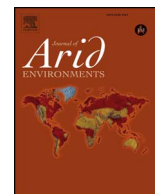




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## Functional perspectives on the dynamics of desert lizard assemblages

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## ABSTRACT

Ecology has long sought whether there are general assembly rules that underlie patterns of community organization. However, new perspectives of community disassembly and reassembly have emerged as environments depart from baseline conditions due to agents of global change. A trait-based approach can provide insights as to how changes affect performance of a species and their subsequent loss, gain, or persistence in an assemblage. We quantified the spatiotemporal dynamics in species and functional diversity from systematic surveys of local lizard assemblages distributed along an elevation gradient from three surveys in a 50-year period (1950s–2000s) in Big Bend National Park (BBNP), USA. BBNP was subjected to and then released from intensive grazing, which has resulted in changes to vegetative composition and cover. We examine changes in local assemblages in the context lizard functional traits, including thermal niche breadth. We hypothesized that temperature specialists were more likely to colonize or be lost from local sites. Species richness was lowest in the 1950s ( $N = 3$  species), and subsequent surveys revealed that species richness increased in both the 1960s and 2000s ( $N = 6$  and  $N = 8$  species, respectively), but not all sites responded uniformly. We found that functional diversity in this system was not affected by this drastic increase species richness, indicative of functional redundancy in species traits. Lizards that were added to sites tended to be smaller bodied with lower thermal tolerances. Lizards with high preferred body temperatures were locally extirpated from high elevation sites that experienced high shrub encroachment, likely due to a reduction in the preferred thermal gradients these species. These results reveal that long-term desert lizard functional diversity was maintained, but the consequences of changes to functional diversity at the local scale need to be examined further.

## 1. Introduction

Ecologists have long sought to identify the mechanisms that drive patterns of community organization (i.e., ‘assembly rules’) (Diamond, 1975; Weiher and Keddy, 2001; Chase, 2003). However, concomitant with recent biodiversity loss and land use change, identifying the mechanisms driving community disassembly have become increasingly important (Ostfeld and LoGiudice, 2003; Larsen et al., 2008; Leavitt and Fitzgerald, 2013; Hernández Fernández et al. 2015). Whether these (dis)assembly dynamics occur in a deterministic or stochastic fashion remains a challenge for ecologists because of the complexities of multiple individuals and species interacting with one another as well as the abiotic environment (Brown et al., 1997; Leibold et al., 2004). Community structure and dynamics are dictated by intrinsic and extrinsic factors interacting across multiple spatial and temporal scales (Ricklefs,

1987; Holyoak et al., 2005; Montaña et al., 2014; Schalk and Saenz, 2016; Vellend, 2016; Sullivan et al., 2017). Gaining a clear understanding how these factors affect community dynamics is critical to determine and design resource conservation baselines and trajectories.

Chief among the intrinsic factors that affect community dynamics are functional traits of species (McGill et al., 2006). Functional traits influence an organism's performance and are a useful means for describing an organism's niche and indirectly explain community dynamics (Stevens et al., 2003; McGill et al., 2006; Petchey et al., 2007). While traditionally, community structure and dynamics have been examined in the context of changes in species diversity, understanding patterns and dynamics of functional traits of community members can provide insight to underlying assembly processes (Petchey and Gaston 2002; Petchey et al., 2007). Further, traits can be extended beyond community structure to how communities are organized across scales (Díaz and Cabido, 2001;

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McGill et al., 2006), how communities change in time (Petchey et al., 2007), and how they affect ecosystem processes (de Bello et al., 2010). Understanding (dis)assembly dynamics requires consideration of functional diversity (FD) within community assemblages and examining sources of redundancy over time (Petchey et al., 2007).

Recent and historic anthropogenic activities, such as overgrazing, industrialization, and shifts in climate (e.g., increased drought severity), throughout the arid ecosystems of the world have altered natural ecological processes (Van Auken, 2000; Whitford, 2002). Arid ecosystem community organization is constrained by water availability (Brown et al., 1997) and this is often reflected in organismal traits (Reich et al., 1999; Donovan et al., 2007; Schalk et al., 2015; Petry et al., 2016). Disruption of ecological processes in arid ecosystems has occurred by multiple pathways including changes in vegetative cover (reduced or increased), increased soil erosion, alternation of nutrient dynamics, and establishment and loss of invasive and native species (Schofield and Bucher, 1986; Brown et al., 1997; Foley et al., 2005; Martin et al., 2003; Van Auken, 2000; Whitford, 2002). Recovery of these systems to release from these anthropogenic pressures is slow as they exhibit time lags on the scale of decades (Valone et al., 2002). Therefore change in arid systems may be abrupt, but the dynamics that follow may be very slow or still in transition (Hastings, 2001).

From a functional perspective, lizards play important roles in arid ecosystems (Morton and James, 1988; Pianka and Vitt, 2003). They are mid-level consumers within desert food webs serving as an important link for energy transfer and can comprise a substantial portion of biomass (Morton and James, 1988). Additionally, lizards are model organisms for understanding ecological change (Pianka, 1966; Dunham, 1980; Pianka and Vitt, 2003) as they are short-lived (average lifespan 1–5 years), span the spectrum of reproductive strategies, and as ectotherms, many aspects of their ecology and life-history are constrained by temperature (Huey and Slatkin, 1976; Pianka and Vitt, 2003). Their ectothermic nature has received considerable attention in the context of global climate change (Huey et al., 2009; Sinervo et al., 2010). One macroclimate model of climate change suggests that ectotherms will increase the time spent in thermal refugia limiting their foraging opportunities thereby constraining other functions such as growth and reproduction, and in turn increasing their extinction risk (Sinervo et al., 2010). However, these models can be too simplistic and ignore the fine-scaled (i.e., microclimate) variation in thermal gradients that are experienced by ectotherms such as lizards (Gunderson and Leal, 2015, 2016). Climate change threatens lizard thermal niches directly and indirectly by altering thermal environments via changes in vegetation cover across time (Van Auken, 2000).

At the regional scale, community structure of Chihuahuan Desert lizards is driven by environmental factors such as soils, vegetation types, and or vegetation structure (Degenhardt, 1977; Whitford and Creusere, 1977; Barbault and Maury, 1981; Menke, 2003). At smaller spatial scales, predator abundance, and vegetative cover affect foraging activity and microhabitat availability, respectively, affecting local assemblage structure (Degenhardt, 1977; Barbault and Maury, 1981; Menke, 2003). Within these local assemblages, lizard abundance is driven by prey availability, which is correlated with rainfall (Whitford and Creusere, 1977). Clearly, multiple factors are driving community organization and dynamics of Chihuahuan Desert lizard assemblages, but these studies have primarily focused on changes in species diversity or abundance across environmental gradients.

Big Bend National Park (BBNP), situated in the Chihuahuan Desert of Texas, USA (Fig. 1), has undergone extensive land use change over the past century. From the late 1800s and up until 1942, much of BBNP was subjected to grazing by goats and cattle (Maxwell, 1985). Subsequent work in this ecosystem has demonstrated that the release from grazing resulted in changes to vegetative composition and cover (Leavitt et al., 2010). Shrubs (e.g. *Larrea tridentata* and *Juniperus pinchotti*) have increased at both low elevation and high elevation sites, while vegetative cover has become increasingly homogenized at mid-

elevation sites due to the invasion of non-native grasses (Leavitt et al., 2010). It is noted that increased vegetative structural complexity is positively correlated with lizard species diversity on a regional scale (Pianka, 1966, 1986; James, 2003). However, changes in vegetative cover, especially in response to anthropogenic factors, can result in reduced lizard diversity or abundance at smaller scales. For example, in central Namibia, species-specific responses to increasing brush encroachment resulted in one species going locally extinct, two decreased in abundance, and one species increasing in abundance (Meik et al., 2002). In Nebraska, two species of lizards dependent on open “blow-out” habitats were extirpated due to an increase in plant densities after cattle were removed (Ballinger and Watts, 1995). While these studies highlight that certain species are prone to shifts, declines, or extinction, these dynamics have not been examined in the context of their functional traits which would provide better insights as to how these changes may scale up to affect higher-level processes.

Here we quantified the spatiotemporal dynamics in species and functional diversity from systematic surveys of lizard assemblages distributed along an elevation gradient from three surveys across a 50-year period (1950s–2000s) at BBNP. To quantify changes in functional diversity, we developed a multidimensional functional trait matrix per species. We hypothesized that functional traits related to the thermal niche would explain assemblage dynamics (presence or absence) in this system (Sinervo et al., 2010), but not all species would exhibit the same responses to environmental drivers of change (Gunderson and Leal, 2015, 2016). We predicted that thermal specialists (i.e., those species that optimally perform at the low and high end of the temperature spectrum) will be the most likely to be added to or removed from local sites compared to thermal generalists that optimally perform over a broader temperature spectrum.

## 2. Methods

### 2.1. Study area and surveys

Five permanent study sites were established in BBNP in the northern Chihuahuan Desert of west Texas by Degenhardt (1960; Fig. 1). The study sites established by Degenhardt (1960, 1966) are located along an elevation gradient established in a southwest-northeast line including the Chisos Mountains and the surrounding desert. From lowest to highest, the sites are: Tornillo Flat (853 m), Grapevine Springs (945 m), Burnham Flat (1036 m), Green Gulch 1 (1280 m), and Green Gulch 2 (1417 m). All sites are 0.40 ha in size with the exception of the Tornillo Flat site, which measures 1.62 ha. Degenhardt (1960) demarcated sites with metal rebar at the four corners of each site. Vegetative composition of these sites varies from low desert creosotebush flats to high elevation pinyon-juniper forest (Leavitt et al., 2010). Lizard surveys were conducted yearly between 1956 and 1960, 1968–1969, and 2005–2006 (hereafter referred to as 1950s, 1960s, and 2000s, respectively). Lizard survey methods were similar in all eras; surveys began when morning substrate temperature reached 35 °C ( $\pm 1$  °C), and ended after ca. 30 min or after the full site was sampled. Surveys consisted of walking ten evenly spaced transects (15 m apart and 60 m long) and identifying each lizard observed to species using binoculars (8 × 42, Eagle Optics, Middletown, Wisconsin). Each study site was sampled yearly between May and August ten times yearly in the 1950s, sampled 20 times yearly in the 1960s, and ten times yearly in the 2000s. Because there were differences in vegetative structure over the survey samples (Leavitt et al., 2010) and lizard detection probabilities can vary by observer bias and species (Smolensky and Fitzgerald, 2010) we evaluate these data with species richness patterns only.

### 2.2. Functional trait diversity

We selected 13 traits that describe multiple dimensions of the functional niche of lizards (Table 1). Some traits related to

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