that large infrequent disturbances (LIDs) may have different implications for the management of forest ecosystems compared to small and frequent disturbances (Dale et al., 1998). These LIDs were defined in terms of their statistical distribution or ecosystem responses or attributes, recognizing also that their effects encompassed large spatial and temporal scales, such as from flooding, fires, hurricanes and volcanic eruptions (Turner and Dale, 1998). More recently, extreme events related to climate became a global concern as they are triggering episodes of widespread tree mortality and consequently modifying forest carbon stocks (Allen et al., 2010; Frank et al., 2015). Extreme climatic events can interact with anthropogenic disturbances (or their legacy: e.g. secondary forests) to produce a synergistic outcome with immediate negative consequences for many ecosystems (Paine et al., 1998; Chazdon, 2003; Buma and Wessman, 2011; but see McGroddy et al., 2013; Bhaskar et al., 2018), challenging our understanding and measurement of biological responses at different spatial and temporal scales and to multiple interacting disturbances.

Extreme events are defined here as climatic or anthropogenic disturbances that lead to extreme biological responses. Extreme anthropogenic disturbances include mainly land-use change, deforestation and induced fires (Moritz, 1997; Foster et al., 1998; Sala et al., 2000; Foley et al., 2005), whereas extreme climatic disturbances include prolonged droughts, severe frosts, high intensity hurricanes, and heat and cold waves (IPCC, 2012). Extreme climatic events exceed a certain threshold of known climate variability over a defined period (IPCC, 2012; van de Pol et al., 2017). By definition, there is a low probability of occurrence of an extreme climatic event and a similarly low likelihood of that event causing an extreme biological response (Smith, 2011; van de Pol et al., 2017). Compared to long-term changes in average climate, the extreme nature of these single climatic events is leading to pressing concerns about the maintenance of ecosystem functions and human well-being (Jentsch and Beierkuhnlein, 2008; Altwegg et al., 2017). Moreover, multiple climatic and anthropogenic disturbances may decrease ecosystem resilience in the short-term due to the sudden disruption of the abiotic or biotic pools (Buma and Wessman, 2011). However, paleoecological records over the past 20,000 years indicate that previous disturbances could actually maintain or increase the resilience of tropical forests to future extreme disturbances (Cole et al., 2014). This suggests that despite short-term ecosystem alteration, past disturbances could help ecosystems to cope

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with future extreme disturbances in the long-term by developing mechanisms to speed recovery such as resprouting in woody plants.

The importance of biological responses to disturbance has been long recognized but scientific agreement on a working definition of resilience and related concepts has proved difficult to conceal (see Grimm and Wissel, 1997; Hodgson et al., 2015; Yeung and Richardson, 2016), limiting their application to ecosystem management (Standish et al., 2014). Biological responses to disturbance can be broadly classified into resilience, resistance and recovery. Resilience was defined by Hollings (1973) as the ability of a system to absorb changes and still persist. Assuming that resilience is achieved through resistance or recovery, then resilience can be defined as the capacity of a system to resist or recover from exogenous disturbance (Hodgson et al., 2015). Resistance is the ability of a system to remain unchanged after disturbance and recovery is the ability to return to pre-disturbance conditions (Grimm and Wissel, 1997; Hodgson et al., 2015). The disturbance regime (i.e. type, extent, frequency, duration, timing and intensity) and ecosystem properties that have a strong influence on the biological responses to disturbance (White and Pickett, 1985), may offer some evidence of ecosystem resilience. For example, several properties of the tropical dry forest (TDF) suggest that this strongly seasonal ecosystem may be highly adapted or resilient to recurrent climatic or anthropogenic disturbances: resprouting capacity of many woody species in response to physical damage (Kennard et al., 2002; Jimenez-Rodríguez et al., 2018; Paz et al., 2018), shorter stature of TDFs regularly exposed to hurricane disturbance (Lugo, 2008), plant phenological adaptations to seasonal droughts (e.g. deciduousness; Bullock and Solis-Magallanes, 1990; Holbrook et al., 1995) or dominance of legumes capable of symbiotic nitrogen fixation which dominate after TDF cleared lands are abandoned (Álvarez-Yépiz et al., 2008; Lebrija-Trejos et al., 2010; Martínez-Ramos et al., 2018). However, beyond the plant community, a more complete understanding of forest resilience should include the study of multiple ecological levels because high variability of responses at one level may be absorbed by the next one, increasing the resilience of higher ecological levels (Felton and Smith, 2017). This scaling up process is poorly understood in TDFs since most studies focus on understanding resilience at a single ecological level, hindering the design of more holistic forest management strategies.

Tropical dry forests once covered 42% of all tropical forests worldwide (Murphy and Lugo, 1986). Despite high diversity and endemism, 97% of the remaining TDF is still at risk mainly from human activities and climate change (Miles et al., 2006). A recent analysis showed that 71% of the potential TDF in Mexico has been converted to other land-uses, and although TDF is poorly represented under the Mexican protected areas network, the country still holds 38% of all Neotropical TDFs (Portillo-Quintero and Sánchez-Azofeifa, 2010). As in many other TDFs worldwide, the Chamela-Cuixmala region on the Pacific coast of Mexico is a landscape composed of active and abandoned croplands and pastures, plantations, successional forests and old-growth deciduous and semideciduous forests (Burgos and Maass, 2004), providing a representative example of TDF complex dynamics globally. This region was colonized by people essentially after the 1970s (Castillo et al., 2005) and still holds 70–80% of TDF (Sánchez-Azofeifa et al., 2009). In addition to this history of forest conversion and land use, in October 2011, this region was directly impacted by the category 2 (Saffir-Simpson Scale) Hurricane Jova and category 4 Hurricane Patricia in October 2015 (Brennan, 2012; Kimberlain et al., 2016); the latter is considered one of the strongest hurricanes recorded in human history. Because water is the most limiting factor that drives TDF dynamics and socio-economical activities (Dirzo et al., 2011), the extra and aseasonal precipitation derived from these two successive hurricanes could have benefited the recovery of the TDF ecosystem and the regional socio-economic activities that depend on land exploitation.

After hurricane Jova and Patricia landfalls, researchers working in the area since the 1980s, continued monitoring the dynamic response of a variety of taxa, ecosystem and landscape/social patterns and processes. The results of these studies and the existing long-term pre-disturbance data allowed us to collectively analyze the resilience of the Chamela TDF to land-use change and to a minor and a major hurricane. In this special issue we synthesize for the first time the scientific information related to TDF resilience to recent extreme disturbance events. One of the main novelties of this special issue is the integration of scientific data across disciplines and ecological levels: population, community, ecosystem and landscape/social. Our main objective was to determine how resilient the Chamela TDF is to extreme climatic and anthropogenic disturbance events across ecological levels. We expected water availability after disturbance to play a vital role on forest resilience by speeding recovery (Fig. 1).

## 2. Resilience of the Chamela tropical dry forest to extreme disturbance events

In this section we summarize by ecological level each of the articles included in this special issue, highlighting their main contributions and commonalities. The 16 manuscripts published come from studies performed in the surroundings and within the Chamela-Cuixmala Reserve, also a Mex-LTER site in the Mexican Pacific Coast and one of the best studied TDF worldwide.

### *2.1. Landscape/social level*

Maass et al. (2018) analyzed the long-term hydrological dynamics in the Chamela TDF. They showed that antecedent precipitation and rainfall intensity were the major factors controlling rainfall-runoff and soil erosion. Interestingly, the timing of the onset of the rainy season was surprisingly very regular, but the length of the rainy season was quite variable. Tapia-Palacios et al. (2018) assessed the link between vegetation greenness, water quality and small mammal diversity at the basin level. During non-hurricane years the lower (coastal) area has a high density of waterborne pathogens that decreases in hurricanes years, possibly due to the increased water flow. At this level, vegetation greenness (measured with EVI index) and small mammal diversity (bats and rodents) also decreased in hurricane years but recovered quickly. Lazos-Chavero et al. (2018) studied how the position in the landscape, economic specialization and land use combine to affect vulnerability of families and vegetation to hurricanes. The main effects associated with the hurricanes were observed in the lower basin, the coastal plain, where they made landfall and natural vegetation had been converted to agricultural land. Vulnerability to hurricanes is thus a precondition that exists prior to the event and landscape modification increases such vulnerability (see also Tapia-Palacios et al., 2018).

### *2.2. Ecosystem level*

Parker et al. (2018) analyzed the immediate and delayed impacts of the two hurricanes on the canopy structure of the forest within the reserve. There were contrasting effects of wind and precipitation because biomass loss was related to hurricane winds whereas the duration of extended greenness was related to the extra aseasonal precipitation post-disturbance. These results suggest that recovery of greenness occurred rapidly, but canopy cover and biomass production may take decades to recover. Martínez-Yrízar et al. (2018) used 35 years of litterfall data to analyze the TDF ecosystem response to hurricanes Jova and Patricia, using litterfall as a proxy of productivity. Hurricane-month litterfall exceeded by far the amount produced in any month of the pre-disturbance period since 1982, suggesting low resistance to hurricanes, but rapid recovery due to the unusually high dry-season precipitation and higher-than-average total annual precipitation. Bhaskar et al. (2018) also used litterfall data to examine to what extent response diversity of old-growth and secondary forests species litterfall confers resilience to biomass production after the two hurricanes struck the area. The interaction between different climatic and anthropogenic