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RESEARCH ARTICLE

Constraints and time lags for recovery of a keystone species (*Dipodomys spectabilis*) after landscape restoration

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Abstract Habitat restoration is typically focused on reestablishing suitable conditions at a local scale, but landscape constraints may be important for keystone species with limited dispersal. We tested for time lags and examined the relative importance of local and landscape constraints on the response of the banner-tailed kangaroo rat (*Dipodomys spectabilis*) to restoration of Chihuahuan Desert grasslands in New Mexico, USA. *Dipodomys spectabilis* is a keystone species that creates habitat heterogeneity and modifies the structure of plant and animal communities. We selected 21 sites and compared density of *D. spectabilis* between areas treated with herbicide to control shrubs (treated areas) and paired untreated areas. We evaluated whether density of *D. spectabilis* depended on treatment age, local habitat quality (vegetation and soil structure), and landscape factors (treatment area and spatial connectivity). Density was greater at treated areas than at untreated areas due to a direct effect of reduced shrub cover. However, the response of *D. spectabilis* to restoration was lagged by a decade or more. Structural equation modeling indicated the time lag reflected a dispersal constraint as opposed to a temporal change in habitat quality. This inference was corroborated by a positive relationship between density at treated areas and connectivity to source populations. Our results indicate that density of *D. spectabilis* depended strongly on the spatial configuration of treated areas, which supports a landscape mosaic approach to restoration. If keystone species commonly exhibit limited dispersal ability, landscape constraints may be broadly important for shaping ecosystem structure and function after habitat restoration.

Keywords Colonization · Connectivity · Conservation · Desertification · Dispersal · Ecosystem engineer · Grassland · Kangaroo rat · Shrub encroachment

Introduction

Keystone species interact strongly with other species through habitat modification, mutualism, competition,

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and predation (Power et al. 1996; Soulé et al. 2005). Because their loss can have cascading effects on community composition across trophic levels (e.g., Crooks and Soulé 1999; Estes et al. 2011), keystone species are critical targets for biodiversity conservation (Lindenmayer et al. 2008). In the context of ecological restoration, reintroduction of keystone species can be important for restoring ecosystem structure and function (Ripple and Beschta 2004; Gibbs et al. 2008). Although ecosystem restoration may be promoted by prioritizing the recovery of keystone species (Palmer et al. 1997; Hobbs and Cramer 2008), successful restoration requires an understanding of factors that constrain responses of keystone species at local and landscape scales.

Responses of species to disturbance are increasingly addressed at multiple spatial scales, but restoration ecology has lagged behind in embracing the concept of scale-dependence. Brudvig (2011) reviewed studies that addressed constraints on restoration outcomes and found 97 % of studies assessed site-level factors, whereas only 11 % considered landscape factors. Reestablishing suitable abiotic and biotic conditions at single sites is often essential for facilitating recovery of target species (e.g., Brawn 2006), but restoration outcomes also can depend on landscape factors (Scott et al. 2001; Matthews et al. 2009). For example, recolonization of restoration sites by target species may be constrained by inadequate connectivity to source populations, and dispersal could maintain long-term persistence through rescue effects (Brown and Kodric-Brown 1977). Given increased institutional demand for restoration approaches that can be applied at broad scales (Menz et al. 2013), developing a mechanistic understanding of scale-dependent constraints on keystone species will help guide decisions about site selection and management to restore degraded ecosystems.

A complex interaction of overgrazing by livestock, drought, fire suppression, and cross-scale feedbacks has led to replacement of grasslands with shrublands in semiarid landscapes throughout the world (e.g., Van Auken 2000; Peters et al. 2006). In the Chihuahuan Desert of southern New Mexico, USA, encroachment by native shrubs—predominately creosotebush (*Larrea tridentata*) and honey mesquite (*Prosopis glandulosa*)—has greatly reduced desert grassland habitat (Grover and Musick 1990). The US Bureau of Land Management (BLM) initiated an extensive shrub-removal program >30 years ago that involves application of herbicide at large spatial scales. More than 200,000 ha of shrubland have been treated, and these efforts were intensified in 2005 with initiation of the Restore New Mexico program, which has an explicit goal to restore grasslands and grassland-dependent wildlife. In general, herbicide applications reduce shrub cover and increase grass cover (Perkins et al. 2006; Cosentino et al. 2013; Supplementary Material 1), creating novel savannah ecosystems that have structural attributes intermediate between invaded shrublands and remnant grasslands (Coffman et al. 2014).

Our primary objective was to evaluate the relative importance of local and landscape-scale constraints on the response of the banner-tailed kangaroo rat (*Dipodomys spectabilis*) to grassland restoration efforts in southern New Mexico. We chose *D. spectabilis* because it is an indicator for desert grassland habitat due to its negative association with shrubs (Krogh et al. 2002; Waser and Ayers 2003) and its dependence on annual and perennial grasses, annual forbs, and seeds (Hope and Parmenter 2007). Furthermore, *D. spectabilis* functions as a keystone species by (1) greatly modifying vegetation structure through selective herbivory and granivory (Brown and Heske 1990; Guo 1996; Davidson and Lightfoot 2006), (2) constructing large mounds that create spatial heterogeneity (Schooley and Wiens 2001) and provide refuge for species from diverse taxa (Hawkins and Nicoletto 1992; Schooley et al. 2000; Davidson and Lightfoot 2007), and (3) outcompeting other small mammals for space and food through its large size and behavioral dominance (Bowers et al. 1987; Bowers and Brown 1992). *Dipodomys spectabilis* affects responses of other species to grassland restoration (Cosentino et al. 2013), and local or landscape-scale constraints on its density should impact restoration trajectories for many biodiversity components.

We predicted that the density of *D. spectabilis* would be greater at areas treated with herbicide than at untreated areas due to improved local habitat quality (i.e., decreased shrub cover, increased grass cover). However, we predicted *D. spectabilis* recovery would be constrained by factors at local and landscape scales. At the local scale, density may be limited by soil structure if shallow soils and soil instability inhibit mound construction (Krogh et al. 2002). At the landscape scale, density may be constrained by size of restoration treatments or distance to other source populations. *Dipodomys spectabilis* has limited dispersal abilities, with most individuals dispersing <100 m (Skvarla et al. 2004; Waser et al. 2006). Thus, we predicted that connectivity to source populations would be particularly important for increasing colonization probability and maintaining rescue effects at restoration sites. Finally, we examined whether *D. spectabilis* exhibited a lagged response to treatments, and we evaluated two hypotheses that could explain a positive relationship between density and treatment age. One hypothesis is that density depends indirectly on treatment age because local habitat quality (e.g., vegetation cover) is poor early in the restoration trajectory (Whitford 2002; Coffman et al. 2014). An alternative hypothesis is that density depends directly on treatment age because of limited dispersal and slow colonization. We used structural equation modeling (SEM) to evaluate the direct and indirect relationships between treatment age and the density of *D. spectabilis*.

Methods

Study area

We conducted our study on 21 sites in a 4,412,000-ha area in the northern Chihuahuan Desert centered near Hatch, New Mexico (Fig. 1; Supplementary Material 2). Each site included an area treated with the herbicide tebuthiuron to target creosotebush, which is the dominant shrub in this region. Other common shrubs included *P. glandulosa*, *Flourensia cernua*, *Ephedra trifurca,* and *Atriplex canescens*. Common grasses were *Sporobolus* spp., *Pleuraphis mutica*, *Bouteloua eriopoda*, *Muhlenbergia porteri*, and *Scleropogon brevifolius*, and other common plants included *Yucca torreyi* and the subshrub *Gutierrezia sarothrae*. Average annual precipitation is 240 mm, with most precipitation occurring from June to October (Throop et al. 2011).

Sampling design

Treated areas were treated once with herbicide at a rate of 0.56 kg/ha between 1982 and 2004 (7–29 years prior to our study). The size of treated areas ranged from 265 to 2,317 ha (mean = 946 ha, SE = 130 ha). At each site, we also established a paired sampling location that was dominated by creosotebush and not treated with herbicide. Treated and untreated areas at each site were within 4.5 km and had similar geomorphology, soil type, and elevation (range = 1,260–1,756 m). We established a pool of 6-ha belt transects (1,000 × 60 m) within treated and untreated areas using ArcGIS (ESRI, Redlands, California, USA), and two transects were randomly selected for sampling within each area. The distance between transects within treated or untreated areas was <1.5 km.

Kangaroo rat surveys

Dipodomys spectabilis mounds are 2–5 m in diameter, up to 0.5 m tall, can include 10 or more burrow openings, and require extensive construction that can take two years to complete (Best 1972). We used visual surveys to count the number of occupied mounds within each belt transect. Mounds are easily detected with visual surveys (Cross and Waser 2000; Schooley and Wiens 2001). A single adult generally occupies a single mound, and a count of occupied mounds is highly correlated with estimates of adult population size from mark-recapture studies ($r^2 = 0.96$; Cross and Waser 2000). Thus, we assumed a strong relationship existed between a count of occupied mounds and adult population size in our study area. We used animal sign (e.g., open burrows, fresh digging, tail drag marks, seed husks) to classify mounds as occupied or unoccupied by *D. spectabilis* (Schooley and Wiens 2001; Krogh et al. 2002). All belt transects on treated and untreated areas at a single site were sampled in a single day between 25 July 2011 and 02 Sept 2011. We subdivided belt transects into two 1,000 × 30-m sections, and we randomly assigned a single observer to each section. The same two observers conducted all surveys concurrently on each belt transect, and the observers had similar experience classifying mounds as occupied or unoccupied. Observers walked in a serpentine path along the length of each section, and all mounds were counted and classified as occupied or unoccupied. Because all belt transects were 6 ha, the number of occupied mounds on each belt transect was a measure of occupied mound density (hereafter “density”).

Environmental covariates

To evaluate whether an effect of herbicide treatment on *D. spectabilis* was mediated by changes in vegetation, we quantified plant cover at treated and

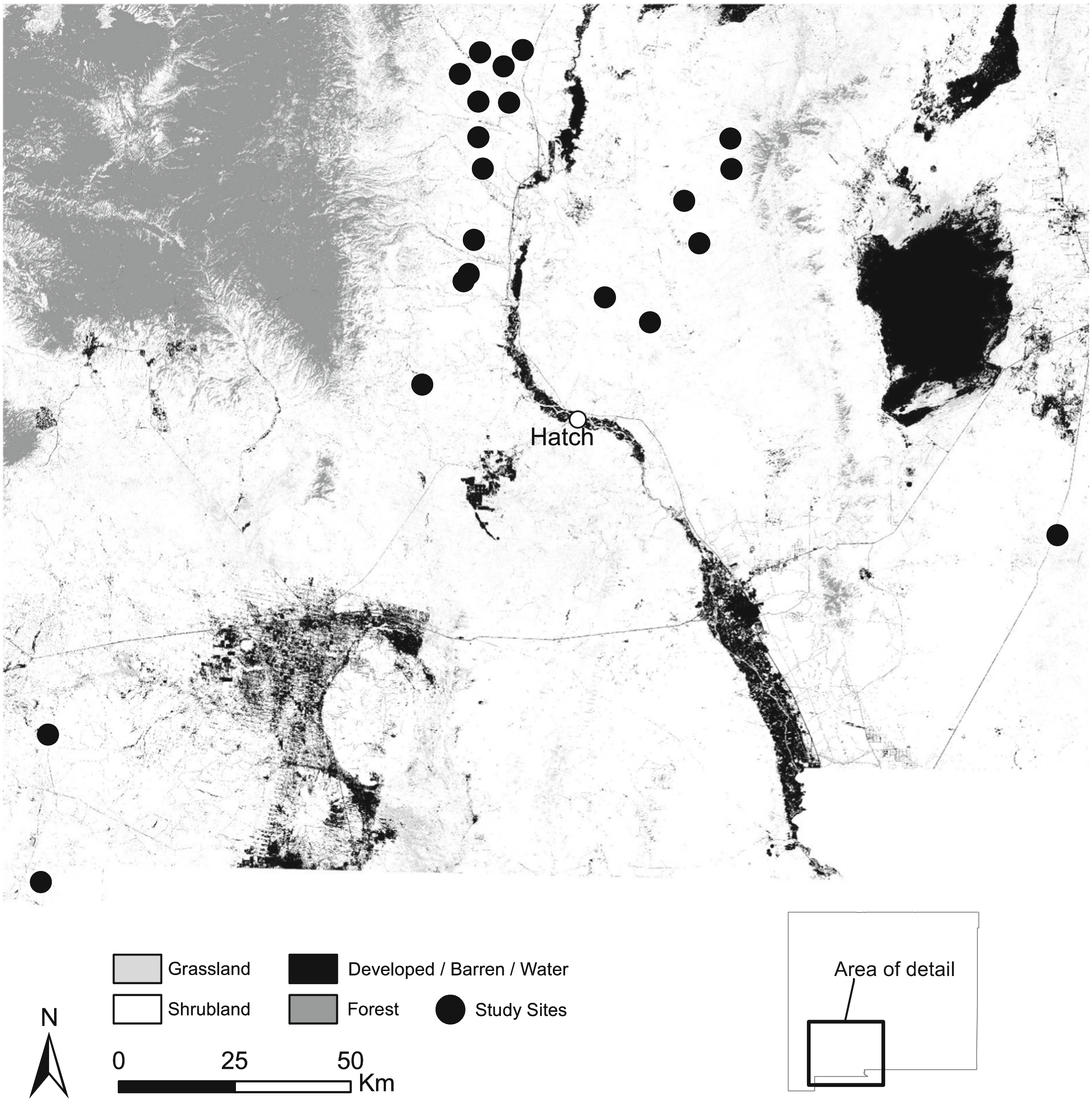

Fig. 1 Map of study sites and land cover in southern New Mexico, USA. *Circles* represent study sites with paired treated and untreated areas. See Supplementary Material 2 for a more detailed map in color with the spatial location of restoration treatments

untreated areas. Two 50-m transects were established on opposite halves of each belt transect (Coffman et al. 2014). Transect centers were separated by 450 m, and they were 30 m offset from the center and oriented parallel to the belt transect. We used the line-point-intercept method (LPI; Herrick et al. 2005) to quantify percent cover by grasses (perennial and annual) and shrubs (live and dead). We averaged vegetation cover across the two LPI transects within each belt transect.

To quantify soil profile characteristics of each area, we dug soil pits to a maximum 80 cm depth or to the top of a restrictive horizon at the center of each LPI transect. We classified each soil pit according to the presence or absence of a restrictive horizon (always indurated calcium carbonate) within 80 cm. Based on the four soil pits within each area, we then classified the area as either having restrictive horizons present at all four soil pits, or having restrictive horizons at <4 soil pits, the latter indicating greater ease of burrow excavation. We also classified each area according to dominant soil texture classes encountered in the subsoil horizons of the four pits, distinguishing those that were predominantly sandy (loamy sands to medium sandy loams) or not sandy (fine sandy loams, loams, gravelly sandy loams, gravelly loams, and gravelly sandy clay loams). Loose sandy soils were postulated to be difficult substrates for maintaining burrow structures compared to the other class.

To evaluate landscape-scale constraints on recovery of *D. spectabilis*, we measured the area and connectivity of treated areas with ArcGIS. We used a connectivity metric that includes a negative exponential dispersal kernel and incorporates distances to potential source populations (Hanski 1994; Moilanen and Nieminen 2002). Because undisturbed grasslands are extremely rare in our study region (Fig. 1), we defined source populations as areas treated with herbicide. We did not use all treated areas as potential source populations because of the short dispersal distances of *D. spectabilis* relative to the large spatial extent of our study area. For each target area, we calculated connectivity using all potential source treated areas within a buffer radius of 3 km, which is consistent with the scale of maximum dispersal by *D. spectabilis* (Skvarla et al. 2004). Connectivity (C_i) of treated area i was defined as

$$C_i = \sum_{j \neq i} \exp(-d_{ij})\, A_j'^{b}$$

where d_{ij} is the distance between target treated area i and source treated area j, A_j' is the effective area of source j, and b is a parameter scaling the association between abundance and source area. Effective area is the patch area (km^2) weighted by the age of source patches (Hanski 1994). Because the abundance of *D. spectabilis* was strongly related to treatment age (see "Results" section), we used treatment age as an index of the abundance of source populations. Effective area A_j' for source j was calculated as $Q_j A_j / Q^*$, where Q_j was the treatment age of source j, Q^* was the maximum treatment age of any potential source, and A_j was the area of source j (Hanski 1994; Schooley and Branch 2009). We set b as 0.5 because emigration is unlikely to have a linear relationship with source effective area (Moilanen and Nieminen 2002). Prugh (2009) showed that the performance of C_i is relatively insensitive to changes in b.

Statistical analysis

We used generalized linear mixed models (GLMM) to evaluate whether density of *D. spectabilis* differed between treated and untreated areas. The number of occupied mounds on each belt transect was the response variable. We specified a Poisson error distribution, and we included random effects of site and treatment nested within site. We examined the effect of treatment on density by comparing the fit of a model with a fixed effect of treatment to a null (intercept-only) model using Akaike's Information Criterion corrected for small sample size (AIC$_C$; Burnham and Anderson 2002). We also compared the null model to models with either a fixed effect of shrub cover or grass cover to evaluate the degree to which a treatment effect was mediated by vegetation. Grass cover was square-root transformed because of a large value. Shrub and grass cover were not included in the same model because of known collinearity (Bestelmeyer et al. 2009). All GLMMs were fit using the lmer function in package *lme4* (Bates et al. 2012) in program R (v. 2.15.1; R Development Core Team 2012).

To identify potential constraints and time lags in the response of *D. spectabilis* to restoration treatments, we first quantified differences in density of occupied mounds between paired treated and untreated areas (Δ = Treated − Untreated). For this analysis, density equaled the total number of occupied mounds across the two belt transects within an area divided by the total area of the two belt transects (12 ha). We then used general linear models (GLM) with a Gaussian error distribution to determine whether differences in density were explained by treatment age (number of years since treatment), area, connectivity, soil texture, and presence of a shallow restrictive zone. We evaluated support for 16 models with different combinations of covariates. The model set included a null model, five models with individual covariates, and 10 models with additive effects of two covariates. We used AIC$_C$ to evaluate the relative support for each model, and Akaike weights were summed across models with the same variable to assess the relative importance of potential constraints on restoration (Burnham and Anderson 2002). Each variable occurred in an equal number of models. GLMs were fit with the glm function in R (R Development Core Team 2012).

Structural equation modeling (Grace et al. 2010) is helpful for illuminating relationships among variables by assessing direct and indirect pathways (Grace et al. 2012). We used SEM to evaluate our two hypotheses that could explain the lagged response of *D. spectabilis* to restoration treatments (see "Results" section): (1) treatment age indirectly affects density of *D. spectabilis* due to changes in vegetation structure over time, and (2) treatment age directly affects density due to the limited dispersal ability of *D. spectabilis*. To evaluate these hypotheses, we used SEM for treated areas and included direct pathways between the density of occupied mounds and treatment age, shrub cover, and connectivity. We evaluated whether shrub cover mediated the effect of treatment age on mound density by including a direct effect of treatment age on shrub cover. We compared the strength of direct and indirect pathways between treatment age and mound density by comparing the strength and significance of standardized regression coefficients for each pathway. We also reported unstandardized coefficients because standardized coefficients can depend on variation in each variable (Grace and Bollen 2005). Site was included as a cluster variable to estimate robust standard errors. We used a χ^2 test to assess model fit. The SEM was fit with the lvm function in the package *lava* (Holst and Budtz-Joergensen 2012) in R.

Results

Overall, we counted 359 occupied mounds. A model with an effect of restoration treatment on density of *D. spectabilis* was strongly supported (Table 1). Mean density (occupied mounds/ha) was greater at treated areas (1.25, SE = 0.22) than at untreated areas (0.17, SE = 0.05; beta estimate = 2.27, SE = 0.48). The best-supported vegetation model indicated that the treatment effect was primarily mediated by changes in shrub cover (Table 1). Density was related negatively to shrub cover (Fig. 2; beta estimate = −0.067, SE = 0.026). A model including grass cover was not supported.

Treatment age and connectivity were the most important predictors of the response of *D. spectabilis* to herbicide treatment (Table 2; Supplementary Material 3). Relative to paired untreated areas, densities of *D. spectabilis* were greatest at treated areas that were old and highly connected to other treated areas (Fig. 3; age beta estimate = 0.088, SE = 0.035; connectivity beta estimate = 0.36, SE = 0.20). Differences in density were more strongly related to treatment age than connectivity based on summed Akaike weights (age = 0.82, connectivity = 0.45). Treatment area and presence of a shallow restrictive zone were generally not important predictors of the response of *D. spectabilis* to herbicide treatment (summed Akaike weights: area = 0.11, restrictive = 0.09). Soil texture was not a strongly supported predictor of differences in density based on Akaike weights (texture = 0.16), but differences in density were greater at non-sandy

Table 1 Model selection statistics for effects of herbicide treatment and vegetation cover on density of occupied mounds of *D. spectabilis* in southern New Mexico, USA

Model set	Model	ΔAIC_C	ω_i	L	K
Treatment effect	Treatment	0.00	1.000	−94.61	4
	Null	12.08	0.000	−102.19	3
Vegetation effects	Shrub cover	0.00	0.756	−99.14	4
	Null	3.02	0.167	−102.19	3
	Grass cover	4.58	0.077	−101.43	4

ΔAIC$_C$ is the difference between AIC$_C$ of each model and the most-supported model, ω_i is the Akaike weight of model *i*, *L* is the log-likelihood, *K* is the number of parameters, and *Null* indicates a model with an intercept only

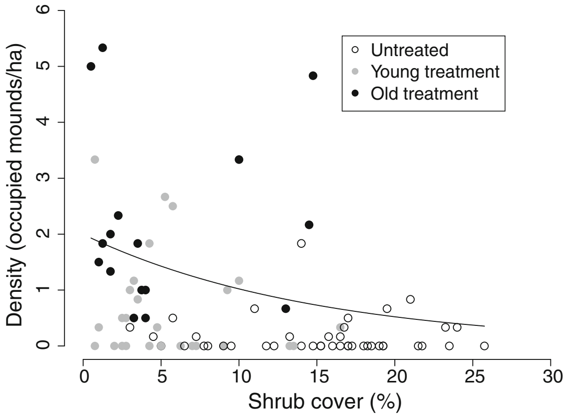

Fig. 2 Relationship between density of occupied mounds of *D. spectabilis* and percent cover of live and dead shrubs at 21 grassland restoration sites in southern New Mexico, USA. Each data point ($n = 84$) is from a 6-ha belt transect in untreated areas (*open circles*), young treated areas (treated 1994–2004; *closed gray circles*), or old treated areas (treated 1982–1989; *closed black circles*). *Best-fit line* is based on parameter estimates from a model that included a fixed effect of shrub cover (Table 1)

Table 2 Model selection statistics for effects of local and landscape constraints on differences in density of occupied mounds of *D. spectabilis* between paired treated and untreated areas (Δ = Treated − Untreated) in southern New Mexico, USA

Model	ΔAIC_C	ω_i	L	K
Age + connectivity	0.00	0.32	−29.58	4
Age	0.36	0.27	−31.30	3
Age + texture	2.42	0.09	−30.79	4
Age + area	2.67	0.08	−30.91	4
Connectivity	3.39	0.06	−32.82	3
Age + restrictive	3.41	0.06	−31.29	4
Connectivity + texture	4.21	0.04	−31.69	4

Main effects included treatment age (years since treatment), connectivity, soil texture (sandy or not sandy), and presence of a shallow restrictive soil horizon. Only models with $\Delta AIC_C < 5$ are displayed

ΔAIC_C is the difference between AIC_C of each model and the most-supported model, ω_i is the Akaike weight of model i, L is the log-likelihood, and K is the number of parameters

sites than at sandy sites (Supplementary Material 4). The lack of soil texture's importance in model selection may be due to the low number of sandy sites ($n = 4$).

The structural equation model of density at treated areas fit the data well ($\chi^2 = 0.04$, $df = 1$, $P = 0.84$). The model indicated that density of *D. spectabilis* depended on treatment age and connectivity (Fig. 4; R^2 for mound density = 43.5 %). Density was greatest at treated areas that were old and connected to other treated areas (Fig. 4). Shrub cover did not depend on treatment age, and shrub cover was not an important predictor of density on treated areas (Fig. 4). Thus, treatment age had a direct effect on density of *D. spectabilis* as opposed to an indirect effect by mediating shrub cover.

Discussion

Our results indicate grassland restoration was generally effective for increasing *D. spectabilis* populations. Density of *D. spectabilis* was greater at areas treated with herbicide than at untreated areas, and the positive response was driven by reduced shrub cover. Density was variable among treated areas, however, indicating improvement of site conditions was not always sufficient to meet restoration objectives. Variation in density was mainly due to a strong time-lagged response to herbicide treatment. Because density was directly affected by treatment age and positively related to connectivity, the time lag likely reflected a dispersal limitation as opposed to changes in local habitat quality. Given its role as a keystone modifier and strong competitor, landscape constraints on reestablishment of *D. spectabilis* will have ramifications for the structure of restored grasslands. If keystone species are typically poor dispersers, landscape constraints may be generally important for determining recovery of biodiversity and ecosystem functioning in degraded landscapes.

Herbicide treatments alter local vegetation structure by reducing shrub cover and increasing grass cover (Perkins et al. 2006; Cosentino et al. 2013; Coffman et al. 2014). Our data indicate the reduction in shrub cover had a direct effect on *D. spectabilis* density as opposed to an indirect effect by mediating grass recovery. Across treated and untreated areas, the density of *D. spectabilis* was related negatively to shrub cover, which is consistent with previous studies (Krogh et al. 2002; Waser and Ayers 2003). *Dipodomys spectabilis* prefers structurally open habitat (e.g., Schroder 1987), and it is hypothesized that high shrub cover decreases foraging efficiency or increases predation risk (Waser and Ayers 2003). In our study, there was a threshold level of shrub cover (15 %; Fig. 2) above which density was uniformly low, and below which density was highly variable. Because most areas with high shrub cover were untreated (Fig. 2; Supplementary Material 1), herbicide treatments likely reduced shrub cover to levels where other factors became limiting to restoration.

Although grass cover responds positively to herbicide treatment, we found no relationship between grass cover and *D. spectabilis* density. Grass seeds and stems can make up a substantial portion of the diet of *D. spectabilis*, but individuals also cache the seeds of forbs, shrubs, and subshrubs (Hope and Parmenter 2007). Given its generalist granivore diet and sensitivity to shrub cover, the positive response of *D. spectabilis* to restoration likely resulted from creation of open habitat structure as opposed to greater access to food from increased grass cover (see also Waser and Ayers 2003). However, we cannot rule out the possibility that *D. spectabilis* responds to flushes in productivity of annual grasses and forbs that our snapshot of vegetation cover did not capture.

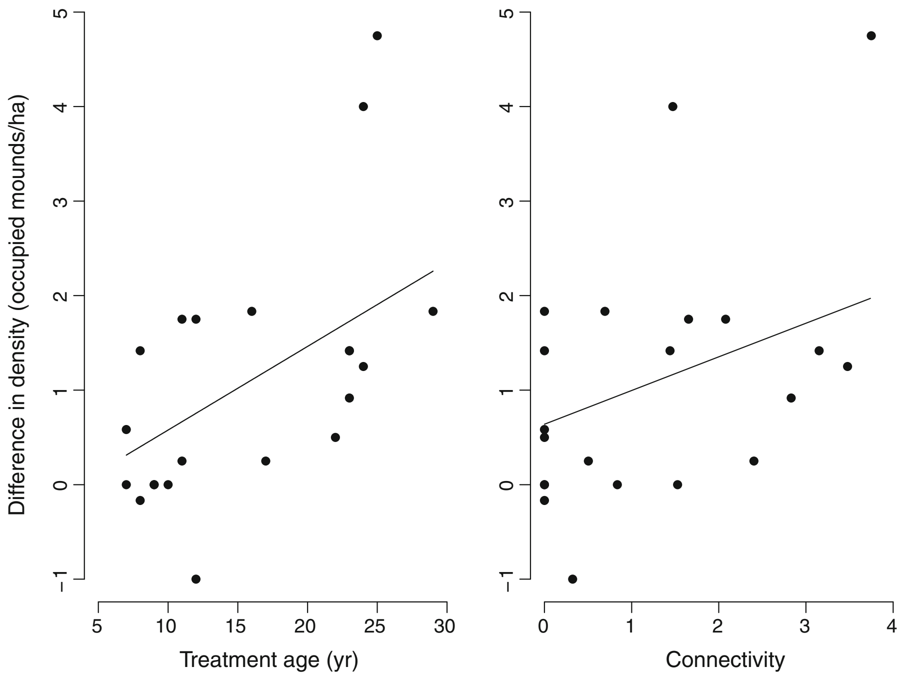

Fig. 3 Difference in density of occupied mounds of *D. spectabilis* between paired treated and untreated areas (Δ = Treated − Untreated) related to treatment age and connectivity. *Best-fit lines* are based on parameter estimates from the most-supported model of differences in density (Table 2)

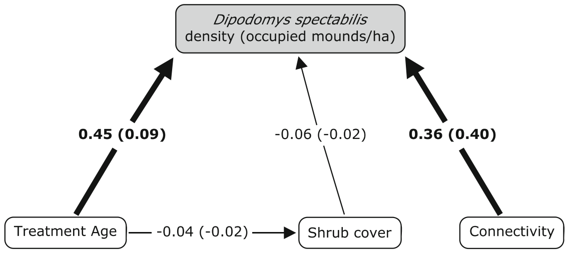

Fig. 4 Structural equation model of the density of *Dipodomys spectabilis* (occupied mounds/ha) at 21 grassland restoration sites in southern New Mexico, USA. Model includes direct effects of treatment age, shrub cover, and connectivity on density, and an indirect effect of treatment age on density. Thickness of pathways is scaled to the magnitude of standardized regression coefficients, which are given. Unstandardized regression coefficients are given in parentheses. Robust SE's were 0.03 for age, 0.06 for shrub cover, 0.20 for connectivity, and 0.13 for the effect of age on shrub cover. *Bold* coefficients are significant at $P < 0.05$

Treatment age was the most important predictor of the response of *D. spectabilis* to restoration. A positive response to habitat restoration can take a decade or longer (Fig. 3). Time lags for restoration responses could be common (e.g., Woodcock et al. 2012), but disentangling the multiple mechanisms that can generate time lags is rare. One hypothesis for our study is that the time lag emerged from changes in habitat quality after herbicide treatment. In situ demographic rates (survival and reproduction) may have tracked slow improvement in habitat quality as shrub cover decreased and grass cover increased. Alternatively, individuals may have perceived habitat quality as low at recently treated areas even if habitat quality was high. Shrubs are killed when herbicide is activated by precipitation, but "shrub skeletons" persist for many years. Colonization may be slow if areas with shrub skeletons are perceived as undervalued resources during habitat selection, creating perceptual traps (Patten and Kelly 2010). Under either mechanism, newly established or remnant populations may exhibit slow population growth early in restoration trajectories. However, shrub cover was <15 % at treated areas regardless of treatment age (Fig. 2), and treatment age was not a strong predictor of shrub cover at treated areas. Furthermore, shrub cover was not a predictor of *D. spectabilis* density at treated areas only. These patterns indicate restoration responses were contingent on other factors after shrub cover was reduced below a threshold level by treatments.

Our results suggest dispersal and landscape context play vital roles in determining the time-lagged response of *D. spectabilis*. The SEM indicated treatment age was the most important direct predictor of density at treated areas. Although a direct effect of treatment age could represent a dynamic aspect of habitat quality not included in our model, the relationship between density and treatment age likely represents a dispersal constraint. *Dipodomys spectabilis* is extremely dispersal limited (Skvarla et al. 2004; Waser et al. 2006), which may lead to slow colonization and low immigration, both of which can result in a positive relationship between density and treatment age. All unoccupied transects that were treated with herbicide and had low shrub cover were recent treatments (Fig. 2), suggesting it can take considerable time for *D. spectabilis* to colonize after herbicide application.

A dispersal constraint was also supported by the consistent positive effect of connectivity on differences in density between treated and untreated areas and overall density at treated areas. The mechanisms producing a positive relationship between density and connectivity should depend on whether treated areas were colonized after herbicide application or occupied by small remnant populations (Banks et al. 2011). At treated areas that are unoccupied, high spatial connectivity is likely important for maximizing colonization probability. However, half of the untreated areas in our study region were occupied by *D. spectabilis* at low densities (Cosentino, unpublished data), suggesting some populations at treated areas represented expanded remnant populations. Population size will be small in both newly established and bottlenecked populations, and immigrant subsidies can be important for rescuing small populations from local extinction (Brown and Kodric-Brown 1977).

Restoration of keystone species

Improving local habitat quality by reducing shrub cover is a critical first step to recovery of *D. spectabilis*. However, recovery can take decades even when shrub cover is reduced, and we attribute this time lag primarily to limited dispersal and inadequate connectivity to source populations. Because *D. spectabilis* is a keystone species, this landscape constraint will shape overall responses of biodiversity to grassland restoration. When targeting future areas for restoration, adopting a landscape mosaic approach and maximizing connectivity to source populations of *D. spectabilis* should be a primary consideration. Connectivity can be facilitated by minimizing the distance between restoration sites and source populations, or by selecting sites that are surrounded by habitats that minimize dispersal costs. Skvarla et al. (2004) found that movement probability of *D. spectabilis* may depend on grass height, suggesting that matrix habitats can differentially affect the probability of colonization and dispersal after herbicide application. More insight into maximizing functional connectivity will require studies on the relative costs of dispersal in common habitats (e.g., grassland, savannah, shrubland) and models of connectivity that account for matrix structure (e.g., McRae et al. 2008).

More generally, identifying local and landscape-scale constraints on restoration of keystone species may be an effective way to integrate responses across levels of biological organization and achieve biodiversity conservation (Likens and Lindenmayer 2012). Landscape constraints may be particularly relevant to restoration of keystone competitors if there is an inverse relationship between dispersal ability and competitive ability (Levins and Culver 1971). Landscape constraints may also be important for keystone modifiers (i.e., ecosystem engineers) if dispersal success trades off with engineering activities and depends on the availability of modified environments. Such a tradeoff may apply to many keystone rodents. For *D. spectabilis*, dispersers prefer to renovate vacant mounds instead of constructing new mounds (Best 1972; Jones 1984; Waser et al. 2006), so emigration to restoration areas is likely limited by the spatial distribution of vacant mounds. Similarly, dispersal by black-tailed prairie dogs (*Cynomys ludovicianus*) is constrained by the spatial distribution of existing burrow systems because dispersers prefer to move to established colonies (Garrett and Franklin 1988). If strong competitors and ecosystem engineers commonly exhibit limited dispersal capacity, long time lags should be expected for recovery of many keystone species to habitat restoration.

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