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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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ABSTRACT

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

(intraspecific) and extrinsic (interspecific interactions, temperature and rainfall and extreme climate events) factors on long-term population trends? (2) What are the implications of changes in these factors, such as the predicted changes in regional rainfall due to global climate disruption, for population dynamics and for forest conservation and management?

2. Materials and methods

2.1. Study site

Data for this study were collected at Chamela-Cuixmala Biosphere Reserve (hereafter, Chamela), 19°30′ N, 105°03′ W, on Mexico's western Pacific coast (*S2*). Chamela includes over 13,000 ha of well-preserved highly seasonal tropical dry forest landscape, with two contrasting forest types; upland and arroyo forests. Upland forest soils are relatively young and shallow (0.5–1 m depth), with tree height from 10 m to 15 m; over 95% of the tree species lose their leaves during the dry season. By contrast, in the arroyo (or riparian) forests, soil is deeper (1–1.5 m), alluvial, and sandy. Canopy height is from 15 m to 40 m, and trees lose from 50% to 75% of leaves during the dry season (Bullock and Solís-Magallanes, 1990; Lott et al., 1987).

The climate is AwO(x′)I (García, 1973). Average rainfall for 1989–2007 was 819.6 mm/year (standard deviation [SD] 303.2 mm/year). Eighty percent of the rainfall in Chamela falls between June and October (Fig. 2), causing highly contrasting seasonal climatic conditions (Bullock and Solís-Magallanes, 1990; Lott et al., 1987). An atypical rainfall period was recorded in January 1992, when 648.7 mm of rain fell in four severe events, compared with the monthly mean of 41.8 mm.

This region is rich in small mammal species, particularly rodents, over 60% of them endemic (Ceballos González et al., 1998; Valdez and Ceballos, 2005). The small mammals in Chamela include the only endemic terrestrial carnivore known in Mexico (*Spilogale pygmaea*), four monotypic and endemic genera, four endemic species, and a marsupial (Ceballos González et al., 1998; Ceballos et al., 2005). These species constitute a rich and redundant functional assemblage, including specialized and generalist species that depend highly on exogenous forcings to remain diverse and to provide ecoservices to the forests they inhabit—from seed predation to insect control. These rodent assemblages include several arboreal and semi-arboreal species sharing similar size and feeding habits. The most abundant rodent in the region is an specialized granivorous heteromyid that is fundamental to determining the forest structure by predating certain tree species. (Ceballos, 1990; Mason-Romo et al., 2017; Vazquez-Dominguez et al., 1999)

2.2. Small-mammal live trapping

Small mammals were sampled monthly from 1990 to 1995 and bimonthly from 1996 to 2007 in six 0.5 ha grids: two in arroyo forest and four in upland forest. Each grid had 64 Sherman traps, 10 m apart and baited with a mixture of rolled oats, vanilla, and peanut butter (Ceballos, 1990). All the small mammals captured were identified and measured (i.e., total length, tail length, left hind foot length, left ear length); recording their sex, reproductive state and approximate age. All animals were immediately released on the same site where they were captured. All processing procedure took no longer than 10 min per animal, to minimize stress. No animal was sacrificed or marked, nor tissue samples were taken for this study. We strictly followed the guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of The American Society of Mammalogists, 2016).

2.3. Primary productivity data

Net primary productivity (NPP) was measured using litterfall (fine dead plant material). Since the great majority of the species renew their foliage every year, we suggest litterfall can be used as a proxy of NPP, considering that the ratio of total NPP to leaf-litter production is 4.2 on average (Maass et al., 2005, 2002; Martínez-Yrizar et al., 1996). Litterfall was collected from conical fiberglass mesh traps (1.4 mm mesh size), 50 cm in diameter and 50 cm deep, supported by three 1 m aluminum stakes fixed into the ground. The litter traps were systematically distributed within two 80 m × 30 m plots (24 traps per plot). The plots were located within a small (approximately 16 ha) well-preserved watershed: one in the middle position of the watershed (at 130 m altitude) in upland forest, and the other in the lower position in arroyo forest, near Arroyo El Zarco. Both plots were near the rodent-trapping sites. Litterfall samples consisted of all fine dead plant material accumulated in the litter traps (i.e., leaves, reproductive structures, and woody debris). Dead branches larger than 2 cm in diameter were discarded. Litterfall was collected monthly during the dry season and biweekly during the rainy season since 1982. The data used in this study cover the 1989–2007 period. For analysis, the monthly litterfall samples were grouped by season: rainy season (June–November), transition season (December–February), and dry season (March–May).

2.4. Climate

Temperature and precipitation data from 1989 to 2007 were obtained from the Chamela meteorological station (Estación Chamela, Instituto de Biología, n.d.). The rainfall data from each year were analyzed by season: rainy season (June–November) which accounts for 80% of the yearly rainfall; transition season (December–February), a period of increased leaf fall; and dry season (March–May), during which trees normally remain leafless (Bullock and Solís-Magallanes, 1990; Lott et al., 1987).

2.5. Population dynamics modeling

To model population dynamics using Royama's framework, the time series for their abundance, or density, must not have any trends (principle of stationarity). This means that time series must be detrended, unless some of the exogenous variables explain the trend, in which case there is no need to detrend the series. Therefore, for species that showed temporal trends, such as changes in their population trajectories between years, the data were linearly detrended using a density/time regression analysis (Berryman, 2003, 1992; Lima et al., 2008a,b; Royama, 1992). To understand how the influence of intraspecific interactions (feedback structure), abiotic influences (rainfall, productivity, and temperature), and interspecific interactions shape the population dynamics of the studied species, models based in the per capita population growth rate (*R*) were generated (Lima et al., 2008a,b). To understand whether the intraspecific interactions act on population dynamics immediately or after a lag period (the order of the feedback structure), a partial rate correlation function (PRCF) analysis was performed (Berryman, 2003, 1992; Lima et al., 2008a,b; Royama, 1992).

After understanding the order of the feedback structure, and detrending population dynamics that exhibited a trend (either to grow or decrease), several models were created using Ricker's discrete logistic model (Ricker, 1954):

$$N_t = N_{t-1} \cdot r_m \cdot exp(-c \cdot N_{t-1}^a)$$

where N_t represents the rodent abundance at time *t*, r_m is a positive constant representing the maximum finite reproductive rate, *c* is a constant representing competition and resource depletion, and an indicates the effect of interference on each individual as density increases (Royama, 1992); a > 1 indicates that interference intensifies with

density and a < 1 indicates habituation to interference. By defining this equation in terms of the *R*-function, by defining $R_t = \log_e (N_t/N_{t-1})$, log-transforming and defining the population density in logarithm $X_t = \log_e (N_t$Fig. 3, we obtain a *R*-function formula selected for modeling these population dynamics because all of its arguments have direct biological value and because of its simplicity and parsimony (Berryman, 2003, 1992; Lima et al., 2008a,b; Royama, 1992). The chosen modeling method was the nonlinear minimal square (NLS) function of the statistics library of R (R Core Team, 2013), as follows:

$$R_t = R_m - \exp(aX_{t-1} + C)$$

where R_t is the per capita change rate, *Rm* is the maximum per capita change, *a* is the effect of individual interference as density increases, X_{t-1} is the log transformed abundance and *C* is a constant representing intraspecific competition and resource depletion (Berryman, 2003, 1992; Lima et al., 2008a,b; Royama, 1992).

From this basic equation, which only includes intrinsic factors, the influence of exogenous factors can be added, as direct (vertical) or additive to *R* and *d*, the parameter measuring the effect of an exogenous factor *W*:

$$(R_t = R_m - exp(aX_{t-1} + C) + d*logW)$$

or indirect (lateral) or non-additive to *R*, as *W*, again, an exogenous factor:

$$(R_t = R_m - exp(aX_{t-1} + C + d*logW))$$

Thus, models were made more complex by adding exogenous factors (Berryman, 2003, 1992; Lima et al., 2008a,b; Royama, 1992), including rainfall, temperature, primary productivity and temperature, and the effect of each season. The interspecific interactions and the atypical rainfall events of January 1992 were also accounted for by subtracting them from the data to see if they affected the fitness of the models. For models in which rainfall showed indirect (lateral) effects, it was substituted for primary productivity, to prove it functioned as a proxy for the change in the availability of resources (De La Maza et al., 2009; Melillo et al., 1993; Nolet et al., 2013; Royama, 1992; Yachi and Loreau, 1999).

2.6. Statistical analyses

To draw statistical conclusions from the models, the Informatic-Theoretical approach was followed, using Akaike's criterion for small samples (AICc), the Akaike weights (*wi*), and their related values (Akaike, 1974, 1973, Berryman, 2003, 1992, Lima et al., 2008a,b, 2006b; Royama, 1992).

To compare the projections provided by the models with the real data, a bias parameter was calculated as: $\Sigma \frac{Oi - Pi}{17}$, where *Oi* is observed data and *Pi* is predicted data. Graphical projections were generated from these comparisons using a specially made *R* script. This script compares the real data with the model results, both from the first value (whole-model projection) and from the immediately anterior value (step-before projection) (Lima et al., 2008a,b; Royama, 1992). All statistical and population dynamics analyses were performed with the statistical software R 3.02 (R Core Team, 2013).

3. Results

3.1. Species modeled

Our analyses included over 20,000 small mammal captures in both arroyo and upland forests (Fig. 1). Seven species accounted for 96% of all total captures: *Liomys pictus* (painted spiny pocket mouse), *Nyctomys sumichrasti* (vesper rat), *Oryzomys melanotis* (black-eared rice rat), *Oryzomys mexicanus* (Mexican rice rat), *Osgoodomys banderanus* (Michoacan deer mouse) and *Peromyscus perfulvus* (tawny deer mouse; Fig. 1). These species were abundant enough in the arroyo forest to be

modeled (Figs. 1 and 2). Interestingly, only *L. pictus* was sufficiently abundant in the adjacent upland forest to be modeled (Fig. 1).

3.2. Long-term population dynamics

All the populations showed marked annual changes in their abundance, exhibiting similar peaks of abundance in 1996, 1998, and 2004, which suggests common drivers underlying these variations (Fig. 1). Population variations were of different scales: less than 75% in *Osgoodomys banderanus* (Fig. 1e); twofold in populations of *Liomys pictus* (Fig. 1a), *Nyctomys sumichrasti* (Fig. 1b) and *Oryzomys mexicanus* (Fig. 1d); threefold in *Oryzomys melanotis* (Fig. 1c); and fourfold in *Peromyscus perfulvus* (Fig. 1f). During 1992, there was a sharp decline in the abundances of all species except *Oryzomys mexicanus*, an opportunistic species (Fig. 2). The most abundant species, *Liomys pictus*, was extirpated for over 16 months from upland forest sites, with abundances going from around 1400 individuals to zero (Fig. 2). Despite these patterns, all but two of these populations fulfilled Royama's (2) stationarity criteria—that is, their populations showed no trend towards increase or decrease over the entire period. The two populations that did show a trend were *Liomys pictus* and *Nyctomys sumichrasti* in arroyo forest, which exhibited negative population trends that had to be detrended to model their abundances.

Partial rate correlation analysis showed that all dynamics modeled were non-cyclic and simple first-order, caused by a combination of intraspecific structure and abiotic factors. This suggests that populations were strongly structured by intraspecific interactions (i.e., biotic factors) and climate effects (i.e., abiotic forcing) that acted immediately, from the season before the one modeled, showing no time lag. It also suggests that interspecific interactions (biotic factors) were less important. Modeling these populations with nonlinear models based on Ricker's formula supported these suggestions and provided further detail about them, as well as some surprises. The main forces driving the population dynamics of these small mammals were, in order of importance, intraspecific interactions, rainfall variability (both directly and indirectly by triggering changes in net primary productivity), atypical climate events and interspecific interactions (Figs. 2 and 3).

3.3. Intrinsic factors

Intrinsic (intraspecific or density-dependent) interactions prevailed over any other factor for most species (Fig. 3). Although very important for some species, intraspecific interactions were not the only driving force for most populations, which were also strongly influenced by abiotic forcings and interspecific interactions (Fig. 3).

3.4. Extrinsic factors: Interspecific interactions

Interspecific interactions were only important for the population of *Liomys pictus* in arroyo forest, which exhibited positive interactions with *Oryzomys melanotis*, and for *Nyctomys sumichrasti*, which showed positive interactions with both *Oryzomys melanotis* and *Osgoodomys banderanus* (Fig. 3).

3.5. Extrinsic factors: Temperature and rainfall

Our results indicated that temperature was an unimportant factor for the population dynamics of all species. In contrast, rainfall influenced all populations directly, through enhancing the reproductive rate, or indirectly, through changes in net primary productivity, which proved to be an adequate proxy of the indirect (or lateral) effects of rainfall changes for the dynamics of every species except *Liomys pictus* in upland forest and *Oryzomys mexicanus* (Figs. 3 and S5).
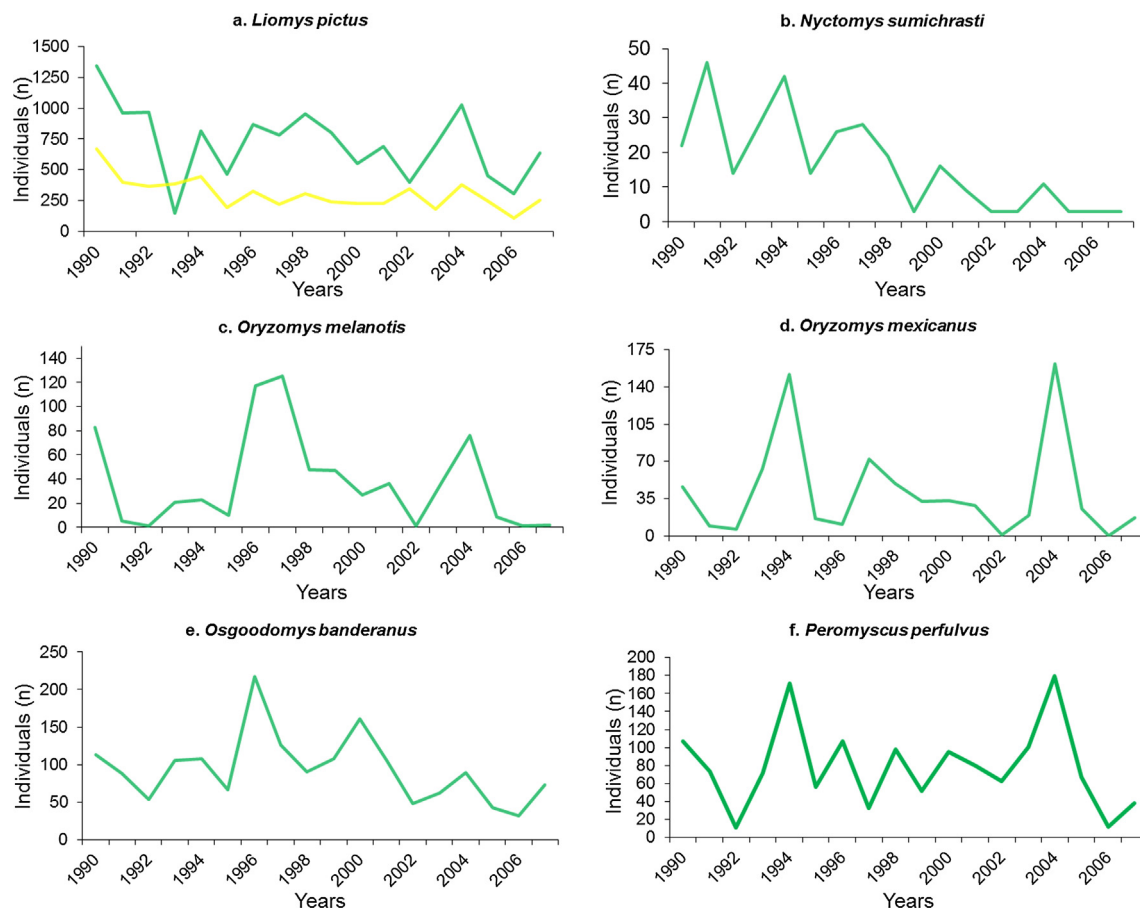
Fig. 1. Population trends and annual variation in relative abundance of the small mammal species in an 18-year period in upland (yellow) and arroyo (green) forests in the Chamela-Cuixmala Biosphere Reserve, Mexico. Although all species showed high variability over time, with different periods for peaks and lows in abundance, their population dynamics fulfil Royama's stationarity principle: dynamics were stable, not showing any increasing nor decreasing trend over the entire study period. This is true for all populations, but those of *Liomys pictus* and *Nyctomys sumichrasti* showed a negative overall trend in arroyo forest, indicating statistically significant population decline over time. These population dynamics were detrended (see Methods). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.6. Extrinsic factors: Extreme climate events

In January 1992, an extraordinary total rainfall of 648 mm was recorded for the month, whereas the average rainfall (1990–2007) for this month is 41.8 mm (for 13 out of the 18 years in this study, January rainfall was 0, and the rainiest January in the time series, 2004, never exceeded 95 mm), and annual rainfall for the same period is 819.6 mm (SD 303.2 mm) (Fig. 1). These extreme out-of-season rainfall events triggered a catastrophic decline of *Liomys pictus* in upland forest. This decline was so disastrous that this population—the most abundant, constituting 95% of the small mammals captured on upland forest sites—fell from over 1,400 individuals on 1990 to zero for the next 16 months (Fig. 1a). This population of *Liomys pictus* recovered from virtual extirpation to an abundance of over 750 individuals in 1994, yet this resilient population never again attained an abundance of over 1400 individuals, as observed in 1990, in the remainder of the time series (Fig. 1a). Both *Osgoodomys banderanus* and *Peromyscus perfulvus* also suffered this event and exhibited sharp reductions (50% and 90%, respectively). *Oryzomys melanotis* and *Oryzomys mexicanus*, both opportunistic species, they benefited from the extreme rainfall event, as their populations grew tenfold and 25 times, respectively, in the next two years.

3.7. Effects of projected rainfall patterns

Our models show that all species would be negatively affected by the lower rainfall predicted; even moderate reduction in rainfall would cause a decline. This population reduction would be less severe for species whose dynamics do not depend on rainfall: *Liomys pictus* in arroyo forest (Fig. 3b), *Nyctomys sumichrasti* (Fig. 3c), and *Peromyscus perfulvus* (Fig. 3g). By contrast, for species such as *Liomys pictus* in upland forest (Fig. 3a) and *Osgoodomys banderanus* (Fig. 3f), the effects are stronger, as the scenarios become more extreme. Both *Oryzomys* species (Fig. 3d and e) are the species most affected, as their abundance would be severely jeopardized.

4. Discussion

4.1. Drivers of population dynamics

The population dynamics of this group of tropical dry forest mammals vary among species and between the two forest habitats (arroyo and upland). For most species, like some of their non-tropical counterparts, intrinsic factors are the basis of their dynamics (e.g., effects on cyclic dynamics of small mammals in northern Fennoscandia are intrinsic second-order effects of predation) (Aars and Ims, 2002; Hansen et al., 1999; Johannesen et al., 2003). This might suggest that their populations have strategies to reduce intraspecific competition processes (Royama, 1992). We found little interspecific competition; only *Oryzomys melanotis*, an opportunistic species, was positively affected by the dynamics of *Liomys pictus*, and *Nyctomys sumichrasti* was similarly positively affected by *Osgoodomys banderanus*. Every interspecific
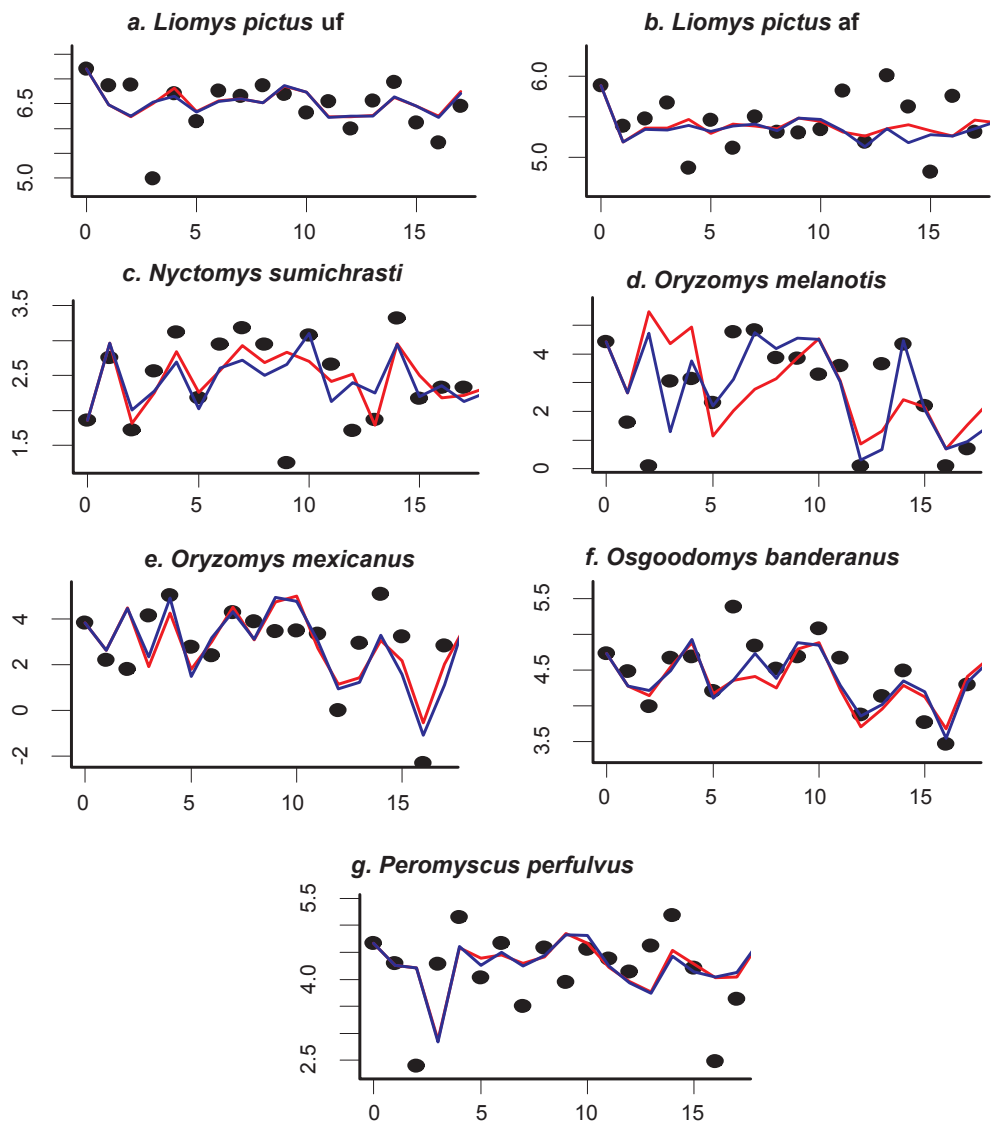
Fig. 2. Population dynamics predictions for small mammal species in an 18-year period (0 = 1990 and 18 = 2007) in upland (only *Liomys pictus*) and arroyo forest in the Chamela-Cuixmala Biosphere Reserve, Mexico. The Y-axis indicates the changes in *R*, per capita rate of change in abundance. The blue line is the whole-model prediction (from the first data) and the red line is the step-wise prediction (from the direct previous dot). uf = upland forest, af = arroyo forest. Note the change of scale in the Y-axis on each graph.

Species		Vegetation type	N	Processes driving their population dynamics				
				Endogenous factors	Exogenous disturbances			
English names	**Scientific names**				**Rainfall**	**Atypical rainfall**	**NPP**	**Interspecific interactions**
Painted Spiny Pocket Mice	*Liomys pictus*	*Upland forest*	13218	■	■	■		
Painted Spiny Pocket Mice	*Liomys pictus*	*Arroyo forest*	5420	■			■	Oryzomys melanotis
Vesper Rat	*Nyctomys sumichrasti*	*Arroyo forest*	290	■	■		■	Oryzomys melanotis, Osgoodomys banderanus
Black-eared Rice Rat	*Oryzomys melanotis*	*Arroyo forest*	410	■		■	■	
Coues's Rice Rat	*Oryzomys mexicanus*	*Arroyo forest*	424	■	■			
Michoacan Deer Mouse	*Osgoodomys banderanus*	*Arroyo forest*	331	■		■	■	
Tawny Deer Mouse	*Peromyscus perfulvus*	*Arroyo forest*	548	■	■	■	■	

Fig. 3. Processes driving population dynamics, determined by the best-sustained (lowest AICc) models, of small mammals of upland forest and arroyo forest in western Mexico. Green = positive effects, red = negative effects.
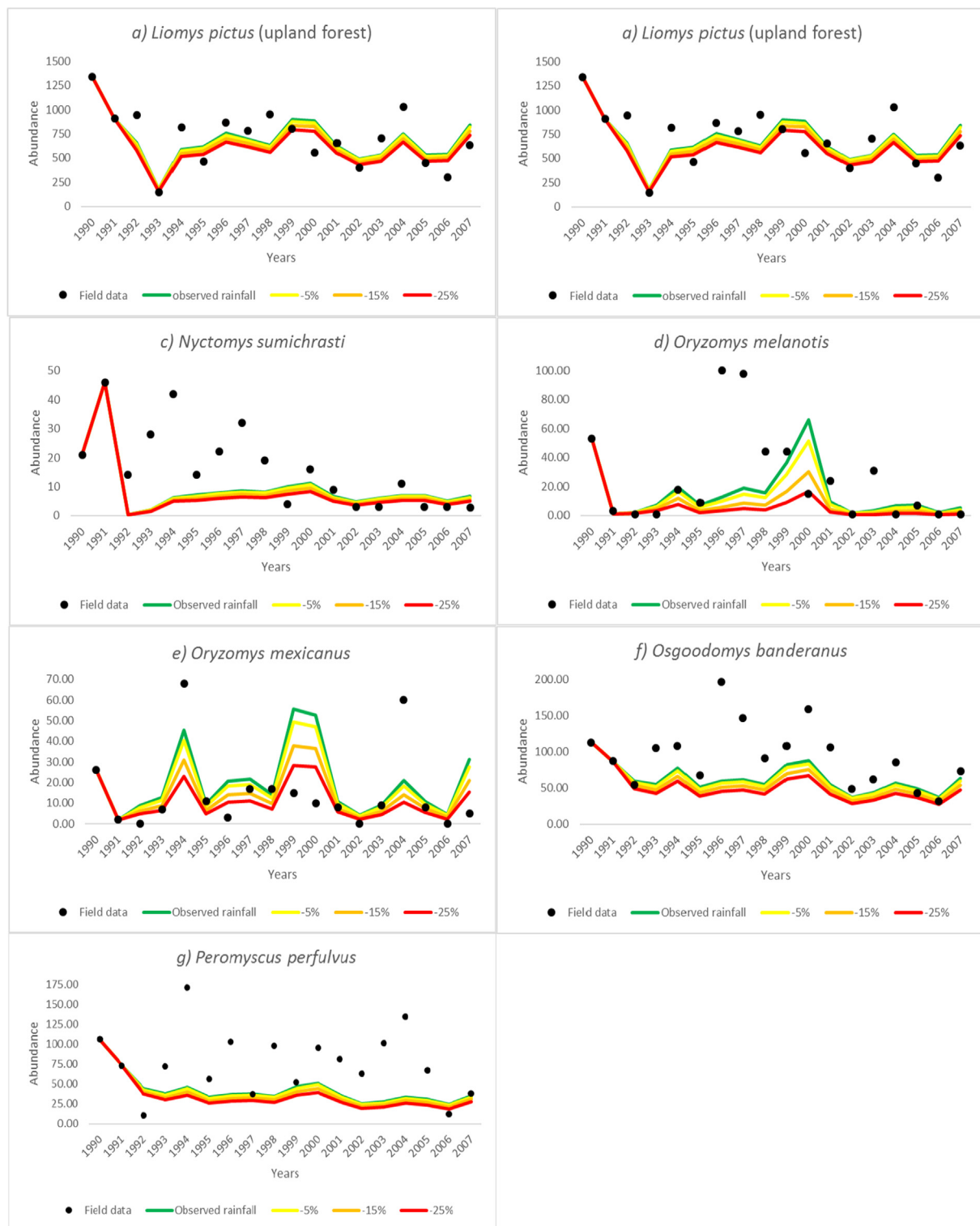
Fig. 4. Model projections, following the regional reductions in rainfall (IPCC, 2014). Field data are represented by the black dots, and the projections generated by our models with the full amount of rainfall recorded from 1990 to 2007 are shown by the green line. The three projections for reduced rainfall are shown according to three different scenarios: conservative (yellow), a 5% reduction in regional rainfall; moderate (orange), a 15% reduction; and severe (red), a 25% reduction.

interaction we found was positive, as reported in other studies with small mammals (Huitu et al., 2004; Lima et al., 2008a,b, 2001). This suggests the presence of common predators or facilitation (Bruno et al., 2003; Stachowicz, 2001).

Temperature is widely recognized as the main driver of population dynamics and diversity in tropical forests (Brown, 2014; Magnusson et al., 2010; Williams et al., 2003). For *Necromys lasiurus*, a small

mammal in the Amazonian savannah, temperature rules its dynamics, and rainfall, except in case of extreme events, is not important (Magnusson et al., 2010). By contrast, we found that temperature was irrelevant for the population dynamics of every species modeled, and rainfall is a pervasive force for most species. This would be expected in seasonal dry forests. The more it rains in a given year, the larger the populations grow, as rainfall affects populations either directly or

indirectly by modifying food availability. Most of the species modeled were strongly dependent on primary productivity (food availability), as has also been found for small mammals in temperate forests, grasslands, and deserts of the Northern Hemisphere (De La Maza et al., 2009; Holmgren et al., 2006; Lima et al., 2008a,b). South American small mammals' population dynamics also rely heavily on changes in food availability caused by El Niño events (Jaksic and Lima, 2003; Lima et al., 2002; Murua et al., 2003), triggering demographic changes such as the "ratadas," in which rodent populations sharply increase, by over a hundredfold (Jaksic and Lima, 2003).

Liomys pictus populations differed between upland and arroyo forests. Although the habitats are contiguous and developed under the same macroclimate regime, they exhibit striking differences in vegetation structure and plant species composition, defined by topography and soil type (Bullock and Solís-Magallanes, 1990; Galicia et al., 1999; Lott et al., 1987; Maass et al., 2002, 1995; Martínez-Yrizar et al., 1996). Soil water dynamics differ between the arroyo forest, where favorable moisture conditions continue for a longer period after the rainy season, to the more limited soil water retention in upland forest.

For this species, our models showed that, in arroyo forest, rainfall acted indirectly on the population dynamics and that primary productivity is a good proxy for measuring these effects. By contrast, in upland forest, direct effects of rainfall variability and extreme climate events played a major role by creating harsher conditions for this species to survive in. In this forest, only *Liomys pictus* had high enough population densities to be modeled.

This species is a heteromyid, meaning it has physiological and ecological characteristics that allow it to survive under high water-stress and high temperatures. It feeds only on seeds that it caches inside its cheek poaches, thus being more effective than any other species in this assemblage in surviving harsh drought conditions (Anderson et al., 2002; Genoways and Brown, 1993; Janzen, 1982; McGhee and Genoways, 1978).

These characteristics allow *Liomys pictus* density to be higher in the upland forest than in the arroyo forest, which is counterintuitive in a system with few effects from interspecific competence and in which upland forest exhibits harsher conditions (Berryman, 2003; Lima et al., 2008a,b; Royama, 1992).

Populations of *Liomys pictus* (in arroyo forest) and *Nyctomys sumichrasti* exhibited negative trends. These declines are alarming, particularly for *Liomys pictus*, the most abundant species, as they may lead to a loss of functional diversity in the region (Boucek and Rehage, 2014; Diaz and Cabido, 2001; Mason-Romo et al., 2017; Naeem et al., 2012) and/or colonization by opportunistic or invasive species (Ceballos et al., 2010a; Fargione et al., 2003; Vitousek, 1990). Understanding and preventing these repercussions is urgent (Ceballos et al., 2010b; Crepet et al., 2002; Naeem et al., 2012).

4.2. Resilience and extreme climate events

Liomys pictus exhibited high resilience to dry years and responded fastest to the increase in seasonal rainfall, critical conditions for their population dynamics in upland forest (Fig. 4a and b); the rest of the assemblage were also resilient to these conditions, but to a lesser extent. This is in agreement with the theory that tropical mammals are most resilient and that there is a gradient in resilience among mammals, decreasing progressively toward the poles (Brown, 2014; Chapin et al., 2004; Moore and Huntington, 2008; Parmesan, 2006; Stork et al., 2009). This resilience might prove fundamental to tropical mammals' survival, as anthropogenically induced global climate disruption further reduces rainfall in the region (Chapin et al., 2004; Stork et al., 2009) and triggers more frequent and intense precipitation events that may be atypical or extreme (Grinsted et al., 2013; Knutson et al., 2010; Meehl et al., 2000).

The extreme rainfall events that struck Mexico's Western Pacific coast in January 1992 (Fig. 2) caused important changes in tree phenology, particularly in the upland forest. This atypical precipitation occurred when the canopy was already leafless, increasing the overland runoff, washing surface litter and seeds down the slope to the arroyo forest. In response to the unexpected precipitation, a second flush of new leaves was produced by most species, followed by another litterfall event at the end of the dry season (Martínez-Yrízar, unpublished). The loss of available or cached seeds had catastrophic consequences for *Liomys pictus* (a strict seed eater) in the upland forest (Fig. 4a). During the following 18 months, it suffered a temporary extirpation (March 1993 to June 1994), leaving upland forest nearly depleted of small mammals (since this species constituted 93% of the captures). *Liomys pictus* was resilient and recovered, perhaps because individuals from the contiguous arroyo forest, unaffected by these events, recolonized the upland forest. This finding suggests source–sink dynamics between arroyo and upland forest, the former providing individuals that might colonize upland forest if its populations are severely reduced by habitat loss or extreme climate events.

The effects of atypical rainfall events have already been reported for other small mammals in the tropics and elsewhere (Hughes, 2003; Thibault et al., 2010; Thibault and Brown, 2008). Extreme climate events cause dramatic increases in mortality rates in other species of small mammals, such as bats in Australia (Hughes, 2003, 2000; Parris and Hazell, 2005; Sherwin et al., 2013) and the Czech Republic (Lučan et al., 2013), or rodents inhabiting Amazonian savannahs (Magnusson et al., 2010).

Our findings confirm that these climate phenomena, predicted to become more common from global warming, can devastate the populations of dominant species and allow invasive ones to thrive. These effects have been reported for desert heteromyid populations of North America: *Dipodomys merriami* (Merriam's kangaroo rat) was permanently extirpated and *Chaetodipus baileyi* (Bailey's pocket mouse) colonized and became exponentially abundant in the community after an atypical rainfall event (Brown et al., 1997; Thibault and Brown, 2008; Valone et al., 1995). Unlike the Chihuahuan desert's rich array of heteromyids that could substitute for *Dipodomys merriami*'s functional role (although imperfectly), our tropical dry forest sites have only one heteromyid. If it were permanently extirpated, its functional role would remain empty, causing deep changes in the forest structure and ecosystem functionality, as *Liomys pictus* is the most abundant small mammal in the region (95% of captures in upland forest) and the only heteromyid in the region. Its functional role is highly specialized and non-redundant, as it is the only territorial, arid-resistant, strict seed-eater in the assemblage (Ceballos, 1990; Mason-Romo et al., 2017).

4.3. Global climate disruption, predictions and risks

Although most populations are affected by reductions in rainfall, populations exhibiting dynamics unrelated to rainfall are the least affected. These effects are similar, independent of the scenario intensity, although more severe scenarios could potentiate the existing negative trends in these populations and might jeopardize their existence. *Oryzomys* species population reductions are increasingly affected as rainfall is reduced, by limiting the capacity of these species to recover after dry years.

Most of the small mammal species inhabiting tropical dry forests in Western Mexico are geographically restricted, dispersal-limited and endemic. This poses a threat similar to the one faced by mammals inhabiting Arctic or high-mountain habitats – these species have "nowhere to go" as climate shifts to conditions outside their ecological niches (Moritz et al., 2008; Sánchez-Cordero et al., 2005; Schloss et al., 2012; Vázquez-Domínguez et al., 2004). This is critical for arroyo forest, the source in this system, which might work as a "highway" for the mammals inhabiting tropical dry forests. Arboreal species' life history makes this source–sink system more efficient if vegetation is contiguous (Eigenbrod et al., 2015; Pulliam and Danielson, 2016). Species surviving in these habitats suffer from other human-caused

disturbances that make them least able to adapt to climate change and, thus, the most endangered species (Janzen, 1988; Maass et al., 2005; Schloss et al., 2012).

4.4. Preserving these highly managed source–sink ecosystems

Our results demonstrate and extend the validity of the ideas first explored by Elton (Elton, 1924) almost a hundred years ago: encouraging long-term population monitoring of small mammal species, particularly in tropical ecosystems. Small mammals are fundamental to the structure and functioning of tropical dry forests because they are abundant in conserved forests, efficient seed and insect predators, controllers of recruitment of plant species in the forest, and common prey for carnivorous species (Ceballos, 1990; Ceballos et al., 2005; Murray et al., 2006).

Plasticity, dispersal abilities, and reproductive capacity are critical to maintain small mammal populations and the services they provide, mitigating the effects of global climate disruption and extreme climate events on biodiversity in these highly endangered tropical dry forests (Brown, 2014; Ceballos and Ehrlich, 2009; Schloss et al., 2012). Yet these characteristics of small mammals might prove insufficient to meet the challenge if we do not secure enough refugia (such as our study site) for species to replenish the defaunated and vanishing tropical dry forests (Ceballos et al., 2007; Dirzo et al., 2014; Eigenbrod et al., 2015; Ghanem and Voigt, 2014).

Unfortunately, tropical dry forests are becoming increasingly disturbed and fragmented at alarming rates. This jeopardizes the resilience of these forests to overcome the effects of global climate disruption (Herrerías-Diego et al., 2006; Miles et al., 2006; Quesada et al., 2009). This disturbance is particularly intense at the neotropics, as climate is recognized as a particularly important threat to these forests (Miles et al., 2006). This makes even more urgent to increase the amount of protected areas on the region, such as the protected area where this study was conducted. (Quesada et al., 2009) This makes our study site unique in providing clues as to how a protected, unmanaged and unaltered tropical dry forest could work as a refuge to buffer the impacts of global climate disruption on the adjacent disturbed and managed regions. Thus, it is a vital resource in this climate crisis (Ashcroft, 2010; Maestri and Patterson, 2016; Myers, 2003; Myers et al., 2000; Stork and Habel, 2014), particularly to for us to learn the mechanisms of natural refaunation for highly managed and defaunated habitats, such as neotropical dry forests (Dirzo et al., 2014).

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.05.058.

References

Aars, J., Ims, R.A., 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology 83, 3449–3456. http://dx.doi.org/10.1890/0012-9658(2002) 083[3449:IACDOP]2.0.CO;2.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control ACI 19, 716–723.

Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary, pp. 267–281.

Anaya, C.A., Jaramillo, V.J., Martínez-Yrízar, A., García-Oliva, F., 2012. Large rainfall pulses control litter decomposition in a tropical dry forest: evidence from an 8-year study. Ecosystems 15, 652–663. http://dx.doi.org/10.1007/s10021-012-9537-z.

Anderson, R.P., Gómez-Laverde, M., Peterson, A.T., 2002. Geographical distributions of spiny pocket mice in South America: insights from predictive models. Glob. Ecol. Biogeogr. 11, 131–141. http://dx.doi.org/10.1046/j.1466-822X.2002.00275.x.

Ashcroft, M.B., 2010. Identifying refugia from climate change. J. Biogeogr. 37, 1407–1413. http://dx.doi.org/10.1111/j.1365-2699.2010.02300.x.

Bateman, B.L., Vanderwal, J., Williams, S.E., Johnson, C.N., 2012. Biotic interactions influence the projected distribution of a specialist mammal under climate change. Divers. Distrib. 18, 861–872. http://dx.doi.org/10.1111/j.1472-4642.2012.00922.x.

Berryman, A.A., 2003. On principles, laws and theory in population ecology. Oikos 103, 695–701.

Berryman, A.A., 1992. On choosing models for describing and analyzing ecological time series. Ecology 73, 694–698.

Berryman, A.a., 2001. Basic and applied ecology functional web analysis: detecting the structure of population dynamics from multi-species time series. Basic Appl. Ecol. 321, 311–321 doi: 10.1078/1439-1791-00069.

Berryman, A., Lima, M., 2006. Deciphering the effects of climate on animal populations:/ rDiagnostic analysis provides new interpretation of/rSoay sheep dynamics. Am. Nat. 168, 784–795. http://dx.doi.org/10.1086/508670.

Boucek, R.E., Rehage, J.S., 2014. Climate extremes drive changes in functional community structure. Glob. Chang. Biol. 20, 1821–1831. http://dx.doi.org/10.1111/gcb.12574.

Brown, J.H., 2014. Why are there so many species in the tropics? J. Biogeogr. 41, 8–22. http://dx.doi.org/10.1111/jbi.12228.

Brown, J.H., 1973. Species diversity of seed eating desert rodents in sand dune habitats. Ecology 54, 775–787. http://dx.doi.org/10.1002/job.305.

Brown, J.H., Valone, T.J., Curtin, C.G., 1997. Reorganization of an arid ecosystem in response to recent climate change. Proc. Natl. Acad. Sci. U. S. A. 94, 9729–9733. http://dx.doi.org/10.1073/pnas.94.18.9729.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18, 119–125. http://dx.doi.org/10.1016/S0169-5347(02)00045-9.

Bullock, S.H., Solís-Magallanes, J.A., 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 1 (22), 22–35.

Ceballos, G., 1990. Comparative natural history of small mammals from tropical forests in Western Mexico. J. Mammal. 71, 263–266.

Ceballos, G., Davidson, A., List, R., Pacheco, J., Manzano-Fischer, P., Santos-Barrera, G., Cruzado, J., 2010a. Rapid decline of a grassland system and its ecological and conservation implications. PLoS One 5. http://dx.doi.org/10.1371/journal.pone.0008562.

Ceballos, G., Ehrlich, P.R., 2009. Discoveries of new mammal species and their implications for conservation and ecosystem services. Proc. Natl. Acad. Sci. U. S. A. 106, 3841–3846. http://dx.doi.org/10.1073/pnas.0812419106.

Ceballos, G., Ehrlich, P.R., Ceballos, G., Ehrlich, P.R., 2007. Global mammal distributions, biodiversity hotspots. Proc. Natl. Acad. Sci. U.S.A. 103, 19374–19379. http://dx.doi.org/10.1073/pnas.0609334103.

Ceballos, G., García, A., Ehrlich, P.R., 2010b. The sixth extinction crisis loss of animal populations and species. J. Cosmol. 8, 1821–1831.

Ceballos, G., Oliva, G., Gisselle, O., 2005. Los mamíferos silvestres de México 10.1017/CBO9781107415324.004.

Ceballos González, G., Rodríguez, P., Medellín, R.A., 1998. Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemicity, and endangerment. Ecol. Appl. 8, 8–17.

Chapin, F.S., Peterson, G., Berkes, F., Callaghan, T.V., Angelstam, P., Apps, M., Beier, C., Bergeron, Y., Crépin, A.-S., Danell, K., Elmqvist, T., Folke, C., Forbes, B., Fresco, N., Juday, G., Niemelä, J., Shvidenko, A., Whiteman, G., 2004. Resilience and vulnerability of northern regions to social and environmental change. Ambio 33, 344–349. http://dx.doi.org/10.1639/0044-7447(2004) 033[0344:ravonr]2.0.co;2.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234–242. http://dx.doi.org/10.1038/35012241.

Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Sci. Adv. 1, 1–7. http://dx.doi.org/10.1126/sciadv.1400082.

Crepet, W.L., Nixon, K.C., Anther, T., Leins, P., Erbar, C., Acta, B., Museum, P.B., Ceballos, G., Ehrlich, P.R., Crepet, W.L., Nixon, K.C., Anther, T., Museum, P.B., 2002. Mammal population losses and the extinction crisis. Science (80.-) 296, 904–907. http://dx.doi.org/10.1126/science.1069349.

Crespin, L., Lima, M., 2006. Adult survival and population dynamics in the leaf-eared mouse Phyllotis darwini in central Chile. Rev. Chil. Hist. Nat. 79, 295–308.

De La Maza, M., Lima, M., Meserve, P.L., Gutiérrez, J.R., Jaksic, F.M., 2009. Primary production dynamics and climate variability: Ecological consequences in semiarid Chile. Glob. Chang. Biol. 15, 1116–1126. http://dx.doi.org/10.1111/j.1365-2486.2008.01796.x.

Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science (80-.) 345, 401–406. http://dx.doi.org/10.1126/science.1251817.

Eigenbrod, F., Gonzalez, P., Dash, J., Steyl, I., 2015. Vulnerability of ecosystems to climate change moderated by habitat intactness. Glob. Chang. Biol. 21, 275–286. http://dx.doi.org/10.1111/gcb.12669.

Ekerholm, P., Oksanen, L., Oksanen, T., 2001. Long-term dynamics of voles and lemmings at the timberline and above the willow limit as a test of hypotheses on trophic interactions. Ecography (Cop.) 24, 555–568. http://dx.doi.org/10.1034/j.1600-0587.2001.d01-211.x.

Elton, C., Nicholson, M., 1941. The Ten-Year Cycle in Numbers of the Lynx in Canada. J. Animal Ecol. 11, 215–244.

Elton, C.S., 1924. Periodic fluctuations in the numbers of animals: their causes and effects. Br. J. Exp. Biol. 2, 119–163.

Ergon, T., Ergon, R., Begon, M., Telfer, S., Lambin, X., 2011. Delayed density-dependent onset of spring reproduction in a fluctuating population of field voles. Oikos 120, 934–940. http://dx.doi.org/10.1111/j.1600-0706.2010.18983.x.

Ernest, S.K.M., Brown, J.H., Parmenter, R.R., 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88, 470–482. http://dx.doi.org/10.1034/j.1600-0706.2000.880302.x.

Estación Chamela, Instituto de Biología, U., n.d. http://www.ibiologia.unam.mx/ebchamela/www/clima.html [WWW Document].

Fargione, J., Brown, C.S., Tilman, D., 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proc. Natl. Acad. Sci. U.S.A. 100, 8916–8920. http://dx.doi.org/10.1073/pnas.1033107100.

Filip, V., Dirzo, R., Maass, J.M., Sarukhan, J., 1995. Within-year and among-year variation in the levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. Biotropica 27, 78–86. http://dx.doi.org/10.2307/2388905.

Galicia, L., López-Blanco, J., Zarco-Arista, A., Filips, V., García-Oliva, F., 1999. The relationship between solar radiation interception and soil water content in a tropical deciduous forest in Mexico. Catena 36, 153–164. http://dx.doi.org/10.1016/S0341-8162(98)00121-0.

García, E., 1973. Modificaciones al sistema de clasificación de Köppen. Instituto de Geografía, UNAM.

Genoways, H.H., Brown, J.H., 1993. Biology of the Heteromyidae. Am. Soc. Mammalogists 9422846.

Ghanem, S.J., Voigt, C.C., 2014. Defaunation of tropical forests reduces habitat quality for seed-dispersing bats in Western Amazonia: An unexpected connection via mineral licks. Anim. Conserv. 17, 44–51. http://dx.doi.org/10.1111/acv.12055.

Giam, X., Scheffers, B.R., Sodhi, N.S., Wilcove, D.S., Ceballos, G., Ehrlich, P.R., 2012. Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. Proc. R. Soc. B Biol. Sci. 279, 67–76. http://dx.doi.org/10.1098/rspb.2011.0433.

Grinsted, A., Moore, J.C., Jevrejeva, S., 2013. Projected Atlantic hurricane surge threat from rising temperatures. Proc. Natl. Acad. Sci. U. S. A. 110, 5369–5373. http://dx.doi.org/10.1073/pnas.1209980110.

Hansen, T.F., Stenseth, N.C., Henttonen, H., Tast, J., 1999. Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. Proc. Natl. Acad. Sci. U. S. A. 96, 986–991. http://dx.doi.org/10.1073/pnas.96.3.986.

Herrerías-Diego, Y., Quesada, M., Stoner, K.E., Lobo, J.A., 2006. Effects of forest fragmentation on phenological patterns and reproductive success of the tropical dry forest tree Ceiba aesculifolia. Conserv. Biol. 20, 1111–1120. http://dx.doi.org/10.1111/j.1523-1739.2006.00370.x.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Lima, M., López, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtali, M.A., Richter, M., Sabaté, S., Squeo, F.A., 2006. Extreme climatic events shape arid and semiarid ecosystems. Front. Ecol. Environ. 4, 87–95. http://dx.doi.org/10.1890/1540-9295(2006) 004[0087:ECESAA]2.0.CO;2.

Hoset, K.S., Le Galliard, J.F., Gundersen, G., 2009. Demographic responses to a mild winter in enclosed vole populations. Popul. Ecol. 51, 279–288. http://dx.doi.org/10.1007/s10144-008-0130-4.

Hughes, L., 2003. Climate change and Australia. Austral Ecol. 28, 423–443. http://dx.doi.org/10.7882/FS.2012.015.

Hughes, L., 2000. Biological consequences of global. Trends Ecol. Evol. 15, 56–61. http://dx.doi.org/10.1111/j.1749-4877.2010.00200.x.

Huitu, O., Huitu, O., Norrdahl, K., Norrdahl, K., Korpima, E., Korpima, E., 2004. Competition, predation and interspecific synchrony in cyclic small mammal communities. Ecography (Cop.) 2, 197–206. http://dx.doi.org/10.1111/j.0906-7590.2003.03684.x.

IPCC, 2014. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovern-mental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jaksic, F.M., Lima, M., 2003. Myths and facts on ratadas: Bamboo blooms, rainfall peaks and rodent outbreaks in South America. Austral Ecol. 28, 237–251. http://dx.doi.org/10.1046/j.1442-9993.2003.01271.x.

Janzen, D.H., 1988. Tropical dry forests, in: E.O, W. (Ed.), Biodiversity. pp. 130–137.

Janzen, D.H., 1982. Fruit traits, and seed consumption by rodents, of Crescentia alata

(Bignoniaceae) in Santa Rosa National Park, Costa Rica. Am. J. Bot. 69, 1258–1268. http://dx.doi.org/10.2307/2442750.

Johannesen, E., Aars, J., Andreassen, H.P., Ims, R.A., 2003. A demographic analysis of vole population responses to fragmentation and destruction of habitat. Popul. Ecol. 45, 47–58. http://dx.doi.org/10.1007/s10144-003-0139-7.

Knutson, T.R., McBride, J.L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J.P., Srivastava, A.K., Sugi, M., 2010. Tropical cyclones and climate change. Nat. Geosci. 3, 157–163. http://dx.doi.org/10.1038/ngeo779.

Krebs, C.J., Boonstra, R., 1978. Demography of the Spring Decline in Populations of the Vole, Microtus townsendii. J. Anim. Ecol. 10.2307/3684.

Letnic, M., Dickman, C.R., 2006. Boom means bust: Interactions between the El Ni??o/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. Biodivers. Conserv. 15, 3847–3880. http://dx.doi.org/10.1007/s10531-005-0601-2.

Lima, M., 2001. The dynamics of natural populations: feedback structures in fluctuating environments. Rev. Chil. Hist. Nat. 74, 317–329. http://dx.doi.org/10.4067/S0716-078X2001000200009.

Lima, M., Berryman, A.A., Stenseth, N.C., 2006a. Feedback structures of northern small rodent populations. Oikos 112, 555–564. http://dx.doi.org/10.1111/j.0030-1299.2006.14439.x.

Lima, M., Keymer, Juan E., Jaksic, F.M., 1999. ENSO-driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America: linking demography and population dynamics. Am. Nat. 153, 476–491.

Lima, M., Harrington, R., Salda??a, S., Estay, S., 2008a. Non-linear feedback processes and a latitudinal gradient in the climatic effects determine green spruce aphid outbreaks in the UK. Oikos 117, 951–959. http://dx.doi.org/10.1111/j.0030-1299.2008.16615.x.

Lima, M., Jaksic, F.M., 1999. Population dynamics of three Neotropical small mammals: time series models and the role of delayed density-dependence in population irruptions. Austral Ecol. 24, 25–34. http://dx.doi.org/10.1046/j.1442-9993.1999.00943.x.

Lima, M., Previtali, M.A., Meserve, P.L., 2006b. Climate and small rodent dynamics in semi-arid Chile: The role of lateral and vertical perturbations and intra-specific processes. Clim. Res. 30, 125–132. http://dx.doi.org/10.3354/cr030125.

Lima, M., Stenseth, N.C., Jaksic, F.M., 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecol. Lett. 5, 273–284. http://dx.doi.org/10.1046/j.1461-0248.2002.00312.x.

Lima, M., Stenseth, N.C., Yoccoz, N.G., Jaksic, F.M., 2001. Demography and population dynamics of the mouse opossum (Thylamys elegans) in semi-arid Chile: seasonality, feedback structure and climate. Proc. Biol. Sci. 268, 2053–2064. http://dx.doi.org/10.1098/rspb.2001.1735.

Lima, M., Ernest, S.K., Brown, J.H., Belgrano, A., Stenseth, N.C., 2008b. Chihuahuan Desert kangaroo rats: Nonlinear effects of population dynamics, competition, and rainfall. Ecology 89, 2594–2603. http://dx.doi.org/10.1890/07-1246.1.

Lott, E.J., Bullock, S.H., Solís-Magallanes, J.A., 1987. Floristic diversity and structure of upland and riparian forests in coastal Jalisco. Biotropica 19, 228–235.

Lučan, R.K., Weiser, M., Hanák, V., 2013. Contrasting effects of climate change on the timing of reproduction and reproductive success of a temperate insectivorous bat. J. Zool. 290, 151–159. http://dx.doi.org/10.1111/jzo.12021.

Maass, J.M., Balvanera, P., Castillo, A., Daily, G.C., Mooney, H.A., Ehrlich, P., Quesada, M., Miranda, A., Jaramillo, V.J., García-oliva, F., Martínez-yrizar, A., Cotler, H., López-blanco, J., Pérez-jiménez, A., Búrquez, A., Tinoco, C., Ceballos, G., Barraza, L., Ayala, R., 2005. Ecosystem services of tropical dry forests : insights from long- term ecological and social research on the pacific coast of Mexico. Ecol. Soc. 10, 17 17/nArtn 17.

Maass, J.M., Martínez-Yrízar, A., Patiño, C., Sarukhán, J., 2002. Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall quality in a Mexican tropical deciduous forest ecosystem. J. Trop. Ecol. 18, 821–834. http://dx.doi.org/10.1017/S0266467402002535.

Maass, J.M., Vose, J.M., Swank, W.T., Martínez-Yrízar, A., 1995. Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. For. Ecol. Manage. 74, 171–180. http://dx.doi.org/10.1016/0378-1127(94)03485-F.

Maestri, R., Patterson, B.D., 2016. Patterns of species richness and turnover for the South American rodent fauna. PLoS One 11, 1–18 10.1371/journal.pone.0151895.

Magnusson, W.E., Layme, V.M.G., Lima, A.P., 2010. Complex effects of climate change: population fluctuations in a tropical rodent are associated with the southern oscillation index and regional fire extent, but not directly with local rainfall. Glob. Chang. Biol. 16, 2401–2406. http://dx.doi.org/10.1111/j.1365-2486.2009.02140.x.

Malhi, Y., Doughty, C., Galbraith, D., 2011. The allocation of ecosystem net primary productivity in tropical forests. Philos. Trans. R. Soc. B Biol. Sci. 366, 3225–3245. http://dx.doi.org/10.1098/rstb.2011.0062.

Martínez-Yrizar, A., Maass, J.M., Pérez-jiménez, L.A., Sarukhán, J., 1996. Net primary productivity of a tropical deciduous forest ecosystem in Western Mexico. In: Martinez-Yrizar, A., Maass, J.M., Perez-Jimenez, L.A., Sarukhan, J. (Eds.), Cambridge University Press. Stable URL: http://www.jstor.org/stab. J. Trop. Ecol. 12, 169–175.

Mason-Romo, E.D., Farías, A.A., Ceballos, G.J., 2017. Two decades of climate driving the dynamics of functional and taxonomic diversity of a tropical small mammal community in western. PLoS One 12, 1–25 10.1371.

McGhee, M.E., Genoways, H.H., 1978. Liomys pictus. Mamm. Species. doi: 10.2307/3504048.

Meehl, G.A., Zwiers, F., Evans, J., Knutson, T., Mearns, L., Whetton, P., 2000. Trends in extreme weather and climate events: Issues related to modeling extremes in projections of future climate change. Bull. Am. Meteorol. Soc. 81, 427–436. http://dx.doi.org/10.1175/1520-0477(2000) 081 < 0427:TIEWAC > 2.3.CO;2.

Mei, W., Primeau, F., McWilliams, J.C., Pasquero, C., 2013. Sea surface height evidence for long-term warming effects of tropical cyclones on the ocean. Proc. Natl. Acad. Sci.

U. S. A. 110, 15207–15210. http://dx.doi.org/10.1073/pnas.1306753110.

Melillo, J.M., McGuire, a.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature. http://dx.doi.org/10.1038/363234a0.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 491–505. http://dx.doi.org/10.1111/j.1365-2699.2005.01424.x.

Milly, P.C.D., Dunne, K.A., Vecchia, a.V., 2005. Global pattern of trends in streamflow and water availability in a changing climate. Nature 438, 347–350. http://dx.doi.org/10.1038/nature04312.

Moore, S.E., Huntington, H.P., 2008. Arctic marine mammals and climate change: impacts and resilience. Ecol. Appl. 18, s157–s165. http://dx.doi.org/10.1890/06-0571.1.

Moritz, C., Agudo, R., 2013. The future of species under climate change: resilience or decline? Science (80.-) 341, 504–508. http://dx.doi.org/10.1126/science.1237190.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C., Beissinger, S.R., 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science (80.-) 322, 261–264. http://dx.doi.org/10.1126/science.1163428.

Murray, A.L., Barber, A.M., Jenkins, S.H., Longland, W.S., 2006. Competitive environment affects food-hoarding behavior of Merriam's Kangaroo Rats (Dipodomys merriami). J. Mammal. 87, 571–578. http://dx.doi.org/10.1126/science.95.2469.427-b.

Murua, R., Gonzalez, L., a., Lima, M.,, 2003. Population dynamics of rice rats (a Hantavirus reservoir) in southern Chile: feedback structure and non-linear effects of climatic oscillations. Oikos 102, 137–145. http://dx.doi.org/10.1034/j.1600-0706.2003.12226.x.

Myers, N., 2003. Biodiversity hotspots revisited. Bioscience 53, 916. http://dx.doi.org/10.1641/0006-3568(2003) 053[0916:BHR]2.0.CO;2.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. http://dx.doi.org/10.1038/35002501.

Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The Functions of biological diversity in an age of extinction. Science (80.-) 336, 1401–1406. http://dx.doi.org/10.1126/science.1215855.

NOAA, 2015. http://www.prh.noaa.gov/hnl/pages/examples/2015_HurricaneSeasonSummary_MediaAdvisory.pdf [WWW Document].

Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y., Ebbinge, B.S., 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. J. Anim. Ecol. 82, 804–813. http://dx.doi.org/10.1111/1365-2656.12060.

Palacios-Vargas, J.G., Castaño-Meneses, G., Gómez-Anaya, J.A., Martínez-Yrizar, A., Mejía-Recamier, B.E., Martínez-Sánchez, J., 2007. Litter and soil arthropods diversity and density in a tropical dry forest ecosystem in Western Mexico. Biodivers. Conserv. 16, 3703–3717. http://dx.doi.org/10.1007/s10531-006-9109-7.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Ecol. Evol. Syst. 37, 637–669. http://dx.doi.org/10.2307/annurev.ecolsys.37.091305.30000024.

Parris, K.M., Hazell, D.L., 2005. Biotic effects of climate change in urban environments: The case of the grey-headed flying-fox (Pteropus poliocephalus) in Melbourne, Australia. Biol. Conserv. 124, 267–276. http://dx.doi.org/10.1016/j.biocon.2005.01.035.

Pulliam, H.R., Danielson, B.J., 2016. Sources , sinks , and habitat selection: a landscape perspective on population dynamics. In: Ronald Pulliam, H., Brent, J. Danielson Source: The American Naturalist, vol . 137, Supplement: Habitat Selection (June, 1991), pp . Published 137.

Quesada, M., Sanchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F. de S., Rosas-Guerrero, V., Sayago, R., Sanchez-Montoya, G., 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. For. Ecol. Manage. 258, 1014–1024. http://dx.doi.org/10.1016/j.foreco.2009.06.023.

R Core Team, 2013. R: A language and environment for statistical computing.

Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. 5, 559–623.

Rosenzweig, M., 1992. Species diversity gradients : we known more and less than we thought. J. Mammal. 73, 715–730.

Royama,, 1992. Analytical Population Dynamics. Chapman, Hall, London, Uk.

Sánchez-Cordero, V., Illoldi-Rangel, P., Linaje, M., Sarkar, S., Peterson, A.T., 2005. Deforestation and extant distributions of Mexican endemic mammals. Biol. Conserv. 126, 465–473. http://dx.doi.org/10.1016/j.biocon.2005.06.022.

Schloss, C., Nuñez, T., Lawler, J.J., 2012. Dispersal will limit ability of mammals to track

climate change in the Western Hemisphere. Proc. Natl. Acad. Sci. U. S. A. 109, 8606–8611. http://dx.doi.org/10.1073/pnas.1116791109.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316, 1181–1184. http://dx.doi.org/10.1126/science.1139601.

Sheffield, J., Wood, E.F., Roderick, M.L., 2012. Little change in global drought over the past 60 years. Nature 491, 435–438. http://dx.doi.org/10.1038/nature11575.

Sherwin, H.A., Montgomery, W.I., Lundy, M.G., 2013. The impact and implications of climate change for bats. Mamm. Rev. 43, 171–182. http://dx.doi.org/10.1111/j.1365-2907.2012.00214.x.

Sikes, R.S., Animal Care and Use Committee of The American Society of Mammalogists, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J. Mammal. 97, 663–688.

Stachowicz, J.J., 2001. The structure of ecological communities. Bioscience 51, 235–246.

Steneck, R., Graham, B.J., Bourque, D., Corbett, J.M., Erlandson, M.H., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future.

Stier, S.C., Mildenstein, T.L., 2005. Dietary habits of the World'S Largest Bats: the Philippine Flying Foxes, Acerodon Jubatus and Pteropus Vampyrus Lanensis. J. Mammal. 86, 719–728. http://dx.doi.org/10.1644/1545-1542(2005) 086[0719:DHOTWL]2.0.CO;2.

Stork, N.E., Coddington, J.A., Colwell, R.K., Chazdon, R.L., Dick, C.W., Peres, C.A., Sloan, S., Willis, K., 2009. Vulnerability and resilience of tropical forest species to land-use change. Conserv. Biol. 23, 1438–1447. http://dx.doi.org/10.1111/j.1523-1739.2009.01335.x.

Stork, N.E., Habel, J.C., 2014. Can biodiversity hotspots protect more than tropical forest plants and vertebrates? J. Biogeogr. 41, 421–428. http://dx.doi.org/10.1111/jbi.12223.

Terborgh, J., 2013. Using Janzen-Connell to predict the consequences of defaunation and other disturbances of tropical forests. Biol. Conserv. 163, 7–12. http://dx.doi.org/10.1016/j.biocon.2013.01.015.

Thibault, K.M., Brown, J.H., 2008. Impact of an extreme climatic event on community assembly. Proc. Natl. Acad. Sci. U. S. A. 105, 3410–3415. http://dx.doi.org/10.1073/pnas.0712282105.

Thibault, K.M., Ernest, S.K.M., Brown, J.H., 2010. Redundant or complementary? Impact of a colonizing species on community structure and function. Oikos 119, 1719–1726. http://dx.doi.org/10.1111/j.1600-0706.2010.18378.x.

Turchin, P., Taylor, A.D., 2007. Complex dynamics in ecological time series. 73, pp. 289–305.

Valdez, M., Ceballos, Y.G., 2005. (Spermophilus Mexicanus Y.S. Perotensis) En El Centro De México pp. 40–48.

Valone, T.J., Brown, J.H., Jacobi, C.L., 1995. Catastrophic decline of a desert rodent, dipodomys spectabilis - insights from a long-term study. J. Mammal. 76, 428–436.

Vázquez-Domínguez, E., Ceballos, G., Cruzado, J., 2004. Extirpation of an insular subspecies by a single introduced cat: the case of the endemic deer mouse Peromyscus guardia on Estanque Island, Mexico. Oryx 38, 347–350. http://dx.doi.org/10.1017/S0030605304000602.

Vazquez-Dominguez, E., Pinero, D., Ceballos, G., 1999. Linking heterozygosity, demography, and fitness of tropical populations of Liomys pictus. J. Mammal. 80, 810–822.

Vitousek, P.M., 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57, 7–13. http://dx.doi.org/10.2307/3565731.

Wang, G., Edge, W.D., Wolff, J.O., 2001. Rainfall and Guthion 2S interactions affect gray-tailed vole demography. Ecol. Appl. 11, 928–933. http://dx.doi.org/10.1890/1051-0761(2001) 011[0928:RAGIAG]2.0.CO;2.

Welbergen, J.A., Klose, S.M., Markus, N., Eby, P., 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. Proc. R. Soc. B Biol. Sci. 275, 419–425. http://dx.doi.org/10.1098/rspb.2007.1385.

Williams, S.E., Bolitho, E.E., Fox, S., 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. Proc. R. Soc. London B 270, 1887–1892. http://dx.doi.org/10.1098/rspb.2003.2464.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Natl. Acad. Sci. U. S. A. 96, 1463–1468. http://dx.doi.org/10.1073/pnas.96.4.1463.

Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X., Liu, J., Yan, J., Zhang, D., Chu, G., 2013. A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. Glob. Chang. Biol. 19, 1197–1210. http://dx.doi.org/10.1111/gcb.12128.