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Long-term population dynamics of small mammals in tropical dry forests, effects of unusual climate events, and implications for management and conservation☆

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A B S T R A C T

Understanding the consequences of biotic and abiotic variability on population dynamics is fundamental to assessing anthropogenic impacts, such as global climate disruption, on populations and species. Our understanding from studies to date is poor, although some long-term studies of small mammals in temperate ecosystems have elucidated the roles of climate and of interspecific interactions in their population dynamics. However, the lack of long-term studies in the tropics is a major impediment to understanding species and ecosystems in these regions. We analyzed the long-term population dynamics of seven species of small mammals from two adjacent tropical dry forests with contrasting phenology in a protected area of western Mexico. We modeled these dynamics using data from an 18-year live-trapping database, and we evaluated the effects of intra- and interspecific interactions, primary productivity, temperature, precipitation, and unusual climate events. Intraspecific interactions were the most common factors in every population, while interspecific interactions had only a mild positive interaction between few species. While we found that the effect of temperature was not relevant to population dynamics, precipitation caused positive effects on all species, either by directly enhancing the reproductive rate or, indirectly, by triggering changes in primary productivity. Extreme climate events created intense signals. *Oryzomys melanotis*, an invasive and opportunistic species, benefited from these events, and two populations were harmed by them: *Peromyscus perfulvus* and *Liomys pictus*, the small mammal with the most abundant population of the upland forest, which was extirpated for over 16 months. Our results suggest that sharp reductions in precipitation and more frequent extreme climate events—both predicted by global climate disruption regional models—would have dramatic effects, adding to the other anthropogenic pressures these forests are already suffering (habitat loss, excessive management). These results emphasize the importance of protected and unmanaged refugia, such as our study site, to provide sources for refaunation following local extinctions.

1. Introduction

The fate of any population, in very simple terms, depends on the factors affecting its survival and reproduction. Such factors can be broadly classified as intrinsic (i.e., density-dependent) or extrinsic (i.e., density-independent), based on their relationship or effects on population dynamics (Royama, 1992). Understanding the effects of intrinsic and extrinsic factors on population dynamics is particularly relevant in the face of the current massive human-induced environmental impacts (Brown, 2014)

In Royama's framework, simple climate factors (temperature, rainfall and wind) are exogenous factors that may affect survival and reproduction directly, as there is a relationship between per capita rate of change and population density. The effect of exogenous variables on the per capita rate of population change can therefore be analyzed independently of population density. However, climate may also affect

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populations by influencing a limiting resource, such as food and water sources. In this case, its effect can be evaluated only in conjunction with population density (Royama, 1992). Thus, the relationship between climate and population density characterizes the per capita share of the resources and the competition strength for a given species (Berryman, 2003, 2001; Lima et al., 2008a,b; Royama, 1992; Valone et al., 1995).

Long-term population dynamics studies have spearheaded the development of this discipline (Elton and Nicholson, 1941; Elton, 1924; Lima et al., 2008a,b). From these seminal works, we have been able understand that population dynamics of small mammals at higher-latitude temperate forests and grasslands are commonly related to predation and seasonality. Such populations show nonlinear dynamics with complex time lags. Extrinsic events in previous years can be major factors influencing dynamics (Ekerholm et al., 2001; Ergon et al., 2011; Hoset et al., 2009; Krebs and Boonstra, 1978; Lima, 2001; Lima et al., 2006a; Wang et al., 2001). However, aside from these well-known studies, most studies of population dynamics to date have been short-term, which can be misleading in understanding population patterns and processes (Berryman, 2003, 1992, 2001, 2006; Elton and Nicholson, 1941; Elton, 1924; Turchin and Taylor, 2007).

Recent studies of small-mammal dynamics have attempted to determine some of the factors affecting these dynamics. In northern mid-latitudes, in arid areas, some studies have found that small-mammal populations are affected by interspecific interactions and climatic factors, particularly atypical rainfall events, leading to local extinction and community-structure changes that can diminish taxonomic and functional diversity (Brown, 1973; Ernest et al., 2000; Fargione et al., 2003; Lima et al., 2008a,b). In South American arid and semi-arid grasslands and shrublands, climate, especially El Niño–Southern Oscillation (ENSO), can strongly influence small-mammal population dynamics by causing sudden increases in resource availability (primary productivity), triggering effects such as spectacular population blooms of invasive species (Crespin and Lima, 2006; Jaksic and Lima, 2003; Letnic and Dickman, 2006; Lima, 2001; Lima et al., 1999; Lima and Jaksic, 1999). However, evaluations of long-term population dynamics are lacking, especially for tropical regions (Brown, 2014).

Human-induced global climate disruption is a major cause of biodiversity loss, and it is expected to worsen. Projections include temperature increase, changes in rainfall patterns, and higher probabilities of extreme climate events (Ernest et al., 2000; Lima et al., 2008a,b; Thibault and Brown, 2008). For instance, strong hurricanes have increased by up to 20% in Australia (Hughes, 2003, 2000; Williams et al., 2003). The most recent years have been climatically atypical for North America, with simultaneous high-category hurricanes in the Pacific Ocean. The strongest hurricane ever recorded in the eastern Pacific Ocean, Patricia, made landfall exactly where this study was performed in October 2015 (NOAA, 2015).

Rainfall changes and extreme events cause diverse effects on mammals, including changes in dominance patterns, local extinctions, mass mortality, reproductive failure, population booms, colonization by invasive species, and loss of functional diversity (Bateman et al., 2012; Lučan et al., 2013; Sherwin et al., 2013; Welbergen et al., 2008).

The tropics are extremely diverse and also increasingly under threat (Brown, 2014; Ceballos et al., 2007; Ceballos and Ehrlich, 2009; Rosenzweig, 1992). Tropical dry forests are threatened—and heavily managed—environments (Brown, 2014; Janzen, 1988; Rosenzweig, 1992; Stier and Mildenstein, 2005; Terborgh, 2013). Among the threats to these highly diverse habitats, recent studies point to extreme climate phenomena—particularly unusually strong hurricanes, higher temperatures, and longer droughts (IPCC, 2014; Mei et al., 2013; Milly et al., 2005; Seager et al., 2007).

The most diverse terrestrial ecosystems are the tropical forests, comprising over 60% of the mammal species on Earth (Brown, 2014). The most widely distributed are the tropical dry forests, which are seasonal ecosystems that depend on the precipitation and temperature patterns for their existence (Brown, 2014; Giam et al., 2012; Janzen, 1988; Rosenzweig, 1992). Although less exuberant than their tropical rain forests counterparts, tropical dry forests are extraordinarily rich, both in taxonomic and functional diversity, as well as in physiological and ecological strategies (Brown, 2014; Mason-Romo et al., 2017; Rosenzweig, 1992).

For extensive tropical dry-forest regions, international climate change models forecast reductions in precipitation of about 20% (IPCC, 2014). Thus, extreme climate phenomena have especially negative effects on tropical forests, where long-term data sets are particularly scarce (Cook et al., 2015; IPCC, 2014; Milly et al., 2005; Seager et al., 2007; Sheffield et al., 2012) and concrete predictions for species-specific impacts have hardly been addressed (Parmesan, 2006). Tropical forests are subject to extensive human activity, including forestry, animal grazing, clearing for agriculture, housing and development, causing a highly fragmented landscape (Quesada et al., 2009). To clearly separate the effects of climate from anthropogenic causes (such as poor management, intensive cattle grazing, and deforestation), studies must be conducted in well-preserved and protected habitats, which can function as refugia for biodiversity to recover after human-induced disturbances (Eigenbrod et al., 2015). Tropical species have also been documented to be more resilient than their non-tropical counterparts to climatic and anthropogenic disturbances (Moore and Huntington, 2008; Moritz and Agudo, 2013; Stork and Habel, 2014), but their resilience has been poorly studied in tropical dry forests.

Tropical dry forests in Western Mexico are seasonal ecosystems where rainfall (June to October) is the main driving factor of plant phenology and productivity (Anaya et al., 2012; Maass et al., 2005, 2002; Martínez-Yrizar et al., 1996). Primary productivity and temperature are known to be driving factors for the biodiversity in these ecosystems (Brown, 2014). One proxy for net primary productivity in deciduous forest is litterfall (Malhi et al., 2011), as it enables us to understand how much biomass was produced during the growing season. This remains true for the tropical dry forests because their very marked phenology can provide us with a precise measure of productivity throughout the year (Martínez-Yrízar et al. this issue). Most tropical dry forests are heavily populated and poorly managed by humans (Herrerías-Diego et al., 2006; Janzen, 1988; Miles et al., 2006). Such forests can be categorized as arroyo or upland. In the Chamela region in Jalisco, Mexico, arroyo forests (canopy height up to 25 m) are confined to lowlands and floodplains. Approximately 75% of the tree species in arroyo forests drop their foliage yearly, during the dry season (March to May). By contrast, upland forests occupy the far larger slopes and face dryer conditions. Trees are shorter (up to 15 m), and virtually all species remain leafless during dry season. These two ecosystems are found contiguously, but they differ in floristic composition and are phenologically contrasting (Anaya et al., 2012; Filip et al., 1995; Lott et al., 1987; Martínez-Yrizar et al., 1996; Palacios-Vargas et al., 2007).

The striking differences between these ecosystems and the populations inhabiting them are caused by processes we do not yet fully understand. Thus, it is pivotal to shed light on how the combined forces of intrinsic and extrinsic factors affect the long-term population dynamics of small mammals inhabiting these forests, how resilient these species are to such forces, and how will they perform in the projected global climate-disruption scenarios. Answering these questions is fundamental to properly manage and protect biodiversity and tropical forest ecosystems in the face of global climate disruption (Chapin et al., 2004, 2000; Moritz and Agudo, 2013; Steneck et al., 2002; Stork et al., 2009; Zhou et al., 2013).

To answer those questions, we monitored the populations of seven native small mammals over an 18-year period in these two diverse and complex types of tropical dry forests. Through mathematical modeling of the species' population dynamics, we assessed the influence of biotic factors (i.e., interactions within and between species and the influence of changes in net primary productivity) and abiotic factors (i.e., rainfall, temperature) in their population dynamics. We specifically addressed the following questions: (1) What are the effects of intrinsic