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Response diversity and resilience to extreme events in tropical dry secondary forests☆

Radika Bhaskar[a,b,*], Felipe Arreola[a], Francisco Mora[a], Angelina Martinez-Yrizar[c], Miguel Martinez-Ramos[a], Patricia Balvanera[a]

[a] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico
[b] College of Design, Engineering, and Commerce, Philadelphia University, Philadelphia, PA, USA
[c] Instituto de Ecología, Universidad Nacional Autónoma de México, Hermosillo, Mexico

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ABSTRACT

Response diversity, defined as the variable responses of species to environmental change, has been proposed as a key determinant of ecosystem resilience. We test this hypothesis along a tropical dry forest successional chronosequence that provides a gradient of species richness and diversity. The system experienced a strong disturbance from Jova, a category 2 hurricane, in 2011. We assessed the resilience of secondary forests to hurricane disturbance by estimating both the resistance and the rate of recovery of standing biomass, comparing data from several years prior- and post-hurricane. We assessed response diversity from variations in species-level litter production in response to fluctuations in precipitation during the annual wet-dry transition period in five pre-hurricane years. The two resilience components, resistance and recovery rate, were negatively correlated, suggesting these measures of resilience are inversely coupled. We found that historic reductions in basal area through human intervention may not necessarily reduce system resilience to additional disturbances, and may in some cases enhance the capacity to absorb hurricane perturbation. This implies old-growth forests can withstand some level of human intervention and structural change, and persist through a subsequent natural disturbance. In accordance with theory, sites with greater response diversity to climate should also be more resilient to disturbance; however, we found a surprising negative relationship between response diversity and rate of recovery. We speculate this contradictory result may be due to the compounding nature of multiple disturbances interacting with climate change, and suggest our understanding of mechanisms that confer resilience to ecosystems might need reevaluation as anthropogenic pressures related to land-use and climate intensify.

1. Introduction

Human-modified landscapes are increasingly dominated by second-growth forests, as areas cleared for human use are abandoned (Chazdon, 2008; Hansen et al., 2013). In the tropics, secondary forests are mostly growing in abandoned agricultural croplands and pastures, due to the widespread representation of this type of disturbance (Gibbs et al., 2010). Studies in the neotropics have found that, with time, regenerating forests in abandoned fields can resemble old-growth forest in various facets, including aboveground biomass (Chazdon, 2008; Poorter et al., 2016), richness (Letcher and Chazdon, 2009), and floristic composition (Norden et al., 2009), though recovery rates may widely vary depending on land-use history (Jakovac et al., 2015; Zermeño-Hernández et al., 2016), local site characteristics, distance to old-growth forest remnants, and several other biophysical factors (Álvarez-Yépiz et al., 2008; Chazdon et al., 2007). Collectively these findings suggest tropical forests possess a strong capacity to recover from this form of human disturbance, when such disturbance is not extensive, long-lasting and severe (Arroyo-Rodríguez et al., 2017; Martínez-Ramos et al., 2016).

However forest ecosystems altered by human intervention are not experiencing disturbance regimes inflicted by agricultural activities in isolation, instead they are recurrently exposed to additional disturbances, such as freezing, drought, and hurricanes, creating a confluence of multiple and overlapping pressures (Chazdon, 2003; Turner, 2010). Changes that result from human-intervention may influence how a forest system responds to subsequent disturbance (McGroddy et al., 2013; Uriarte et al., 2009), particularly as disturbances are compounded (Millar and Stephenson, 2015; Paine et al., 1998; Uriarte et al., 2009). In order to gain a deeper understanding on the capacity of

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* Corresponding author at: College of Design, Engineering, and Commerce, Philadelphia University, Philadelphia, PA, USA.
E-mail address: radika@gmail.com (R. Bhaskar).

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human-altered systems to withstand multiple stressors and continue to provide ecosystem services (Millar and Stephenson, 2015; Paine et al., 1998), it is urgent to examine what mechanisms involving abiotic and biotic factors allow modified ecosystems to persist (Johnstone et al., 2016).

Tropical dry forests are experiencing multiple, interacting disturbances (Miles et al., 2006) of both natural and anthropogenic origin. In addition to widespread clearing for agriculture (Sánchez-Azofeifa and Portillo-Quintero, 2011), they experience natural disturbance in the form of tropical cyclones, with projections that suggest both storm intensity and precipitation rates may be potentially intensified in the near future (Knutson et al., 2010). Hurricanes directly impact forest dynamics related to carbon capture and carbon storage, by stripping branches of twigs and leaves, damaging or snapping stems, or uprooting entire trees (Everham and Brokaw, 1996). These changes can substantially shape forest composition and structure over a long time-frame (Boose et al., 2004). Examining two key components of forest biomass, litter production and basal area, which are sensitive to hurricane impact (Imbert and Portecop, 2008), can inform our understanding of primary production post-disturbance. Secondary tropical forests have high carbon sequestration potential (Chazdon et al., 2016) based on studies of regrowth following clearing, though seasonally dry forests may have lower capacity for recovery than other tropical forest types (Poorter et al., 2016); a deeper understanding of carbon accumulation dynamics following disturbance can clarify what role secondary forests can play in climate change mitigation strategies (Mora et al., 2017).

Central to understanding disturbance response is the concept of resilience, which describes a system's ability to tolerate an external stressor and continue functioning over time (Holling, 1973). Resilience in its broadest sense encompasses both the ability to resist change and to recover from it (Levin and Lubchenco, 2008; Mori, 2016), and thus requires the consideration of multiple components (Hodgson et al., 2015). *Resistance* is generally defined as the ability of a system to withstand or absorb the impact of a disturbance (Connell and Ghedini, 2015; Griffiths and Philippot, 2013). Recovery, on the other hand, is defined as the ability of a system to return to its pre-disturbance state; it can be measured through indicators such as *recovery rate,* the speed with which the system recovers (Grimm and Wissel, 1997; same as elasticity, per Hodgson et al., 2015). The concept of resilience has evolved to be applicable to social-ecological systems (Folke, 2016), and though there has been some disagreement on the inclusion of recovery as a facet of resilience (Connell, Nimmo, Ghedini, Mac Nally, Bennett, 2016; Sundstrom et al., 2016), it may be particularly relevant to examine recovery in order to inform active management and restoration of degraded ecosystems (Lake, 2012). Beyond characterizing the different resilience components, a deeper understanding is needed of the mechanisms that create or enhance resilience, particularly as disturbances overlap and potentially interact (Pulla et al., 2015).

The biological characteristics that confer resilience may arise through factors at the species, community, and landscape level (Oliver et al., 2015). Many theoretical studies have emphasized the importance of the 'insurance hypothesis', which suggests systems with greater diversity should maintain functioning despite environmental fluctuation (Yachi and Loreau, 1999). Specifically, this compensatory mechanism is a function of species response diversity, which measures the variability of species responses to environmental change (Elmqvist et al., 2003). A high response diversity should provide greater ecosystem resilience (Mori et al., 2012; Winfree and Kremen, 2009), because as species respond differently to the environment some may thrive while others may not, thus ensuring at least some continuity of function.

Resilience to hurricane disturbance is also influenced by stand-level structural attributes that modulate the extent of damage experienced as well as the trajectory of recovery. Trees of a greater stature (height and diameter), are more prone to damage by hurricane disturbance (Lugo, 2008; Van Bloem et al., 2005). In transformed tropical landscapes, the structural composition of a particular stand reflects both the species composition as well as land-use history (Mesquita et al., 2015). Because early successional forests are commonly characterized by a lower structural development, they may accordingly be less impacted by hurricanes (McGroddy et al., 2013). Attributes that relate to stand-level structure must be taken into account when assessing what role response diversity may play a role in predicting resilience.

Here we examine to what extent response diversity confers resilience to natural disturbance in tropical dry forests. The region of study along the Pacific coast of Mexico represents a mosaic of old-growth and secondary forest patches of differing ages. In the initial stages of regrowth following abandonment of slash-and-burn agriculture (the most common farming method), net productivity and accumulation of biomass increase over time (Anderson-Teixeira et al., 2016; Guariguata and Ostertag, 2001). With time, secondary forests in this region have been found to resemble old-growth in terms of litter production and chemistry (Bhaskar et al., 2016), forest structure (Mora et al., 2014), and functional diversity (Bhaskar et al., 2014; Mora et al., 2014). This region was directly impacted by a strong hurricane in 2011, Hurricane Jova, a category 3 hurricane (Saffir-Simpson Hurricane Wind Scale) that hit landfall as category 2, with wind speeds that reached 160 km/hour and heavy rainfall (223 mm) over a two-day period (Brennan, 2012; rainfall data from the meteorological station at Chamela). This storm allowed us to examine how human-modified forest ecosystems respond to subsequent natural disturbances. Because forest stands have different mixtures of species as a result of both spatial variation and human impact, they provide a natural experiment to test how variation in response diversity contributes to resilience of function related to biomass production.

Our objective was to empirically evaluate the conceptual framework that higher response diversity enhances resistance and rate of recovery (Fig. 1). Our specific goals were twofold: (1) to characterize the resilience of aboveground biomass in human-modified sites to hurricane impact, by estimating both recovery rate and resistance, and (2), to examine how response diversity could explain variation in resilience among forest plots. Stand-level aboveground biomass was chosen as an indicator that could assess cumulative resilience of the forest, while species' annual litter production was used to assess inter-specific variability in sensitivity to changes in water availability, as a measure of response diversity.

2. Material and methods

2.1. Study area

We conducted fieldwork within and around the Chamela-Cuixmala Biosphere Reserve, on the Pacific coast of the state of Jalisco, Mexico (19°230–19°300N, 104°560–105°040W). This tropical dry forest region experiences seasonal rainfall, and a typical annual dry season extending from November through May (Bullock, 1986). Mean annual rainfall, from 1983 to 2015, was 800.4 mm, with 87% falling between June and October (Maass et al., 2017). However inter-annual precipitation is highly variable in this region, both in terms of total and timing of rainfall (Anaya et al., 2012; García-Oliva et al., 1995; Maass et al., 2017). Areas surrounding the reserve have been largely cleared for cattle pastures and agricultural fields; some areas are subsequently left unmanaged resulting in a patchwork of secondary forests of varying age (Burgos and Maass, 2004).

2.2. Sampling

We used data from 11 sites, representing secondary forests in three categories of regrowth (young, intermediate, and advanced) as well old-growth forest with little evidence of human intervention. Secondary forests were aged 1–2 years (young), 3–5 yrs (intermediate) and 8–12 yrs (advanced) when sites were initially established in 2004. The original design had 12 sites, but the third replicate for old-growth was

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