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Short communication

Effects of grassland restoration efforts on mound-building ants in the Chihuahuan Desert

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ABSTRACT

Shrub encroachment is a serious problem in arid environments worldwide because of potential reductions in ecosystem services and negative effects on biodiversity. In southwestern USA, Chihuahuan Desert grasslands have experienced long-term encroachment by shrubs including creosotebush (*Larrea tridentata*). Land managers have attempted an ambitious intervention to control shrubs by spraying herbicides over extensive areas to provide grassland habitat for wildlife species of conservation concern. To provide a broader assessment of how these restoration practices affect biodiversity, we evaluated responses by four mound-building ant species (*Pogonomyrmex rugosus*, *Aphaenogaster cockerelli*, *Myrmecocystus depilis*, and *Myrmecocystus mexicanus*). We compared colony densities between 14 pairs of treated areas (herbicide applied 10–30 years before sampling) and untreated areas (spatially matched and dominated by creosotebush). *P. rugosus* and *A. cockerelli* responded positively to restoration treatments likely due to an increased abundance of seeds associated with increased grass cover. Variation in *P. rugosus* densities among different-aged treatments suggests a substantial time lag in response that could reflect temporal changes in habitat quality or facilitation by a keystone rodent, *Dipodomys spectabilis*. Colony densities of the scavenging ant *M. mexicanus* were reduced on treated areas, and *M. depilis* exhibited a similar trend, likely reflecting a reduction of liquid food resources associated with shrubs. Our results demonstrate that ongoing efforts to restore Chihuahuan Desert grasslands are having both positive and negative effects on non-target taxa such as ants and support the need for a landscape mosaic approach to restoration.

1. Introduction

Shrub encroachment is a common phenomenon in semiarid and arid environments worldwide (Archer, 2010; Eldridge et al., 2011). The shift from grasslands to shrublands often results in reduced forage production for livestock and increased soil erosion (Archer, 2010). Moreover, loss of grassland habitats poses concerns for maintenance of animal biodiversity in these ecosystems (Archer, 2010; Meik et al., 2002; Sirami et al., 2009).

In southwestern United States, Chihuahuan Desert grasslands have experienced a long-term encroachment by shrubs, primarily creosotebush (*Larrea tridentata*) and honey mesquite (*Prosopis glandulosa*). This landscape conversion is thought to be triggered by livestock overgrazing during extended drought periods alongside a reduction of fires and cross-scale feedbacks among shrub encroachment, soil erosion, and local climate (Archer, 2010; Peters et al., 2006). Reversal of these transitions is difficult and, where possible at all, requires intensive management intervention. The Bureau of Land Management (BLM) in New Mexico, USA has sprayed herbicides over vast areas in an attempt to control shrubs. These efforts to restore desert grasslands started in the1980s but were expanded in 2005 with the Restore New Mexico Program (Coffman et al., 2014; Cosentino et al., 2013, 2014). Restoration efforts have focused on recovering suitable habitat for wildlife species of conservation concern such as regionally declining birds

(Coffman et al., 2014). A comprehensive understanding of effects of these restoration practices on biodiversity requires assessments of non-target taxa as well (Cosentino et al., 2013, 2014).

Ants have been promoted as useful indicators for environmental monitoring and assessment of land management practices (Andersen and Majer, 2004; Underwood and Fisher, 2006). For our evaluation of grassland restoration efforts in the Chihuahuan Desert, we focused on four species of mound-building ants—*Pogonomyrmex rugosus*, *Aphaenogaster cockerelli*, *Myrmecocystus depilis*, and *Myrmecocystus mexicanus*. These ant species have large colonies and distinctive nest structures (Wheeler and Wheeler, 1986) that make them ideal to census over large spatial extents. Harvester ants such as *P. rugosus* also have strong effects on ecosystem functioning through selective seed predation, seed dispersal, and alteration of soil conditions (MacMahon et al., 2000). In general, we expected the focal ant species would respond to restoration treatments primarily because anticipated changes in vegetation (reduced shrub cover, increased grass cover) would affect availability of food resources. Abundances of Chihuahuan Desert ants can also strongly depend on soil texture (Bestelmeyer and Wiens, 2001; Johnson, 1992), so we expected that responses could be constrained by soils.

We predicted that *P. rugosus* would respond favorably to grassland restoration treatments because it is a granivore that feeds on seeds of perennial grasses (Whitford, 1978; Zimmer and Parmenter, 1998) and annual grasses and forbs (Rissing, 1988; Whitford, 1978). Furthermore, if the positive association between *P. rugosus* and mounds of banner-tailed kangaroo rats (*Dipodomys spectabilis*) observed at fine scales (Edelman, 2012) translates to broader scales, we predicted a time lag in response of *P. rugosus* to restoration treatments because *D. spectabilis* exhibits a lagged response (Cosentino et al., 2014). Because *A. cockerelli* is an opportunistic omnivore that scavenges for insects and seeds (Bestelmeyer, 2005; Sanders and Gordon, 2003; Wheeler and Wheeler, 1986), we had no clear prediction how the species would respond to vegetation changes, and we expected other factors such as soil texture could drive abundance patterns (Bestelmeyer and Wiens, 2001). *Myrmecocystus* species (honeypot ants) are also opportunistic foragers (Sanders and Gordon, 2003) including diurnal (*M. depilis*) and nocturnal (*M. mexicanus*) species (Schooley et al., 2000). Among its varied food sources, *Myrmecocystus* collects plant secretions (floral and extrafloral nectar) and honeydew from homopterans that are stored within the replete caste (Wheeler and Wheeler, 1986). Homopteran species are tended by ants on *Larrea* (Schultz et al., 1977), *Myrmecocystus* has been collected from *Larrea* (Rango, 2005), and *M. depilis* was an indicator species for *Larrea* habitat (Bestelmeyer and Wiens, 2001). Hence, we predicted that *M. depilis* and *M. mexicanus* would respond negatively to shrub removal treatments.

2. Materials and methods

We conducted the study in the Chihuahuan Desert in southwestern New Mexico in a region centered on the town of Hatch (see study maps in Cosentino et al., 2013; Coffman et al., 2014). Shrublands were dominated by creosotebush and tarbush (*Flourensia cernua*). Common grasses were dropseeds (*Sporobolus* spp.), tobosa (*Pleuraphis mutica*), bush muhly (*Muhlenbergia porteri*), black grama (*Bouteloua eriopoda*), threeawns (*Aristida* spp.) and burrograss (*Scleropogon brevifolius*).

We selected 14 sites consisting of paired treated and untreated areas spatially matched for soil type, landform, and elevation. Treated areas (mean = 1005 ha; range = 449–1946 ha) were sprayed with the herbicide tebuthiuron at a standard rate of 0.56 kg/ha by the BLM to target creosotebush. Treatments were applied to each site once between 1982 and 2002 (10–30 years before our ant sampling). Matched untreated areas were dominated by creosotebush. Mean elevation for treated and untreated areas was 1529 m (range = 1329–1756 m).

Within each treated and untreated area, two 1-km belt transects were established that were coincident with two of the three transects sampled in Coffman et al. (2014). Each of our belt transects was 1000 m × 8 m (length × width). Belt transects within an area were 300–1500 m apart and ≥100 m from roads.

We measured densities of ant colonies by counting nests for the four focal species (*P. rugosus*, *A. cockerelli*, *M. depilis*, *M. mexicanus*) on each belt transect between 19 September and 19 November 2012. A single observer (MMM) conducted all counts between 800 and 1400 and alternated between starting surveys on treated or untreated areas each day. Nest entrances separated by > 1.5 m were counted as separate colonies. Species identification in the field was based on typical nest structure and observations of foragers entering or leaving nests (Wheeler and Wheeler, 1986). If necessary, the observer agitated the colony with a probe or by blowing on the entrance to bring occupants to the surface. Collected voucher specimens confirmed that sampled dark *Myrmecocystus* ants were from colonies of *M. depilis* and not *M. mimicus*.

To evaluate environmental variables that might explain density patterns for ant species, we measured vegetation cover, soil texture, and the density of *D. spectabilis* mounds. Vegetation cover (shrubs and grasses) was measured using line point intercept (LPI) sampling on two 50-m transects associated with each of the two 1-km belt transects (for details see Coffman et al., 2014). Dominant soil texture was determined at the center of each LPI transect. We used a simple binary classification of soil texture that included 'loam' and 'not loam' (sandy or gravelly) based on a soil pit dug to a depth of 70 cm or to a restrictive horizon. Active mounds for *D. spectabilis* were counted on two 1-km transects using larger belts (1000 m × 60 m; Cosentino et al., 2014). For analysis, we averaged all environmental variables from transects within each treated and untreated area.

We used Wilcoxon signed rank tests to determine if shrub cover, grass cover, and colony densities for the four ant species differed between treated and untreated areas. We then used Spearman's rank correlation coefficients to determine if the difference between ant colony density within treated and untreated pairs was related to time since treatment. A positive correlation would indicate a time lag in treatment effects on colony density. Finally, we applied hierarchical partitioning (hier.part function in R; Walsh and Mac Nally, 2008) to explore relationships between ant species densities and measured environmental factors (shrub cover, grass cover, soil texture class, mound density of *D. spectabilis*) across all areas. Hierarchical partitioning allows one to estimate the independent and joint effects of predictor variables exhibiting collinearity (Cosentino et al., 2013).

3. Results

Restoration treatments affected vegetation cover as we predicted. Shrub cover was reduced ($P = 0.001$, $S = -52.5$, $n = 14$) on treated areas (median = 3.67%) compared to untreated areas (median = 15.13%). Likewise, grass cover increased ($P = 0.009$, $S = 40.5$, $n = 14$) on treated areas (median = 24.21%) compared to untreated areas (median = 15.00%).

Restoration efforts affected densities of three of the four focal ant species (Fig. 1). Densities of *P. rugosus* were greater on treated areas compared to untreated areas ($P = 0.041$, $S = 26$, $n = 14$). Likewise, densities of *A. cockerelli* increased on treated areas compared to untreated areas ($P = 0.035$, $S = 27$, $n = 14$). In contrast, shrub control treatments reduced the densities of *M. mexicanus*