# Functional perspectives on the dynamics of desert lizard assemblages

Daniel J. Leavitt[a,b,*,1,2], Christopher M. Schalk[c,3]

[a] *Big Bend National Park, Panther Junction, TX 79834, USA*
[b] *Sul Ross State University, Alpine, TX 79832, USA*
[c] *Department of Biological Sciences, Sam Houston State University, Huntsville, TX 77341, USA*

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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 becoming 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;

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 "blowout" 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 ( ± 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
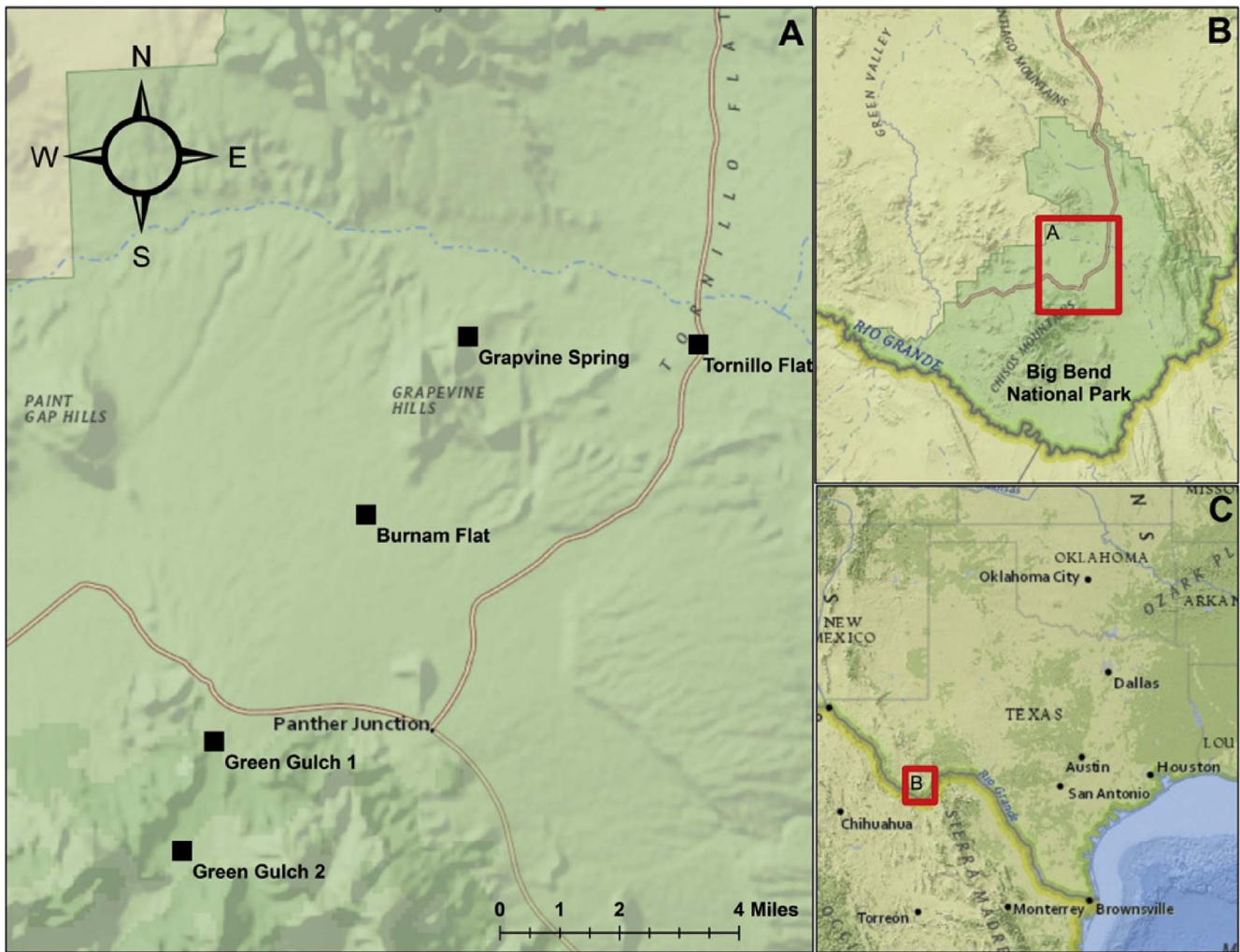
**Fig. 1.** Lizard study site locations (A) in Big Bend National Park, Texas, USA (frame on inset map indicates location of Big Bend National Park (B) in Texas (C).

**Table 1**
Traits used to measure lizard functional diversity. Functional traits for each species were collected from the literature (see Methods). Morphological traits were measured from museum specimens (see Appendix 1).

| Trait Type | Trait |
| --- | --- |
| Thermoregulatory Mode and Foraging Period (TM) | Mean body temperature, thermal niche breadth (°C) |
| Foraging Mode (FM) | Active or sit and wait foragers, head height, head length (mm) |
| Resource Quantity (RQ) | Number of eggs, weight of clutch (g), snout-vent length, body width, body height, (mm) |
| Habitat Use (HU) | Body width, body height, tibia-fibula length, radius-ulna length (mm) |
| Predator Avoidance (PA) | Tail length (mm) |

thermoregulatory mode and foraging period (TM), foraging mode (FM), and resource quantity (RQ) were assembled from the literature (Pianka and Parker, 1975; Schall, 1977; Bashey and Dunham, 1997; Lemos-Espinal et al., 2003; Parker and Pianka, 1973; Vinegar, 1975; Vitt and Price, 1982). Additional traits related to resource quantity (RQ), habitat use (HU), and predator avoidance (PA) were measured from adult specimens collected at or near the study area (Table 1; Appendix 1) with a digital caliper (precision = 0.01 mm). The combined dataset was used to describe the functional niche for all lizard species detected more than twice during this survey.

Morphological traits were size-adjusted by regressing each morphological trait against SVL and using the residuals to represent the trait (Schalk et al., 2015) and then $z$-transformed (Gotelli and Ellison, 2004). To adjust for multicollinearity we removed one of each pair of morphological variables that maintained greater that 90% correlation coefficient as calculated following Zar (1999). To visualize the functional niche space, we conducted a principal co-ordinates analysis (PCoA) on the combined dataset of functional traits and applied the Gower dissimilarity metric (Pavoine et al., 2009) in program PAST (Hammer et al., 2001). To decipher the axes loadings, we examined Pearson correlation coefficients (Zar, 1999) for each trait on all axes that cumulatively account for ≥95% of the variation in the dataset. Finally, to determine lizard functional groupings we conducted simple single linkage cluster analysis on these same axes (Pianka, 1980).

To understand the dynamics of local assemblages in the multivariate trait space, we examined different facets of functional diversity per site per era using unweighted presence–absence data. Using the 'picante' package (Kembel et al., 2010) in R (R Core Development Team), we calculated: 1) Functional diversity (FD), the extent of functional differences among species which is determined from the dendrogram branch length calculated from a cluster analysis conducted with average clustering and Euclidean distances (Petchey and Gaston, 2002), and using the 'FD' package (Laliberté and Legendre, 2010), we calculated: 2) Functional dispersion (FDis) is the spread of species in multidimensional trait space and is calculated from the

**Table 2**
Lizard species detection history at each site within Big Bend National Park, Texas from surveys conducted across three eras: the 1950s, 1960s, and the 2000s. Sites are arrayed along an elevation gradient: Tornillo Flat (853 m), Grapevine Spring (945 m), Burnham Flat (1036 m), Green Gulch 1 (1280 m), Green Gulch 2 (1417 m).

| Species | Site | Era | | |
|---|---|---|---|---|
| | | 1950s | 1960s | 2000s |
| *Aspidoscelis inornata* | Tornillo Flat | | | |
| | Grapevine Spring | | | X |
| | Burnham Flat | | X | X |
| | Green Gulch 1 | | | |
| | Green Gulch 2 | | | |
| *Aspidoscelis marmorata* | Tornillo Flat | X | X | X |
| | Grapevine Spring | X | X | X |
| | Burnham Flat | X | X | X |
| | Green Gulch 1 | X | X | |
| | Green Gulch 2 | X | | |
| *Aspidoscelis scalaris* | Tornillo Flat | | | |
| | Grapevine Spring | X | X | X |
| | Burnham Flat | | | X |
| | Green Gulch 1 | X | X | X |
| | Green Gulch 2 | X | X | X |
| *Cophosaurus texanus* | Tornillo Flat | X | X | X |
| | Grapevine Spring | X | X | X |
| | Burnham Flat | X | X | X |
| | Green Gulch 1 | X | X | |
| | Green Gulch 2 | X | | |
| *Sceloporus consobrinus* | Tornillo Flat | | | X |
| | Grapevine Spring | | X | |
| | Burnham Flat | | X | |
| | Green Gulch 1 | | X | X |
| | Green Gulch 2 | | | |
| *Sceloporus magister* | Tornillo Flat | | | X |
| | Grapevine Spring | | | |
| | Burnham Flat | | | |
| | Green Gulch 1 | | | |
| | Green Gulch 2 | | | |
| *Phrynosoma modestum* | Tornillo Flat | | | |
| | Grapevine Spring | | | |
| | Burnham Flat | | | |
| | Green Gulch 1 | | | X |
| | Green Gulch 2 | | | |
| *Uta stansburiana* | Tornillo Flat | | X | X |
| | Grapevine Spring | | | |
| | Burnham Flat | | X | X |
| | Green Gulch 1 | | | |
| | Green Gulch 2 | | | |
| Era Species Richness | | 3 | 6 | 8 |

mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre, 2010). A site with just a single species is given a FDisp value of zero (Laliberté and Legendre, 2010).

As species richness (SR) of an assemblage changes, FD could exhibit one of three responses: 1) changes in FD are proportional to changes in species richness (i.e., a 1:1 relationship), 2) changes in SR have relatively little effect on FD (i.e., functional redundancy), 3) changes in FD are proportionally greater than changes in species richness (i.e., functional sensitivity) (Petchey et al., 2007). We compared the change in FD through time with the change in SR through time. Specifically, we examined the changes and relationships in FD and SR of each site from the 1950s to the 1960s and the 1960s to the 2000s.

## 3. Results

### 3.1. Lizard surveys

Between 1957 and 2006, eight lizard species were detected on 1660 occasions during 332 surveys conducted at five study sites in BBNP (Table 2; Leavitt, 2007). Overall, species richness of this lizard community increased from 3 to 8 over the eras (Table 2). *Aspidoscelis marmorata* and *Aspidoscelis scalaris* (Family Teiidae) and *Cophosaurus texanus* (Family Phrynosomatidae) were the most frequently detected species across all sites and eras (Table 2). *Aspidoscelis inornata* (Family Teiidae), *Phrynosoma modestum*, *Sceloporus consobrinus*, *Sceloporus magister*, and *Uta stansburiana* (Family Phrynosomatidae) were also detected, but less frequently, and not until after the initial 1950s survey (Table 2).

From the 1950s to the 1960s, species richness increased in all but one site (Green Gulch 2), and from the 1960s to 2000s, species richness increased at the lowest elevation site (Tornillo Flat), remained constant at two mid-elevation sites (Grapevine Springs and Burnham Flat), and decreased at the highest elevation sites (Green Gulch 1 and 2) (Table 2). In the 1960s, *A. marmorata* and *C. texanus* disappeared concurrently from the two high elevation plots (Green Gulch 1 and 2). After the 1960s, *A. scalaris* expanded its distribution from the low and high elevation sites and was found at the mid-elevation site (Burnham Flat) for the first time in the 2000s (Table 2). *Aspidoscelis inornata* was detected at one mid-elevation site (Burnham Flat) in the 1960s for the first time and colonized the second mid-elevation site (Grapevine Springs) in the 2000s. In general, there was a net increase in species richness despite individual species going absent at some sites over time. Two species were detected two times or less (*P. modestum* and *S. magister*, respectively) were not included in multivariate evaluation of functional diversity in this lizard community.

### 3.2. Functional trait diversity

The first three PCoA axes accounted for 96% of the variation in the data set (PCoA 1: 74%; PCoA 2: 19%; PCoA 3: 3%). PCoA axis 1 was correlated with traits associated with lizard foraging modes and predator avoidance (Table 3). PCoA axis 2 was correlated with lizard thermal biology and habitat use (Table 3). PCoA axis 3 was correlated with body size (Table 3). In general, teiids and phrynosomatids segregated on a gradient of body shape and foraging mode (Fig. 2). Clustering of these species revealed nesting of functional groups, which consisted of three teiids and two small-bodied phrynosomatids, with the exception of *C. texanus* (Fig. 3). Within the teiid group, *A. inornata* occupied its own niche space (Fig. 3).

Functional diversity (FD) peaked at the mid elevation site (Burnham Flat), was lower at both the lower and higher elevation sites (Fig. 4A).

**Table 3**
Correlation coefficients (r) between functional traits and PCoA axes for lizard assemblage in Big Bend National Park, Texas, USA. Abbreviations in parentheses are the trait types listed in Table 1.

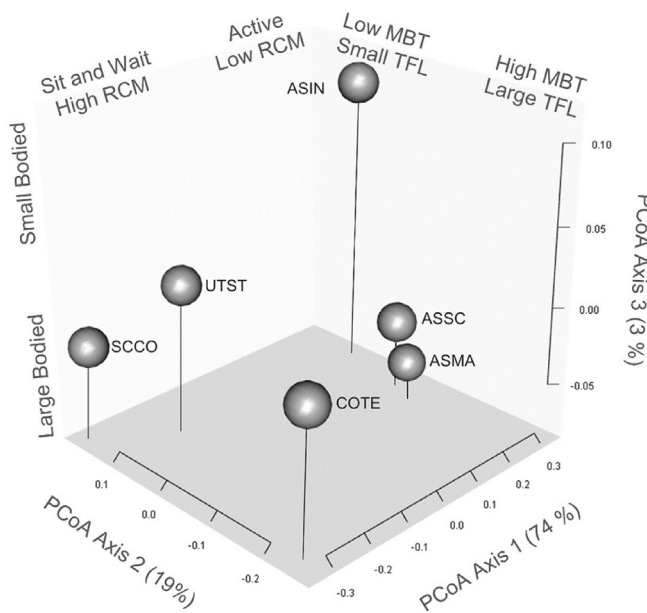| Functional Trait (Trait Type) | PCoA 1 r | PCoA 2 r | PCoA 3 r |
|---|---|---|---|
| Snout-Vent Length (RQ) | 0.63 | −0.49 | −0.49 |
| Body Width (RQ, HU) | −0.73 | −0.60 | −0.33 |
| Body Height (RQ, HU) | −0.92 | 0.04 | 0.01 |
| Head Length (RQ, FM) | −0.75 | 0.39 | −0.47 |
| Tibia-Fibula Length (HU) | −0.62 | −0.74 | 0.04 |
| Radius-Ulna Length (HU) | −0.87 | −0.40 | 0.14 |
| Tail Length (PA) | 0.91 | 0.34 | −0.18 |
| Mean Body Temperature (TM) | 0.81 | −0.56 | 0.09 |
| Thermal Niche Breadth (TM) | −0.72 | −0.56 | 0.19 |
| Foraging Mode (FM) | −0.97 | 0.09 | −0.04 |
| Mean Clutch Size (RQ) | −0.81 | 0.33 | −0.16 |
| Relative Clutch Mass (RQ) | −0.94 | 0.29 | 0.06 |

**Fig. 2.** Principal coordinates analysis (PCoA) ordination of functional traits of the lizard community surveyed from the 1950s–2000s in Big Bend National Park, Texas. Species abbreviations are ASIN: *Aspidoscelis inornata*; ASMA: *Aspidoscelis marmorata*; ASSC: *Aspidoscelis scalaris*; COTE: *Cophosaurus texanus*; SCCO: *Sceloporus consobrinus*; UTST: *Uta stansburiana*. Abbreviations for functional traits are RCM: relative clutch mass; MBT: mean body temperature; TFL: tibia-fibula length.
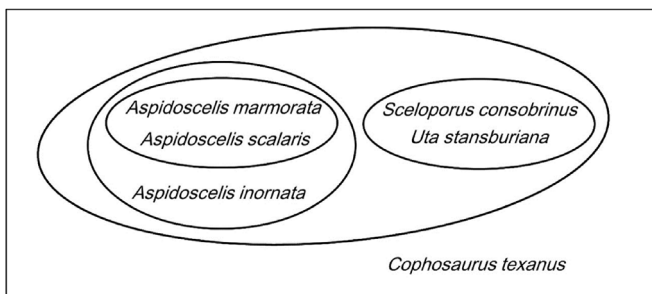


**Fig. 3.** Functional group structure of desert lizards in Big Bend National Park, Texas as determined by single-linkage cluster analysis of principle coordinates (PCoA) scores.

Functional dispersion (FDisp) was fairly consistent across four of the five sites (Fig. 4B). Green Gulch 2 had the lowest FDisp, which coincided with the loss of two species from the site since the 1950s and the persistence of just a single species (*Aspidoscelis scalaris*) (Fig. 4A).

Overall, from the 1950s–2000s, change in the SR ranged from -2 to +2 (mean = 0.3). From the 1950s–1960s change in the SR ranged from -2 to +3 (mean = 0.8) and from 1960s–2000s change in SR ranged from -2 to +3 (mean = -0.2). Changes in SR had relatively little effect on FD, regardless of whether species were added or lost at a site from both the 1950s–1960s (FD = 0.1631*SR - 0.0123; Fig. 5A) and from the 1960s–2000s (FD = 0.1337*SR - 0.0359; Fig. 5B). Functional redundancy was apparent between the species dropped and added. For instance, on sites where *A. marmorata* dropped out, *A. scalaris* entered (Table 2); these species maintain the same thermoregulatory and foraging modes however they differ slightly in microhabitat (Fig. 2).

## 4. Discussion

Ecological communities can be viewed on a continuum as fragile networks that are susceptible to collapse or as fluid ever-changing networks assembling and disassembling (Bascompte and Stouffer, 2009). In the context of species turnover and (dis)assembly, our observations of local assemblages over five decades revealed that they
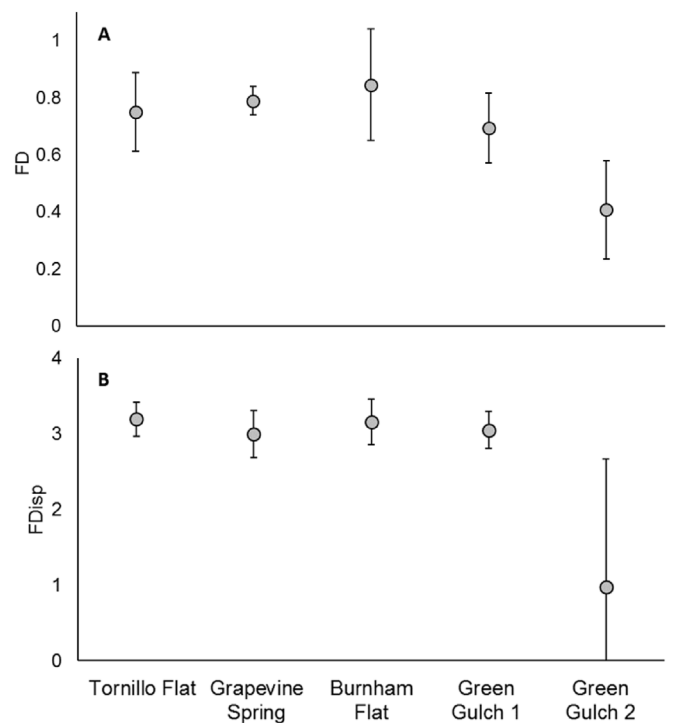


**Fig. 4.** Indices of functional diversity (mean ± SD) from five local desert lizard assemblages surveyed across three eras (1950s, 1960s, 2000s) in Big Bend National Park, Texas: A) functional diversity (FD), and B) functional dispersion (FDisp).

exhibit dynamics consistent with both contraction and expansion, which are consistent with mechanisms of disassembly and assembly, respectively. Species richness increased over time, but not all sites responded uniformly. Our results suggest that individual species loss and gain is due to deterministic factors, and is likely due to traits associated with a species thermal niche. Specifically, thermal specialists are more likely to be added to or lost from local assemblages as compared to thermal generalists. Functional diversity did not increase with increasing species richness and was consistent across space and time due to high functional redundancy of species traits.

### 4.1. Species richness

Overall, lizard species richness increased from the 1950s to the 2000s. In arid systems, animal species richness response to shrub encroachment depends on the study organism, with local assemblages both increasing and decreasing in local species richness (Kazmaier et al., 2001; Kerley and Whitford, 2009; Sirami et al., 2009; Eldridge et al., 2011). The best predictor of the assemblage response is how local spatial heterogeneity changed with subsequent shrub encroachment. Spatial heterogeneity is positively correlated with habitat diversity (Pianka, 1966). If shrub encroachment reduces a site's spatial heterogeneity (*i.e.,* one cover type dominates) then species richness usually decreases (Tews et al., 2004). From the 1950s to the 2000s, only one site consistently lost species (Green Gulch 2) and was the site that experienced the largest increase in percent vegetation cover in large homogeneous patches (Leavitt et al., 2010). An assessment of vegetation richness and composition patterns on these same sites discovered significant increases in vegetation cover on sites Green Gulch 1 and Green Gulch 2 (Leavitt et al., 2010). These increases in vegetation cover were double or triple (respectively) the amount of cover that was observed on them in the 1950s. Further, these two sites lost the same two species from their assemblages over this time (*A. marmorata* and *C. texanus*). In contrast, five other species (*A. inornata, S. consobrinus, S. magister, P. modestum,* and *U. stansburiana*) occurred in more locations
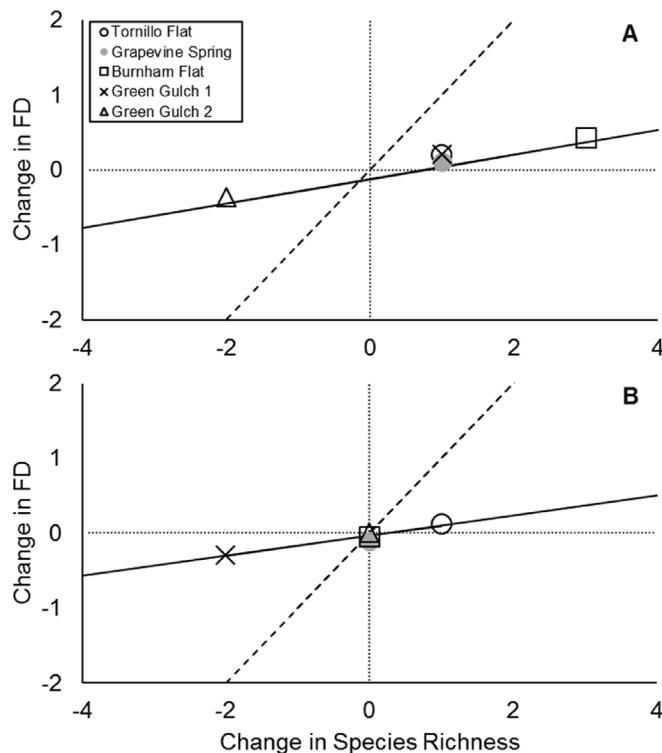
**Fig. 5.** Temporal change in desert lizard functional diversity (FD) and species richness in five sites between the periods of A) 1950s–1960s, and B) 1960s–2000s. The solid lines indicate the relationship between change in FD and change in SR. The dashed lines are the 1:1 relationship. The origin is depicted by the dotted horizontal and vertical lines.

following shrub encroachment over time. These species represent members of the local species pool that occurred in BBNP through the years of heavy grazing and have become regionally more abundant. This too may be due to changes in local spatial heterogeneity, all of the sites where these species became present increased in both forbs and grasses since the 1950s (Leavitt et al., 2010).

### 4.2. Functional diversity

FD did not change uniformly and concomitantly with SR patterns. We observed evidence of high intrinsic redundancy in the temporal dynamics of FD in Chihuahuan Desert lizard assemblages FD were less than proportional to changes in SR, which decreased slightly over time (1950s–1960s slope: 0.1631 vs. 1960s–1950s slope: 0.1337). The five species added to the overall community in our study did not increase the FD proportionally to SR. Comparing temporal dynamics of British bird assemblages, Petchey et al. (2007) observed that changes in FD tended to be nearly proportional to changes in SR, suggesting lower intrinsic redundancy. While their regional species pool had 192 species, local assemblages contained far fewer species, which they attributed to the lack of functional redundancy (Petchey et al., 2007). However, arid ecosystems imposed strong environmental filters on the regional species pool so that coexisting species possess traits that are suited to the environment (Boersma et al., 2014; Schalk et al., 2015). For instance, desert frog assemblages are structured by the process of environmental filtering, which is reflected in their traits, as coexisting species exhibit high morphological similarity (Schalk et al., 2015). Regardless of any changes to the landscape in response to release from grazing pressure, regional environmental filters may already constrain species functional traits (Pianka, 2014). Any colonization or extinction experienced by an assemblage may not result in a proportional or extrinsic functional response because the regional species pool has species with a similar suites of traits adapted to the environmental conditions (Schalk et al., 2017).

Three species of lizards (*A. inornata*, *S. consobrinus*, and *U. stansburiana*) were never detected until the 1960s when they colonized mid-elevation sites that experienced homogenization of cover by grasses (Leavitt et al., 2010). *Aspidoscelis inornata* is the smallest North American teiid with a low mean body temperature and short annual activity window that ceases earlier compared to heterospecifics (Schall, 1977; Persons and Wright, 2009). Both *S. consobrinus* and *U. stansburiana* are small bodied phrynosomatids with low mean body temperatures and short annual activity cycles (Lemos-Espinal et al., 2003). These lizards are patchily distributed within BBNP where grassland habitats are available and are most likely increasing due to the expansion of grassland communities. We propose that the increase in overall grassland cover resulted in cooler temperatures, thus small-bodied lizards with lower thermal tolerances were able to occupy these habitats.

Shrub encroachment can have consequences for ectotherms as it alters the microclimate due to increasing shade cover (Van Auken, 2000). For ectotherms that have a high preferred body temperature, it can be increasingly difficult to locate basking sites to maintain optimal temperatures in encroached sites. *Aspidoscelis marmorata* and *C. texanus* were common at the BBNP high elevation sites (Green Gulch 1 and 2) during the 1950s (Degenhardt, 1966), when later surveys revealed they were locally extirpated these sites. Both species prefer open canopy microhabitats, which enables them to maintain high body temperatures (Bashey and Dunham, 1997; Dixon, 2009). The high elevation sites already have lower ambient air temperature (Leavitt, 2007). When released from grazing pressure, shrub cover at these sites increased at least two-fold (Leavitt et al., 2010), altering the microclimate and the availability of optimal thermal gradients were likely reduced for these high temperature thermal specialists. Further evidence that thermal niches may be driving the observed changes is comparing the species lost from these sites to one that has persisted across the entire study. From a functional perspective, *A. scalaris* is very similar to *A. marmorata* (Barbault and Maury, 1981). Yet *A. scalaris* has persisted in the high elevation sites across the 50-year period and diverges from *A. marmorata* by having a lower preferred body temperature (Barbault and Maury, 1981). The functional redundancy between the two *Aspidoscelis* species likely maintained the consistent patterns of functional diversity, even though one species was locally extirpated. It is important to note that local extirpation in no way indicates an overall reduction to their presence in the ecosystem. For example, *C. texanus* is now commonly found in lower elevation sites that contain open desert wash, rocky outcrops and bajada habitats (Leavitt, 2007).

### 4.3. Implications for conservation

North American deserts have fewer lizard species compared to deserts in Australia or Southern Africa (Pianka, 1986). From a regional perspective, the species functional redundancy buffered against large changes to FD when shrubs encroached at local sites. While regional FD was maintained across time, whether loss or gain of species affects function at local sites needs to be examined further. While functional redundancy may be high in species-rich environments, ecological change often impacts the outliers or functional specialists rather than generalists (Devictor et al., 2008; Leavitt and Fitzgerald, 2013; Hibbits et al., 2013). Most conversation goals target conserving taxonomic diversity, which has taken priority over ecosystem function (Rosenfeld, 2002). For desert ecosystems lizards play functionally important roles as predator, prey, and ecosystem engineers (Pianka and Vitt, 2003). As our study demonstrated, one species that declined (*C. texanus*) was functionally unique. Thus, the loss of these unique species may have a disproportionally greater impact on structure and function of these local communities and ecosystem processes.

Climate change is one of the most imminent threats to ecosystems worldwide (Tewksbury et al., 2008). In the context of the disassembly process, or as termed by Gallagher et al. (2013) "reassembly", functional diversity and local species pools have indicated that temperature

sensitive species may be lost from a community (Deutsch et al., 2008; Gallagher et al., 2013; Sinervo et al., 2010) and our results appear to support these findings. However, it is important to note that no lizard species went regionally extinct, but were extirpated from local sites. Clearly, an approach that incorporates both functional and taxonomic perspectives across multiple spatial and temporal scales will provide insights as the short and long-term consequences of extirpation of redundant and unique species on ecosystem function.

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## Appendix 1. Lizard specimens measured at the Texas Cooperative Wildlife Collection (now Biodiversity Research and Teaching Collection; BRTC) for this study.

*Aspidoscelis scalaris*: TCWC 71833, 72513, 72742, 76354, 79768, 79769, 80510, 80511, 85999, *Aspidoscelis marmorata*: TCWC 91387, 91389, 91396, 91429, 91447, 91448, 91449, 91476, 91477, 91478 *Aspidoscelis inornata*: TCWC 48569, 71724, 71827, 72473, 72749, 72782, 78634, 81621, 81663 *Cophosaurus texanus*: TCWC 62837, 64733, 64734, 64735, 64736, 66998, 68208, 69517, 92139, 93525, *Sceloporus consobrinus*: TCWC 5739, 5760, 5762, 5786, 5787, 5791, 5792, 8859, 9337 *Uta stansburiana*: TCWC 91390, 91392, 92129, 92197, 92202, 92204, 92206, 92207, 92208, 93542, *Sceloporus magister* TCWC 12885, 12286, 23410, 23411, 33270, 62949, 99910, 66986, 88156, 93539, *Phrynosoma modestum* TCWC 62893, 62894, 64728, 76025, 76027, 76030, 77652, 79148, 88062, 88063.

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