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ORIGINAL PAPER

Response of lizard community structure to desert grassland restoration mediated by a keystone rodent

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Abstract Many grasslands in the Chihuahuan Desert have transformed to shrublands dominated by creosotebush (*Larrea tridentata*). Grassland restoration efforts have been directed at controlling creosotebush by applying herbicide over large spatial scales. However, we have a limited understanding of how landscape-scale restoration affects biodiversity. We examined whether restoration treatments in southern New Mexico, USA have influenced the community structure of lizards, which are sensitive to shrub encroachment. We compared lizard community structure on 21 areas treated with herbicide from 7 to 29 years ago with paired untreated areas that were dominated by shrubs and matched by geomorphology, soils, and elevation. To examine mechanisms underlying responses to restoration, we tested whether the abundance of a grassland specialist, *Aspidoscelis uniparens*, depended on time since treatment, treatment area and isolation, and local habitat quality. Because lizards use rodent burrows as habitat, we tested whether community structure and *A. uniparens* abundance depended on the abundance of the keystone rodent, *Dipodomys spectabilis*. Treated areas had reduced shrub cover and increased grass cover compared to untreated areas. Lizard community composition differed strongly between areas, with four species responding to treatments. Divergence in community composition between treated–untreated pairs was greatest for old treatments ($\geq$22 years), and community composition was influenced by *D. spectabilis*. In particular,

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the abundance of *A. uniparens* was greatest on old treatments with a high density of *D. spectabilis*. Overall, our results demonstrate lizard community structure responds to grassland restoration efforts, and keystone species can shape restoration outcomes. Reestablishment of keystone species may be a critical constraint on the recovery of animal biodiversity after habitat restoration.

Keywords *Aspidoscelis* spp. · *Dipodomys spectabilis* · Desertification · Grassland restoration · Keystone species · Shrub encroachment

Introduction

Shrub encroachment into arid and semiarid grasslands has occurred worldwide over the last century (Burrows et al. 1990; Van Auken 2000; Moleele et al. 2002). Livestock overgrazing, fire suppression, and drought have led to increased shrub cover, increased soil erosion, decreased water infiltration, and nutrient redistribution (Schlesinger et al. 1990). Wildlife species are also affected by changes in plant composition. At local scales, alterations in habitat heterogeneity and food resources can affect species distribution, abundance, and community structure (Whitford 1997; Krogh et al. 2002; Bestelmeyer 2005; Valone and Sauter 2005). At landscape scales, the loss and spatial isolation of grassland habitat can lead to the decline of grassland or savanna-dependent species (e.g., Blaum et al. 2007).

Shrub removal has been initiated in desertified ecosystems in an attempt to restore grass cover. In the northern Chihuahuan Desert of the southwestern United States, encroachment by creosotebush (*Larrea tridentata*) and honey mesquite (*Prosopis glandulosa*) has decreased grassland habitat (Buffington and Herbel 1965; Grover and Musick 1990; Peters et al. 2006). Removal of creosotebush in southern New Mexico is accomplished by herbicide application, often at large spatial scales. Since 1980, the United States Bureau of Land Management (BLM) has applied herbicide to >90,000 ha of public land in southern New Mexico (P. Smith, personal communication). Historical restoration efforts were primarily aimed at increasing forage production for livestock, and herbicide application can be effective at reducing creosotebush cover and increasing grass cover (Perkins et al. 2006). Restoration efforts were expanded starting in 2005 under the Restore New Mexico program with an explicit goal of improving habitat for wildlife. Animal biodiversity can provide essential ecosystem services (e.g., Ostfeld and Keesing 2000), and protection of wildlife is regarded as an important component of stewardship on public lands (Burger 2002). Although it is generally assumed that animals respond positively to habitat restoration, this assumption is rarely tested.

Diversity of lizards is high in arid regions (Pianka 1973), and desert lizards function as important consumers of terrestrial arthropods (e.g., ants and termites; Whitford and Bestelmeyer 2006) and prey for a variety of vertebrates (Pianka 1986). Grassland restoration could have a strong impact on lizard community structure. Lizard species have specialized patterns of space use that are directly tied to vegetation composition and cover (e.g., widely-foraging in open spaces vs. sit-and-wait under vegetation; Pianka 1966, 1973; Reilly et al. 2007). Vegetation structure also affects species distribution and abundance by mediating prey abundance (Jones 1981), predation risk (Hawlena and Bouskila 2006), and availability of refuge (Davidson et al. 2008). Thus, lizard community structure can depend strongly on the plant community (Pianka 1966), and lizard communities are sensitive to changes in vegetation cover and microhabitat diversity resulting from shrub encroachment

(Jones 1981; Meik et al. 2002; Menke 2003). However, it is unknown how lizard communities respond to grassland restoration efforts at landscape scales.

We addressed the hypothesis that lizard community structure (i.e., species richness, diversity, evenness, composition) changes in response to landscape-scale efforts to restore perennial grasslands in the Chihuahuan Desert in southern New Mexico. The relative abundance of lizards was documented on replicated areas treated with herbicide to target creosotebush and paired shrub-dominated areas that were untreated. Based on comparisons of community structure of lizards between shrubland and grassland habitats (Menke 2003; Castellano and Valone 2006), we predicted there would be no difference in species richness, evenness, or diversity between treated and untreated areas. However, given the links between vegetation structure and the realized niche of individual species (e.g., space use, food resources), we expected the assemblage of lizard species to vary between treated and untreated areas.

We also evaluated potential mechanisms underlying the response of species to habitat restoration in two ways. First, we tested whether community composition was related to time since herbicide treatment, vegetation and habitat structure, and abundance of the banner-tailed kangaroo rat (*Dipodomys spectabilis*). *Dipodomys spectabilis* is a keystone species that modifies vegetation patterns through selective herbivory and granivory (Guo 1996; Schooley et al. 2000; Davidson and Lightfoot 2006), and it plays an engineering role by constructing large mounds that provide refuge for wildlife species (e.g., Hawkins and Nicoletto 1992; Davidson and Lightfoot 2007). Davidson et al. (2008) showed that lizard abundance was related positively to the availability of mounds of burrowing rodents. However, the distribution of *D. spectabilis* is restricted by shrub cover (Krogh et al. 2002), and the species has limited dispersal abilities (Skvarla et al. 2004). Thus, *D. spectabilis* may exhibit a lagged response to grassland restoration. If the abundance of *D. spectabilis* influences lizard community composition, there may also be time lags in the response of lizards to restoration. Second, we conducted a detailed analysis of the abundance of the desert grassland whiptail (*Aspidoscelis uniparens*), which is associated with grasslands (Menke 2003). We were particularly interested in understanding the relative importance of local and landscape-scale constraints on the response of *A. uniparens* to grassland restoration. We evaluated how the abundance of *A. uniparens* depended on treatment area and isolation, time since herbicide treatment, and habitat quality factors (i.e., vegetation structure and density of *D. spectabilis*).

Materials and methods

Study area

We conducted the study in a 44 120-km^2 area in the northern Chihuahuan Desert centered near Hatch, New Mexico (Fig. 1). Dominant shrubs in the region include *L. tridentata*, *P. glandulosa*, *Flourensia cernua*, *Ephedra trifurca,* and *Atriplex canescens*. The dominant grasses are *Sporobolus* spp., *Pleuraphis mutica*, *Bouteloua eriopoda*, *Muhlenbergia porteri*, and *Scleropogon brevifolius*. Other common plants include *Yucca torreyi* and the subshrub *Gutierrezia sarothrae*. Average annual precipitation is 240 mm, with >60 % of precipitation occurring from June to October (data from the Jornada Experimental Range, Fig. 1; Throop et al. 2011).

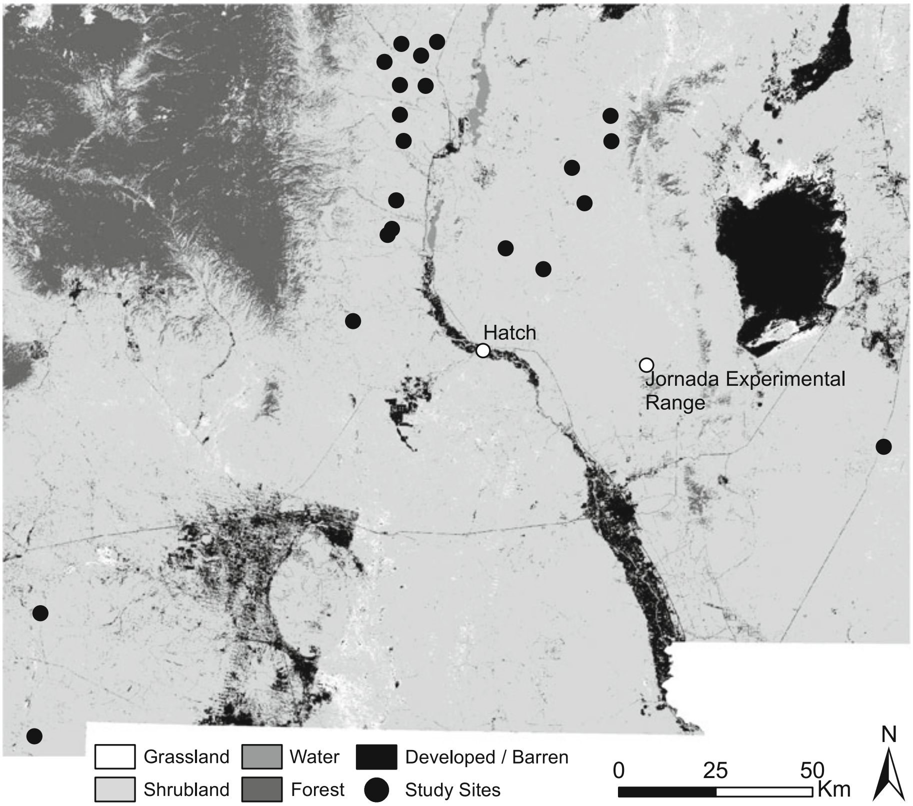

Fig. 1 Map of study sites and land cover in the study region in southern New Mexico, USA. Paired treated–untreated areas were located at each study site. The USDA Cropland Data Layer Map (http://www.nass.usda.gov/research/Cropland/SARS1a.htm) from 2010 was used to generate the land cover map. Hatch, New Mexico and the Jornada Experimental Range are indicated on the map

Sampling design

We selected 21 sites treated with the herbicide tebuthiuron (TEB) used to target creosotebush. Sites were treated with TEB by the BLM at a standard rate of 0.56 kg/ha between 1982 and 2004. The average area of TEB application (i.e., "treated areas") was 946 ha (range = 265–2,317 ha), and the shape of treatments varied among areas. For each treatment area, we also established a paired shrub-dominated area that was not treated with TEB. The distance between treated and untreated areas within pairs was ≤4.5 km, and pairs were matched by geomorphology, soil type, and elevation. The average elevation of treated and untreated areas was 1,509 m (range = 1,260–1,756 m).

Within each treated and untreated area, we used ArcGIS (ESRI, Redlands, California, USA) to generate a pool of 8–10 belt transects that were 1,000 × 60 m (length × width). Transects were at least 300 m apart and 100 m from major roads. From this pool, we randomly selected two transects for lizard sampling. Due to logistical constraints, transects within treated and untreated areas were separated by ≤1.5 km.

Lizard surveys

We used visual surveys to count lizards at each transect within treated and untreated areas (Germaine and Wakeling 2001; Meik et al. 2002; Davidson et al. 2008). All transects for a single treated–untreated pair were sampled on a single day between 25 July and 2 September 2011. Each belt transect was subdivided into two 1,000 × 30 m sections, and a single observer was randomly assigned to each section. We completed surveys between 800 and 1315. Observers walked in a serpentine path along the 1,000-m length of each section and searched the ground for lizards. Binoculars were used to identify lizards to species. Individuals that could not be confidently identified were excluded from analyses. Search time was recorded for each observer, and abundances for each species were pooled across the two transects within each area. Abundances were standardized by search effort (lizards/observer hours) for all analyses.

We took two steps to avoid bias due to differential detection probability between treated and untreated areas. First, the same two observers conducted lizard surveys concurrently on each belt transect. Second, to avoid bias associated with temperature-dependent lizard activity, we alternated between starting surveys on treated versus untreated areas each day. We also used occupancy modeling (MacKenzie et al. 2006; Kendall and White 2009) and information theory (Burnham and Anderson 2002) to demonstrate that detection probability did not strongly differ between treated and untreated areas for five of the six species analyzed (Appendix A, Supplementary Material). Species observed at <5 areas were excluded from analyses. We also excluded species with low detection probability (e.g., arboreal species, species with cryptic coloration or motionless behavior).

Environmental covariates

To record habitat structure, we established two 50-m transects at each belt transect. Transects were located 30 m from the center and at opposite ends of each belt transect. The line-point-intercept method was used to quantify cover by grasses, live shrubs, rocks (gravel and cobble), and bare soil (Herrick et al. 2005). Habitat variables were averaged across vegetation transects located within treated and untreated areas.

We conducted visual surveys to count mounds of *D. spectabilis* within each belt transect used to sample lizards. Mounds of *D. spectabilis* are 2–5 m in diameter and up to 0.5 m tall (Cross and Waser 2000) and easily detected during visual surveys. Mounds were counted during lizard surveys, and we assessed mound activity using animal sign (e.g., open burrows, fresh digging, tail drag marks, seed husks; Jones 1984, Krogh et al. 2002). A single mound is generally occupied by a single adult, and a count of active mounds is highly correlated with mark-recapture estimates of adult population size ($r^2 = 0.96$; Cross and Waser 2000).

Data analysis

Wilcoxon signed rank tests were used to compare habitat structure and lizard community indices (species richness, evenness, and diversity) between treated and untreated areas. We used the Shannon diversity index and Pielou's (1969) index of evenness. To evaluate whether lizard species composition differed between treated and untreated areas, we used a blocked multi-response permutation procedure (MRBP; Mielke and Berry 1982). We used site as the blocking factor, Euclidean distances, and within-block median alignment. The wilcox.test function in program R (v. 2.15.0; R Development Core Team 2012) was used to conduct the Wilcoxon signed rank tests, and PC-ORD (McCune and Mefford 1999) was used to conduct the MRBP.

We used nonmetric multidimensional scaling (NMDS; Kruskal 1964) to visualize potential gradients in species composition between treated and untreated areas. We used Bray–Curtis distances and limited the ordination to two axes. To explore a possible lagged response of lizard community composition to herbicide treatment, we defined treatments as either young (treated 1994–2004) or old (treated 1982–1989). In addition to evaluating whether sites clustered in ordination space based on treatment age, we used a t test to determine whether Bray–Curtis distances between treated–untreated pairs were greater for old treatments than for young treatments. The vegan package (Oksanen et al. 2011) in program R (v. 2.15.0; R Development Core Team 2012) was used to calculate Bray–Curtis distances (vegdist function) and to conduct the NMDS (metaMDS function).

To examine how community composition correlated with environmental factors, we used the envfit function in the vegan package in R (Oksanen et al. 2011). In this procedure, fitted vectors depict how environmental factors correlate with the NMDS ordination (e.g., Pillsbury et al. 2011). Fitted vectors are calculated using a linear model in which the value of an environmental factor is the dependent variable, and the NMDS axes are the independent variables. The direction of each vector in the ordination indicates the most rapid rate of change of an environmental factor, and the length of each vector is proportional to model fit, r^2. A P value was calculated for each environmental factor using 10,000 Monte Carlo permutations. Environmental factors included shrub cover, grass cover, rock cover, bare soil, elevation, and the density of active mounds of *D. spectabilis*. To improve linearity, we used the natural logarithm of grass cover and the square root of *D. spectabilis* mound density.

Generalized linear mixed models (GLMM) were used to evaluate the degree to which the abundance of individual species differed between treated and untreated areas. We specified a Poisson distribution for the response variables. Treatment was used as the fixed factor, and a random intercept was estimated for each site. GLMMs were conducted using the lmer function in package lme4 in R (Bates et al. 2011). We used an alpha of 0.10 for all hypothesis tests.

We used hierarchical partitioning (hier.part function in R; Walsh and Mac Nally 2008) to provide insight into the mechanisms underlying the response of the grassland-associated species, *A. uniparens*, to grassland restoration. Hierarchical partitioning was used to assess how treatment age (young vs. old), metapopulation factors (treatment area and isolation), and habitat quality factors (grass cover, shrub cover, and density of active mounds of *D. spectabilis*) affected the abundance of *A. uniparens* on treated areas. Hierarchical partitioning is useful for isolating the independent and joint effects of predictor variables that are collinear (Heikkinen et al. 2004). Independent and joint effects are computed by running models with all possible combinations of predictor variables and using the increase in the fit of models with a particular variable compared to the corresponding model without that variable (Mac Nally 2000; Heikkinen et al. 2004). Because intact, undisturbed grasslands are extremely limited in our study area, we calculated isolation as the distance to the nearest area treated with herbicide, including treated areas that were not part of this study. Distances were calculated between the center of each area. A Poisson distribution was specified for all models, and log-likelihood was used as the goodness-of-fit measure. Treatment area, isolation, and grass cover were ln-transformed. We defined *D. spectabilis* mound density as a categorical variable based on the median density ($\geq$1.4 mounds/ha = High, <1.4 mounds/ha = Low). We calculated pseudo r^2 (Dobson 2002) to estimate the percent variation in *A. uniparens* abundance explained by treatment age, metapopulation factors, and habitat quality factors.

Results

Habitat structure

Treatment with herbicide was highly effective at influencing vegetation cover (Fig. 2). Treated areas had less shrub cover ($V = 231$, $P < 0.001$) and greater grass cover ($V = 25$, $P = 0.002$) than untreated areas that were not treated with herbicide. Bare soil ($V = 84$, $P = 0.29$) and rock cover ($V = 156$, $P = 0.17$) did not differ between treated and untreated areas.

Lizard community structure

Overall, we identified 1,438 individual lizards representing 13 species. Five species were observed at <5 areas and were excluded from further analyses: *A. exsanguis*, *A. neomexicana*, *Cophosaurus texanus*, *Gambelia wislizenii*, and *Urosaurus ornatus*. *Phrynosoma cornutum* and *Sceloporus cowlesi* were also excluded because of low detection probability. The remaining six species represented 97 % of all identified lizards and were included in all analyses: little striped whiptail (*Aspidoscelis inornata*), checkered whiptail (*A. tesselata*), tiger whiptail (*A. tigris*), *A. uniparens*, greater earless lizard (*Holbrookia maculata*), and common side-blotched lizard (*Uta stansburiana*). *Aspidoscelis uniparens* was the most frequently observed species (61 % of all identified lizards).

There were no differences in lizard species richness ($V = 50$, $P = 0.57$), evenness ($V = 119$, $P = 0.61$), or diversity ($V = 96$, $P = 0.75$) between treated and untreated areas (Appendix B: Fig. B1, Supplementary Material). However, species composition differed between treated and untreated areas (MRBP test, $T = -1.91$, $P = 0.05$). This treatment

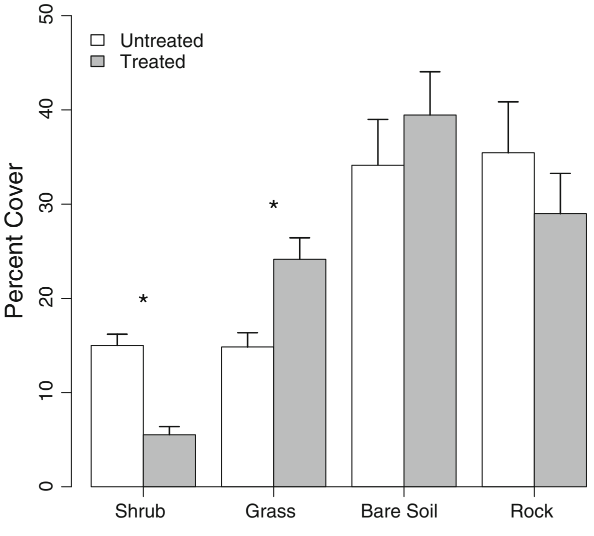

Fig. 2 Comparison of mean (+ 1 SE) vegetation, soil, and rock cover between areas treated with the herbicide tebuthiuron and paired untreated ($n = 21$) in southern New Mexico, USA. *Asterisk* (*) indicates a significant difference ($P \leq 0.05$) between treated and untreated areas based on a Wilcoxon signed rank test

effect was corroborated by the GLMM analyses for individual species and the NMDS ordination (see below).

Abundance differed between treated and untreated areas for four lizard species (Fig. 3). Abundance was greater on treated areas for *A. inornata* (beta estimate = 1.67, SE = 0.51, $P < 0.001$) and *A. uniparens* (beta estimate = 0.48, SE = 0.072, $P < 0.001$), whereas abundance was greater on untreated areas for *A. tesselata* (beta estimate = −0.91, SE = 0.31, $P = 0.003$) and *A. tigris* (beta estimate = −0.33, SE = 0.13, $P = 0.01$). There was no difference in abundance for *U. stansburiana* between treated and untreated areas, and *H. maculata* was marginally greater on treated than on untreated areas (beta estimate = 0.59, SE = 0.42, $P = 0.16$).

The NMDS ordination (stress = 11.5 %) revealed three site groupings (Fig. 4a). Within groupings, the lizard community was dominated by one of three sets of species: *A. inornata*; *A. tigris* and *U. stansburiana*; and *A. tesselata, A. uniparens*, and *H. maculata*. Treated–untreated pairs typically clustered together in ordination space. However, within groupings, treatments tended to be shifted in a consistent direction in ordination space compared to their paired untreated areas. This pattern was most evident for sites with high values on the first NMDS axis. Untreated areas at these sites were dominated by *A. tesselata*, whereas paired treatments were dominated by *A. uniparens* and *H. maculata*.

Divergence in lizard community composition between treated–untreated pairs depended on treatment age. Specifically, Bray–Curtis distances were greater for old treatments than for young treatments (Fig. 4a; $t = 1.90$, $P = 0.076$). Treated areas also tended to separate by age along the first NMDS axis (Fig. 4a). This separation was explained in part by the density of active *D. spectabilis* mounds (Fig. 4b; $r^2 = 0.17$, $P = 0.026$). Scores on the first axis for treated areas only were strongly correlated with mound density ($r_p = 0.58$), but this was not the case for untreated areas ($r_p = 0.12$). Thus, the correlation of mound density to the ordination was primarily driven by *D. spectabilis* activity on treated areas. Overall, elevation exhibited the strongest correlation with the ordination (Fig. 4b; $r^2 = 0.66$, $P < 0.001$). Rock cover ($r^2 = 0.15$, $P = 0.041$) and bare soil ($r^2 = 0.12$, $P = 0.073$) were also correlated with the ordination, but shrub cover ($r^2 = 0.023$, $P = 0.64$) and grass cover ($r^2 = 0.0031$, $P = 0.94$) were not (Fig. 4b).

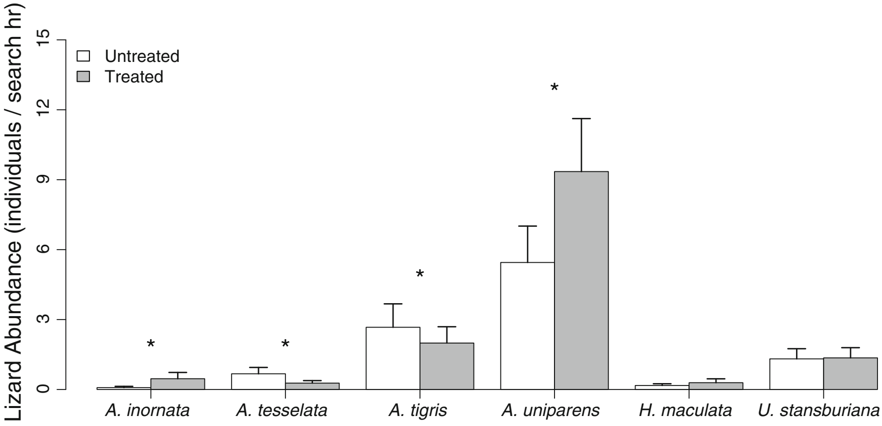

Fig. 3 Comparison of mean (+ 1 SE) lizard abundance for six species between areas treated with the herbicide tebuthiuron and untreated areas ($n = 21$) in southern New Mexico, USA. *Asterisk* (*) indicates a significant difference ($P \leq 0.05$) between treated and untreated areas based on generalized linear mixed models

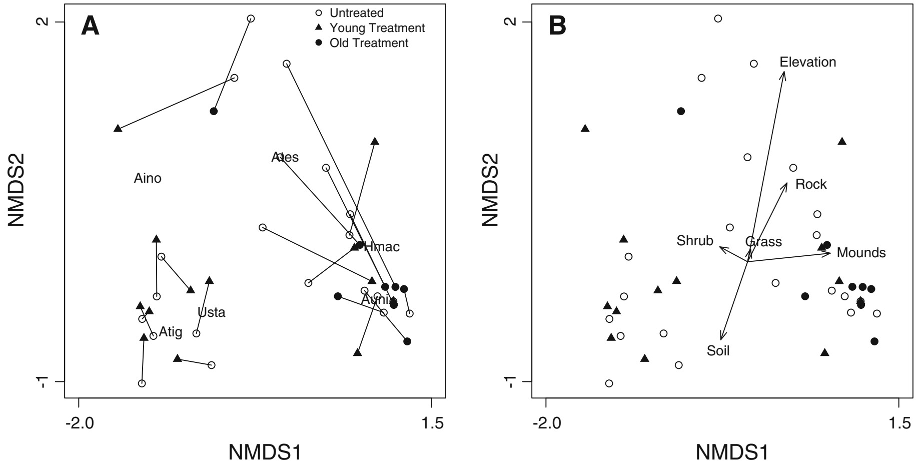

Fig. 4 Nonmetric multidimensional scaling of lizard species composition at 21 areas treated with tebuthiuron herbicide (*filled circles* and *triangles*) and paired untreated areas (*open circles*) in southern New Mexico, USA. Areas were treated with herbicide between 1982 and 1989 (*filled circles*) or 1994 and 2004 (*filled triangles*). Treated–untreated pairs are connected by *lines* and species scores are indicated by abbreviations **a** Aino = *Aspidoscelis inornata*, Ates = *Aspidoscelis tesselata*, Atig = *Aspidoscelis tigris*, Auni = *Aspidoscelis uniparens*, Hmac = *Holbrookia maculata*, Usta = *Uta stansburiana*. Fitted vectors **b** represent the correlation of environmental factors with the ordination. Vector arrows indicate the direction of the most rapid rate of change of environmental factors, and the length of each vector is proportional to r^2. "Mounds" indicates active mound density of *Dipodomys spectabilis*. See **a** for symbol legend

Response of *Aspidoscelis uniparens* to grassland restoration

Treatment age, metapopulation factors, and habitat quality factors accounted for 29 % (pseudo r^2) of the variation in *A. uniparens* abundance. Hierarchical partitioning revealed that treatment age and the abundance of *D. spectabilis* mounds had considerable independent effects on *A. uniparens* abundance (Fig. 5). The abundance of *A. uniparens* was ~3 times higher on old treatments than young treatments (Fig. 6a; $P < 0.001$), whereas *A. uniparens* abundance was greatest on treated areas with a high density of *D. spectabilis* mounds (Fig. 6b; $P < 0.001$). A substantial portion of the explained variation was also due to joint effects for treatment age and *D. spectabilis* mound density. The independent and joint contributions of habitat area, isolation, grass cover, and shrub cover were all low (Fig. 5). The negative joint contribution of shrub cover indicated that it was a suppressor variable (albeit a weak one), which suppressed the independent contribution of other variables (Mac Nally 2000).

Discussion

Our results show that lizards respond to landscape-scale efforts to remove creosotebush and restore perennial grasslands in the Chihuahuan Desert. Herbicide application was effective at reducing shrub cover and increasing grass cover. Although lizard community indices were similar between treated and untreated areas, shrub removal strongly affected community composition. The relative abundances of lizards varied between treated and untreated areas, and differences in community composition increased with treatment age.

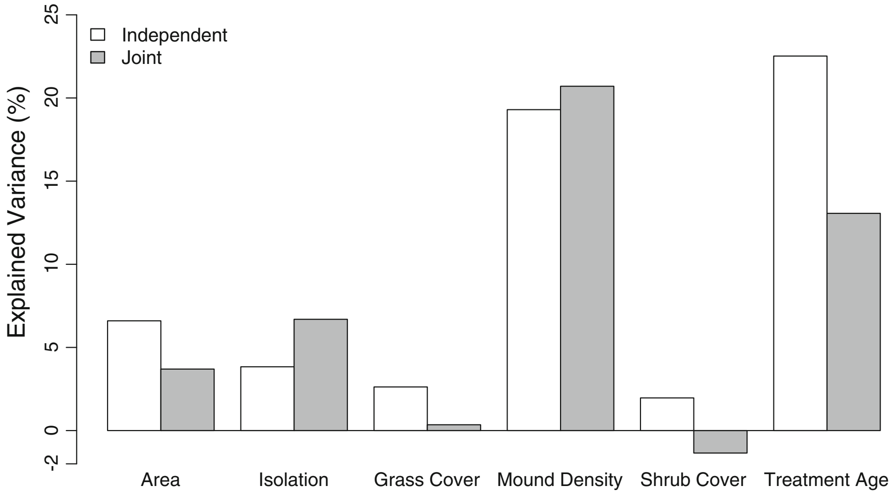

Fig. 5 Independent and joint effects of treatment age, metapopulation factors, and habitat quality factors on the abundance of *Aspidoscelis uniparens* in southern New Mexico, USA. Independent and joint effects were estimated using hierarchical partitioning and are expressed as a percentage of the total variation explained. "Mound density" indicates active mound density of *Dipodomys spectabilis*

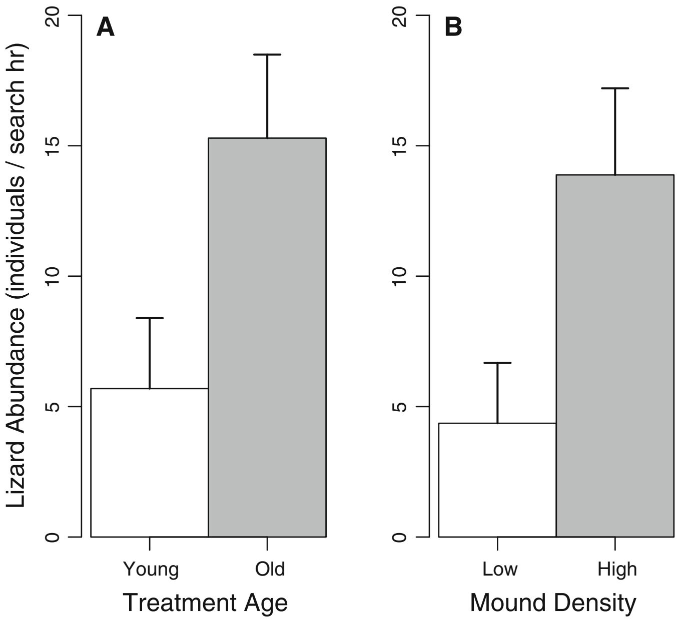

Fig. 6 Effects of **a** treatment age and **b** density of active *Dipodomys spectabilis* mounds on the mean (+ 1 SE) abundance of *Aspidoscelis uniparens* on treated areas in southern New Mexico, USA. "Mound density" indicates active mound density of *Dipodomys spectabilis*

Furthermore, differences in community composition were related to the abundance of *D. spectabilis*, suggesting that keystone species can shape responses of lizard communities to grassland restoration. Our study illustrates the high degree of interdependence of restoration objectives in the Chihuahuan Desert ecosystem and the long time frame necessary to assess restoration efforts.

Species richness, diversity, and evenness of lizards were similar between treated and untreated areas, paralleling other comparisons of lizard communities between shrub-dominated and grassland habitats (Meik et al. 2002; Menke 2003; Castellano and Valone 2006). However, we found considerable variation in community composition. First, the ordination revealed three assemblages differentiated by environmental gradients, primarily elevation. *Aspidoscelis inornata* and *A. tesselata* were represented at high-elevation sites, whereas *A. tigris, A. uniparens, H. maculata,* and *U. stansburiana* were represented more at mid- to low-elevation sites. Elevation affects lizard distribution and abundance by creating gradients in temperature (Fischer and Lindenmayer 2005), vegetation structure (Meik and Lawing 2008), and rock cover (Monasterio et al. 2010). In our system, elevation was correlated with rock cover and bare soil, but it was not correlated with vegetation cover (Fig. 4b). Given that elevation was more strongly correlated with the ordination than was rock cover or bare soil, changes in community composition along the elevation gradient likely reflected changes in environmental temperature.

Second, community composition was influenced by restoration treatments. The ordination revealed differentiation in community composition between treated–untreated pairs within the three site groupings, and four of the six species differed in abundance between treated and untreated areas. Given our paired study design, which controlled for elevation and geomorphology at the site level, observed differences in abundance likely reflect a direct response of each species to shrub removal. Habitat preferences were generally consistent with previous studies for each species (e.g., Christiansen et al. 1971; Whitford and Creusere 1977; Baltosser and Best 1990; Schall 1993; Menke 2003). *Aspidoscelis tigris* is associated with shrublands and occurred at highest abundance on untreated areas, whereas *A. inornata* and *A. uniparens* are associated with grasslands and occurred at highest abundance on treatments. *Aspidoscelis tesselata* was most abundant on untreated areas, but this pattern could reflect greater detection probability on untreated than treated areas (Appendix A, Supplementary Material).

Studies on the response of lizards to habitat restoration have assessed practices including prescribed burning (Mushinsky 1992; Litt et al. 2001; Templeton et al. 2011), livestock removal (Castellano and Valone 2006), and non-native plant removal (Bateman et al. 2008). Consistent with our findings, these studies show effects of restoration practices on lizards are largely species-specific. By evaluating community composition at replicated treated and untreated areas across a broad region, our results demonstrate that restoration changes lizard assemblages at the local scale, which should increase beta diversity at the landscape scale.

The difference in community composition between treated–untreated pairs depended on treatment age. Divergence in community composition was greater for old treatments than for young treatments, indicating a lagged response to restoration. This pattern was likely driven by the slow response of *A. uniparens*, the most abundant species in our system. Specifically, the abundance of *A. uniparens* was greater on old treatments than young treatments. Given the lack of large, undisturbed grasslands in our study area (Fig. 1), low average abundance of *A. uniparens* on young treatments could indicate slow colonization from source populations or limited immigration after herbicide application. However, occupancy probability for *A. uniparens* was similar between treated and untreated areas (BJ Cosentino, unpublished data), suggesting remnant populations occur in creosotebush-dominated habitats before herbicide application. Furthermore, immigration is an unlikely constraint because isolation was not a strong predictor of *A. uniparens* abundance. Because the abundance of *A. uniparens* did not depend on treatment area either, metapopulation factors in general had limited value for predicting the response of *A. uniparens* to grassland restoration.

An alternative explanation for the lagged response of *A. uniparens* abundance is that habitat quality for this species is low at sites during early stages of restoration trajectories. Vegetation structure is a direct component of habitat quality that changes with time since herbicide application, but shrub and grass cover were not important predictors of community composition or the abundance of *A. uniparens*. However, vegetation may indirectly affect the response of lizards to restoration by controlling the abundance of ecosystem engineers (e.g., Shenbrot et al. 1991; Davis and Theimer 2003; Shipley and Reading 2006). Banner-tailed kangaroo rats function as engineers by constructing mounds that provide critical space for thermoregulation, foraging, and refuge during predation attempts (Davidson et al. 2008). Davidson et al. (2008) found lizard abundance was greater on *D. spectabilis* mounds than on nearby areas off mounds, and lizard abundance was greatest in areas with mounds constructed by *D. spectabilis* and Gunnison's prairie dogs (*Cynomys gunnisoni*). Consistent with this pattern at a regional scale, we found that lizard community composition was sensitive to the density of *D. spectabilis*—particularly on areas treated with herbicide—and that there was a strong, positive effect of *D. spectabilis* density on the abundance of *A. uniparens*. Because *D. spectabilis* is negatively affected by creosotebush cover (Krogh et al. 2002), our results indicate shrub removal indirectly affects lizard community composition by mediating the abundance of *D. spectabilis*.

The slow increase in abundance of *A. uniparens* likely occurred in response to a lagged response of *D. spectabilis* to shrub removal. Young treatments had high shrub cover and low density of *D. spectabilis*, whereas old treatments had low shrub cover and high density of *D. spectabilis* (BJ Cosentino, unpublished data). The abundance of *A. uniparens* may have been constrained on young treatments by limited refuge space constructed by *D. spectabilis*. This hypothesis is supported by the hierarchical partitioning analysis. Treatment age and density of *D. spectabilis* had the greatest joint contribution in explaining the abundance of *A. uniparens*, indicating that some of the variation in *D. spectabilis* density among sites is explained by treatment age. However, treatment age and density of *D. spectabilis* also had strong independent effects. The independent effect of *D. spectabilis* indicates that kangaroo rats had a direct effect on *A. uniparens* abundance, whereas the independent effect of treatment age suggests that lizards responded to additional aspects of habitat quality correlated with treatment age (e.g., predator abundance; Hawlena and Bouskila 2006).

Burrowing rodents can function as keystone species by having dramatic impacts on vegetation structure and animal communities in desert ecosystems (Heske et al. 1993; Kotliar et al. 1999; Schooley et al. 2000; Davidson et al. 2008). Our results indicate that burrowing rodents may also play a key role in controlling the response of wildlife species to habitat restoration, most likely through their engineering effects. However, keystone rodents have been negatively impacted by desertification (Whitford 1997; Krogh et al. 2002) and eradication programs (Delibes-Mateos et al. 2011), and little is known about the response of these species to habitat restoration. When the goal is to restore habitat for wildlife, our results support the notion that the success of restoration can depend in part on the reestablishment of keystone species (Hobbs and Cramer 2008). Studies on mechanisms underlying the response of keystone species to restoration should be useful for generating management recommendations to facilitate the recovery of animal biodiversity.

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