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Resilience and vulnerability of herpetofaunal functional groups to natural and human disturbances in a tropical dry forest☆

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Natural and anthropogenic disturbances alter animal populations in complex ways. Shifts in population size and taxonomic species diversity as such may not always completely reflect the effects of forest disturbance on faunal communities. In this study, we used a functional ecological approach to detect resilient and vulnerable species including anurans (frogs and toads), lizards and snakes, after Hurricane Jova hit the Pacific Coast of Mexico in 2011. Using population abundances, we compared functional traits including habitat preference, body size and reproductive type of the herpetofauna inhabiting tropical dry forest vegetation under a chronosequence of successional stages: active pastures, 0 y; early-forests, 5–6 y; young-forests, 8–10; intermediate-forests 15–17 y; and old-growth continuous forests. A total of 4093 individuals representing 17 species of anurans, 18 lizard species and 25 snake species were recorded. Overall, successional stage and Hurricane Jova affected the number of anurans and lizards in contrasting ways. For example, while the total number of anurans declined significantly after the hurricane in all successional stages (from 736 to 512 individuals), lizard populations significantly increased (from 1084 to 1612), except in old-growth forests. In contrast, neither disturbance type significantly affected the density of snakes (from 81 to 69). Regarding functional traits, there were complex trajectories of change in species abundances according to successional stage after the hurricane. For lizards, abundance within different functional traits was correlated with the chronosequence after Hurricane Jova. Density of terrestrial and medium-sized lizard species increased with successional age, while arboreal and small-sized lizards decreased. For anurans, terrestrial and large-sized species declined elsewhere, while medium- and small-sized species increased in pastures after Hurricane Jova. Furthermore, riparian frogs with aquatic reproduction were recorded only in pastures. The herpetofauna of the tropical dry forest on the Pacific Coast of Mexico is composed of a mixture of species resilient and/or vulnerable to the synergetic impact of human and natural disturbances. Under the present scenario of land-use and land-cover change, therefore, the preservation of old-growth forest tracts in the human-dominated landscape of the study region is extremely important.

1. Introduction

Tropical forests are the most biodiverse terrestrial ecosystems in the world and face high deforestation and fragmentation rates (Dirzo and Raven, 2003; Laurance et al., 2012). As the deforestation of old-growth tropical forests proceeds, complex landscapes in which secondary forests and agricultural land uses coexist are the most common scenery in several tropical regions (Bowen et al., 2007; Chazdon et al., 2009; Sánchez-Azofeifa et al., 2009). Sometimes human activities (e.g. changes of land use and cover) and dramatic environmental disruptions (e.g., landslides, fires, droughts and hurricanes) co-occur, generating important and drastic modifications in tropical ecosystems (Lugo, 2008; Lugo et al., 2010; Sousa, 1984). In some tropical landscapes, effects of agricultural clearings could be as severe as hurricane disturbances, and when acting simultaneously, they could maintain a complex and diverse assembly of animal species with dynamic rates of local invasions and extinctions (Boucher et al., 2000). These dynamic faunal communities are the result of vegetation structure that changes through successional time and space affecting the physical environment (e.g., light, moisture and temperature). In this context, habitat specialist species are

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the most likely to be negatively affected. Nevertheless, several native species can persist and sustain viable populations within highly altered landscapes, maintaining the basic structure and function of original ecosystems (Ávila-Cabadilla et al., 2009; Becker et al., 2007; Bowen et al., 2007; Laurance et al., 2012; Suazo-Ortuño et al., 2008).

There is a great amount of information regarding the dynamics of secondary forests and forest succession across the Neotropics (Chazdon et al., 2016; Pooter et al., 2016. This knowledge, however, has been focused mostly on tree species, leaving aside successional trajectories of faunal assemblages (but see Ávila-Cabadilla et al., 2009; Bowen et al., 2007; Chazdon et al., 2011; Fraga-Ramírez et al., 2017; Suazo-Ortuño et al., 2015. The impact of natural and anthropogenic habitat disturbance on animal populations and communities is a complex process that involves several interacting factors (physical and biological). Reductions of population sizes and taxonomic species loss, therefore, may not always completely reflect all changes, pervasive or not, on animal assemblages after a disturbance (Duckworth et al., 2000; Lavorel and Garnier, 2002). Considering the functional diversity of faunal assemblages – morphological, physiological, behavioral and life history traits – would allow detecting the ways in which species face novel environmental conditions after a disturbance (Becker et al., 2007; Petchey and Gaston, 2002; Walker, 1992). Theory predicts that species with similar functional attributes tend to respond in the same way to changes in the environmental conditions (Duckworth et al., 2000; Lavorel and Garnier, 2002).

Previous studies in the tropical dry forest along the Pacific Coast of Mexico (i.e., the Chamela region) have shown different responses of herpetofaunal groups to forest disturbance. For example, while anuran populations have been shown to be negatively affected lizard species increased their populations in pastures; while snakes have shown no change (Suazo-Ortuño et al., 2008, 2011). These findings, however, considered only two contrasting habitats, namely cattle pastures and old-growth forests, leaving aside secondary forests, which have become an important feature of tropical landscapes (Burgos and Maass, 2004; Chazdon et al., 2009, 2011, 2016, Fraga-Ramírez et al., 2017; Pooter et al., 2016). In contrast, when secondary forests of different ages were included in the analysis, the herpetofaunal community in the Chamela region has been shown to be highly resilient to forest disturbance, since the mosaic of secondary forests at different ages provides adequate and novel habitats (Fraga-Ramírez et al., 2017; Suazo-Ortuño et al., 2015).

In this study, we used a functional ecological approach to detect changes in herpetofaunal assemblages in a tropical dry forest after Hurricane Jova hit the Pacific Coast of Mexico in 2011 (Olguín-López et al., 2015). For this, we compared the functional traits that have been used to classify the herpetofauna, including the following: habitat preference, reproductive type and body length at two time intervals, before and after the hurricane. These functional traits are representative of the species of anurans, lizards and snakes inhabiting the tropical dry forest of Chamela (according to García and Ceballos (1994), Ramírez-Bautista (1994)). Furthermore, because the successional stages considered showed differences in several habitat traits (e.g., canopy cover, basal area, exposed roots and depth of the litter layer), which are important for the incidence of amphibians and reptiles (Suazo-Ortuño et al., 2008), we expected a stronger impact of Hurricane Jova on amphibian and reptile populations inhabiting active pastures and old-growth forests.

The former habitats represent the extremes of our successional chronosequence and, therefore, present the greater contrasts regarding habitat attributes (Chazdon et al., 2011; Maza-Villalobos et al., 2011; Suazo-Ortuño et al., 2008, 2015). Forest succession has been proceeding in the secondary forests sites, while active pastures and old-growth forests have been maintained as such during the course of the present study. For instance, active pastures are devoid of tree cover, while for several tree species basal area and canopy cover increase with the successional stage being greater in old-growth forests. These changes in vegetation structure affect the incidence of several arboreal herpetofaunal species as has been shown for other vertebrates (Ávila-Cabadilla et al., 2009; Bowen et al., 2007; Chazdon et al., 2011), while changes in litter amount and quality on the ground throughout the chronosequence affect the incidence of terrestrial and fossorial species (Suazo-Ortuño et al., 2008, 2015). Therefore, we expected a correlation between herpetofauna abundance and successional stage (i.e., time elapsed since pasture abandonment) for the different functional groups considered in this study (Chazdon et al., 2011).

Thus far, there is evidence of only minor effects of successional stage, Hurricane Jova or of their interaction with herpetofauna species richness and diversity (Lara-Uribe, 2014; Marroquín, 2014; Suazo-Ortuño, unpublished data). In contrast, strong changes have been observed in the composition of amphibian and reptile communities (Lara-Uribe, 2014; Marroquín, 2014; Suazo-Ortuño et al., 2015; Suazo-Ortuño, unpublished data). Therefore, our analysis is focused only on the abundance of species within the functional traits considered. An important aspect for the conservation of the herpetofauna should be the determination of species traits associated with their vulnerability to extinction or to their persistence (resilience) in the agricultural mosaics currently composing tropical landscapes (Becker et al., 2007; Petchey and Gaston, 2002).

2. Materials and methods

2.1. Study landscape

This study was conducted in the tropical dry forests of the Chamela region encompassing the Chamela-Cuixmala Biosphere Reserve (CHCBR, 13,142 ha), located on the coast of Jalisco in the Mexican Pacific (19°230–19°300 N, 104°560–105°040 W) (Fig. 1). The CCBR's average annual temperature is 25.6 °C (1980–2015) with minor variation between years. Monthly mean minimum and maximum temperatures are 16.4 °C (March) and 32.6 °C (August), respectively. Rainfall is highly seasonal and with a variable annual precipitation (annual range from 366 to 1329 mm). Mean annual rainfall is 800.4 mm (1983–2015), with 87% falling between June and October; and September (215 mm) is the wettest month on average (data from the meteorological station at Chamela, IBUNAM and the "Watershed Project," UNAM). Although only 7% of the rainfall events are greater than 50 mm, hurricanes deliver 42% of the total precipitation when coming ashore (Garcia-Oliva et al., 2002). The study region is part of the Mexican Pacific lowlands, which constitute a hot spot of herpetofaunal species richness and endemism and support one-third of the species of amphibians and reptiles known in Mexico (García, 2006).

Human development in the area began in the 1960s. Presently, the landscape configuration consists of subsistence agriculture areas (e.g., corn, squash, and bean), cattle pastures (45% of the area) and selective extraction of trees for firewood and other uses. The remaining vegetation consists of a mixture of old-growth forest patches and secondary forests in different stages of succession (Fraga-Ramírez et al., 2017; Suazo-Ortuño et al., 2015). In the region, 25–45% of the landscape corresponds to secondary forests and 55–75% to old-growth forest (Sánchez-Azofeifa et al., 2009).

Hurricane Jova in October 2011, reached category 3 (Saffir-Simpson Hurricane Wind Scale), making landfall as category 2 on the Jalisco coast (Brennan, 2012). Hurricane Jova accumulated 330 mm of mean rainfall (min 230 mm–max 490 mm), increasing runoff in river channels and causing severe floodings. Hurricanes are infrequent in the study area, but their occurrence damages the vegetation even within the biosphere reserve and along forest edges (Olguín-López et al., 2015). Around 4% of adult trees in the continuous old-growth forest were damaged by Hurricane Jova (R. Ahedo, UNAM, unpublished data; Fig. 1).

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