

# Long-term experimental loss of foundation species: consequences for dynamics at ecotones across heterogeneous landscapes

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**Abstract.** Biome transition zones where species co-exist near their geographic limits are expected to be among the most responsive to changes in climate that result in mortality of foundation species. Long-term (>13 years) patterns in dominance and cover of functional types were examined following the annual experimental removal of one of three foundation species at an arid-semiarid biome transition zone. Objectives were to identify key processes influencing these patterns, and to predict future landscape-scale dynamics following mortality of different foundation species. Aboveground biomass of dominant species was removed from 3 × 4 m plots. Cover by species on control and removal plots was estimated annually in communities with a single dominant species, and in ecotonal communities with two dominant species across two types of ecotones (semiarid grassland-arid grassland, arid grassland-arid shrubland).

For most species and functional types, trends in cover through time were related to the remaining species assemblages rather than to variable climatic conditions. In ecotonal communities, resident co-dominant species increased to dominance following the loss of a foundation species with little change in community composition. In mono-dominated communities, dominant species loss resulted in a shift to species that are currently sub-dominants of the same functional type as the species that was removed. Subdominant perennial grass and shrub species increased rapidly following removals in most grassland locations. Annuals and perennial forbs had variable cover values through time that were not clearly related to pulses in precipitation and were not synchronized across locations. The most common response regardless of the identity of the foundation species removed or the community type was an increase in cover by sub-dominant grasses and by the arid grass species (*Bouteloua eriopoda*). The rate of increase by *B. eriopoda* depended on initial cover, and resulted from both vegetative growth and seedling recruitment from other locations. Seed dispersal and seedling recruitment from other locations were not found for the semiarid grass, *Bouteloua gracilis* or the arid shrub, *Larrea tridentata*. Because *B. eriopoda* is more susceptible to shrub invasion, drought, and livestock grazing than the other two foundation species, widespread loss of either of the other species and subsequent increase in *B. eriopoda* is expected to result in an increase in landscape-scale vulnerability to these environmental drivers. The extent and magnitude of this change in vulnerability will depend on the ability of *B. eriopoda* to respond based on the micro-environmental conditions of the site regardless of which species (*B. gracilis*, *L. tridentata*) is lost.

**Key words:** arid; biome transitions; Chihuahuan Desert; dominant species; experimental removals; grasslands; mortality; semiarid; Shortgrass Steppe; shrublands.

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## INTRODUCTION

Directional changes in climate are affecting nearly every ecosystem on Earth (MEA 2005, IPCC 2007). One of the potentially most important effects of climate change is the loss of long-lived dominant species that provide the foundation for the structure and function of ecological systems (Dayton 1971, Ellison et al. 2005). Responses following mortality of foundation species depend on a number of factors, including life history characteristics of species available for recovery, legacies of the foundation species, and climatic and micro-site environmental conditions (e.g., Drake 1991, Rejmánek and Richardson 1996, Foster et al. 1998, Hooper et al. 2005, Suding et al. 2006, Wootton 2010). Disentangling the relative importance of these factors is critical to predicting future dynamics under climate change (Clark et al. 2011, Rubidge et al. 2011). Ecotones between communities dominated or co-dominated by different species located at their geographic limits provide opportunities to evaluate the importance of these biotic and abiotic factors to future dynamics (Peters et al. 2006*a, b*, Stuve et al. 2011). The goal of this study was to determine how different factors influence species dominance and community composition through time in order to predict future dynamics at a biome transition zone following the loss of different foundation species.

Different outcomes following species mortality depend on the processes governing patterns in dominance and community assembly (Drake 1991). For ecotones located across a landscape with similar climate and no barriers to dispersal, competition for resources and spatial heterogeneity in local environmental factors are expected to have different effects on species responses (Von Holle and Simberloff 2005). If competition governs current patterns, then the loss of a foundation species at an ecotone would result in dominance by resident co-dominant species with a complementary niche based on resource acquisition (Tilman 1982, 1988, Fargione et al. 2003, Bret-Harte et al. 2008). For landscapes with more than one co-dominant species, the species with the most complementary resource-based niche to the foundation species is expected to dominate through time following its mortality (Diaz et al. 2003). Responses can be symmetric

when mortality of either species results in similar magnitude of responses that lead to dominance by the other species (Cahill and Casper 2000). Responses can be asymmetric where loss of one species results in a response that differs in magnitude or direction compared to responses following the loss of a second species (Freckleton and Watkinson 2001).

Alternatively, if resource partitioning and environmental filtering associated with temporal or spatial heterogeneity govern current dominance patterns (Sala et al. 1989, Cipriotti and Aguiar 2010), then co-dominant resident species would have a limited ability to respond to foundation species loss. Morphological constraints on resource acquisition and edaphic conditions that influence recruitment and survival would limit species responses (Watson and Casper 1984, Neilson 1986, Laycock 1991, Lebrija-Trejos et al. 2010). These constraints can also arise from biotic and abiotic legacies associated with mortality of the foundation species (Foster et al. 1998). As a consequence, resident sub-dominant species, or potentially invasive species, would increase to dominance rather than existing co-dominant species (Symstad and Tilman 2001). These species may be from the same or different growth form as the foundation species that was lost (Bret-Harte et al. 2008), and novel assemblages can emerge as a result of species-specific responses (Williams and Jackson 2007, Seastedt et al. 2008, Hobbs et al. 2009).

These dominance responses are not necessarily mutually exclusive. For example, niche complementarity and competitive release can operate at fine scales, and environmental filtering and resource partitioning can become important as environmental heterogeneity increases with spatial extent (Cavender-Bares et al. 2004). One approach to examining responses at multiple scales is to conduct experimental removals of different combinations of dominant species across a spatially heterogeneous landscape. Species removals in natural communities can be used to examine biotic interactions and abiotic constraints without the artificial conditions that result when seed additions are used to create communities (Diaz et al. 2003, Munson and Lauenroth 2009). In addition, long-term observations following loss of species are needed for systems with large year-to-year variability in

climate and where patterns in dominance and composition require years to decades to emerge, such as communities dominated by long-lived grasses and shrubs (Wardle et al. 1999, Wootton 2010).

In this study, effects of long-term loss of different foundation species on community dynamics were examined at a semiarid-arid biome transition zone. This landscape consists of a mosaic of grassland and shrubland communities and their ecotones, each dominated by one or more species with different life history traits. Long-term experimental manipulations (>13 years) of two dominant grasses and one dominant shrub were used to address the following questions: (1) What are long-term patterns in dominance by resident co-dominant species and functional types following loss of different foundation species? (2) What are trends in cover through time for co-dominant species and functional groups? We then used these results to infer the relative importance of competition, resource partitioning, legacies, and environmental conditions across a heterogeneous landscape. Finally, we discuss the consequences of these fine-scale changes in dominance to future landscape-scale dynamics.

## METHODS

### Study area

This study was conducted on the McKenzie Flats at the Sevilleta National Wildlife Refuge (SEV) Long Term Ecological Research site in central New Mexico (NM), USA (34.4 N, 106.7 W, 1600 m asl). Grazing by cattle has been excluded from the site since 1973, although native herbivores occur at low densities (pronghorn antelope, rabbits) or infrequently at high densities (e.g., grasshoppers). Long-term (80 yr) mean annual precipitation at a nearby weather station is 23.2 cm (SD = 7.9 cm) (Socorro: 34.05 N, 106.91 W, 1432 m asl) (Hochstrasser et al. 2002). Long-term mean monthly temperature over the same time period ranges from 2.6°C (January) to 24.6°C (July). Precipitation data from two weather stations located near the northwestern (Deep Well) and southern boundary (Five Points) of the study area show little spatial variation, and no long-term trends over the 16 years of the study (Fig. 1A). Based on annual rainfall amounts and

the monthly Palmer Drought Severity Index (PDSI; Palmer 1965, Heim 2002), the study was initiated during a 1-year drought (negative PDSI from spring 1995 through summer 1996) followed by two wet years (positive PDSI in 1997–1998) and a series of average to dry years through 2003 (Fig. 1B). Recent years have been generally wet (2004–2007) or dry to average (2008–2010).

### Species and community descriptions

Landscapes at the SEV are representative of central NM where a biome transition zone occurs between the northern extreme of the Chihuahuan Desert and the southern boundary of the Shortgrass Steppe to result in communities dominated or codominated by two of three species. Two Chihuahuan Desert species, the C<sub>4</sub> perennial grass, *Bouteloua eriopoda* (black grama) and the C<sub>3</sub> shrub, *Larrea tridentata* (creosotebush), form ecotones with each other, and *B. eriopoda* forms ecotones with the Shortgrass Steppe species, the perennial C<sub>4</sub> grass, *B. gracilis* (blue grama). Ecotones between *B. gracilis* and *L. tridentata* rarely occur at this site (Peters et al. 2006a). These species share some characteristics, but also differ in life history traits and morphology that were expected to affect: (1) their ability to dominate following the removal of one of the other species, and (2) the response of other species and functional types to their removal.

*Bouteloua gracilis* is a short-statured (<20 cm tall), shallow-rooted (<50 cm deep) bunchgrass that recovers slowly (sub-decadal to centuries) following disturbance as a result of infrequent recruitment by seedlings and slow tillering rates (Hyder et al. 1971, Briske and Wilson 1977, Coffin et al. 1996, Peters 2002a, b). Rate of recovery depends on disturbance size (Coffin and Lauenroth 1988, Munson and Lauenroth 2009). Because undisturbed *B. gracilis* clones can live hundreds of years, the well-developed crown structure and high density of roots concentrated under a plant (Coffin and Lauenroth 1991, Sun et al. 1998) likely result in well-defined areas of long-term plant-soil interactions with legacy effects that are expected to influence recovery of other species following its removal.

*Bouteloua eriopoda* is a medium-height (<50 cm tall), shallow-rooted (<50 cm deep) grass that responds rapidly following disturbance by pro-

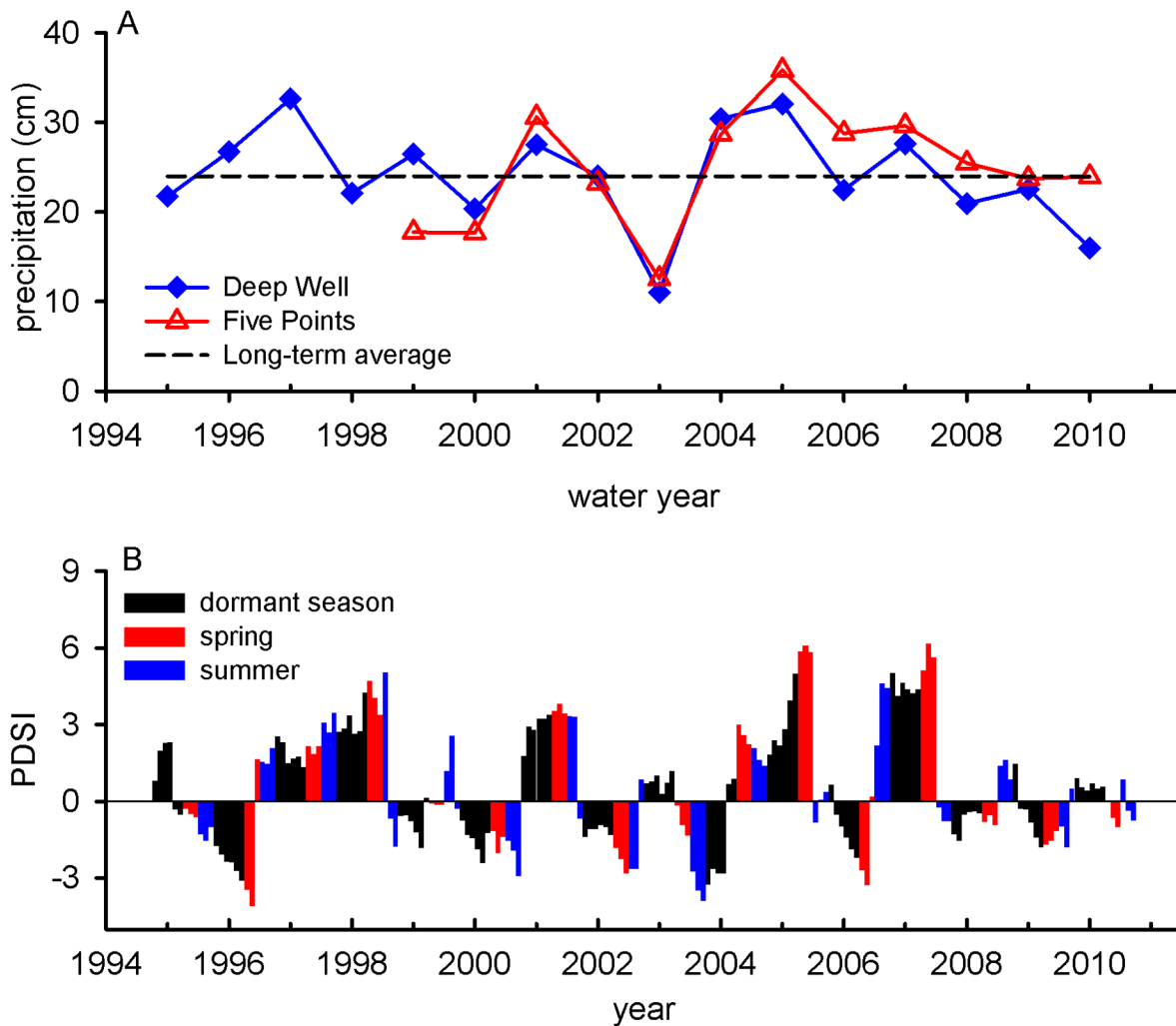


Fig. 1. (A) Water-year (Oct. 1–Sept. 30) precipitation at the Sevilleta LTER site from the Deep Well (mean: 24.0 cm/yr) and Five Points (mean: 24.8 cm/yr) stations located at the study site for the years 1995 to 2010 and for a nearby long-term weather station (Socorro, New Mexico; long-term avg = 24.0 cm/yr), (B) Palmer Drought Severity Index (PDSI) calculated monthly for the National Climate Data Center region (NM 5) for central NM (<http://www7.ncdc.noaa.gov/CDO/cdo>). Negative values indicate drought and positive values occur in wet months.

ducing stolons (Valentine 1970, Fields et al. 1999). This species is short-lived (35–40 years) with an open canopy structure and loose collection of stolons and shallow roots (Gibbens and Lenz 2001) that are expected to result in a diffuse pattern of short-term soil legacies near the soil surface following its removal.

*Larrea tridentata* is a relatively short (<2 m tall)  $C_3$  shrub that has expanded its distribution throughout the Chihuahuan Desert over the past

several centuries, primarily through seedling recruitment rather than vegetative spread (Dick-Peddie et al. 1999, Peters et al. 2006b). Leaves and roots of these plants contain chemicals that can potentially inhibit growth of other plants (Hyder et al. 2002). This deep-rooted species (>1 m) is long-lived (hundreds of years) with an extensive system of fine and coarse roots (Gibbens and Lenz 2001) that is expected to result in patchily distributed, loosely defined soil legacies at



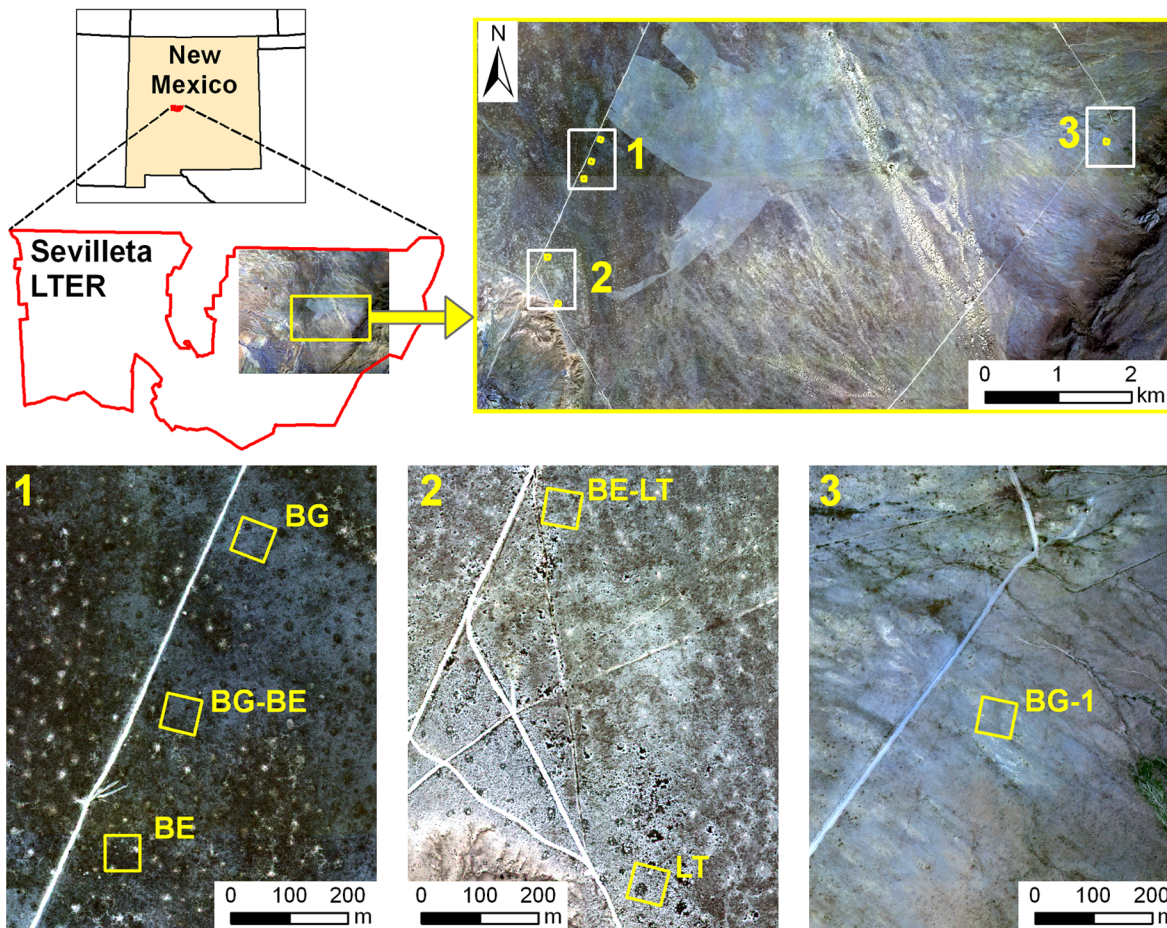


Fig. 2. ADAR image showing the six locations where long-term experimental removals of foundation species were conducted at the SEV LTER within central New Mexico, USA. In general, *Bouteloua gracilis* locations are light blue, *B. eriopoda* locations are black, and *Larrea tridentata* locations are very light gray. Plots were not located in kangaroo rat mounds (white dots). Three locations occur across a Shortgrass Steppe (*B. gracilis*-dominated, BG) to Chihuahuan Desert grassland (*B. eriopoda*-dominated, BE) ecotone with co-dominance by both *Bouteloua* species in the middle (BG-BE). Three locations occur across a Chihuahuan desert grassland (BE) to Chihuahuan Desert shrubland (dominated by *L. tridentata*; LT) with co-dominance by these species in the middle (BE-LT). The final location (BG-1) is a *B. gracilis*-dominated community on different soils.

shallow and deep depths.

Communities dominated by these species tend to be spatially distributed across the study area based on soil properties, although there is overlap in soils where different foundation species dominate. In general, grasslands are found on sandy loam and sandy clay soils; *B. eriopoda* dominates sandy loam soils and *B. gracilis* increases in dominance as clay content increases and depth to the petrocalcic horizon decreases (Kröel-Dulay et al. 2004). *Larrea tridentata* dominates locations

with large amounts of surface gravel found over fine-textured soils with shallow depth to the petrocalcic layer (<30 cm) (Buxbaum and Vanderbilt 2007).

#### Experimental design

Five locations were selected in a 2 km<sup>2</sup> area in 1995, and a sixth location on a different soil and topographic position was added in 1998 within a 10 km distance from the first five locations (Fig. 2). None of the locations experienced fire over the

Table 1. Initial cover (%) for treatment and control plots,† and their similarity in functional type composition at six locations spanning two ecotones.

Community type	Soil‡	TRT§	Total¶	BG¶	BE¶	LT¶	Other perennials				SII
							Grasses	Shrubs	Forbs	Annuals#	
<i>B. gracilis</i> -1 (BG-1)	SCL	C	17	9	2	0	1	0	5	0	NA††
		U	11	0	7	0	3	0	1	0	
<i>B. gracilis</i> (BG)	SL	C	30	26	0	0	2	2	1	0	1.00
		U	28	24	0	0	1	2	1	0	
<i>B. gracilis</i> - <i>B. eriopoda</i> ecotone (BG-BE)	SL	C	40	25	13	0	1	0	1	1	0.99
		U	43	24	17	0	1	0	1	0	
		A	38	22	13	0	1	0	0	1	
<i>B. eriopoda</i> (BE)	SL	C	36	2	28	0	1	1	1	3	0.95
		A	27	1	17	0	4	1	1	3	
<i>B. eriopoda</i> - <i>L. tridentata</i> ecotone (BE-LT)	SL-SCL	C	46	2	13	18	7	7	1	0	0.95
		A	45	2	18	15	5	4	0	0	
		L	50	1	16	19	8	5	1	0	
<i>L. tridentata</i> (LT)	SCL-C	C	30	0	0	25	0	4	0	0	1.00
		L	26	0	0	22	0	4	0	0	

† Cover means were calculated from five plots in 1995 for all locations except BG-1 (1998).

‡ Soil types: SCL: sandy clay loam; SL: sandy loam; SCL-C: sandy clay loam, shallow caliche layer.

§ TRT: Treatment codes. C: control; U: removal of *B. gracilis*; A: removal of *B. eriopoda*; L: removal of *L. tridentata*.

¶ Total plant cover excludes cacti and yucca. BG: *B. gracilis*. BE: *B. eriopoda*. LT: *L. tridentata*.

# Annuals include forbs and grasses.

|| SI: simplified Morisita Index of Similarity (Horn 1966 cited in Krebs 1999) between treatment and control plots at the same location. For all locations except BG-1: the 1995 cover by dominant species and sub-dominant functional types was used.

†† NA: Not available because cover of *B. gracilis* before the removal treatment was not recorded.

history of the Sevilleta LTER (1989 to present). The five locations selected either were dominated by single species (BG: *B. gracilis*, BE: *B. eriopoda*, LT: *L. tridentata*) or were ecotones codominated by two species (BG-BE: *B. gracilis* and *B. eriopoda* at the grassland ecotone; BE-LT: *B. gracilis*/*L. tridentata* at the grassland-shrubland ecotone). The sixth location (BG-1) represents a *B. gracilis* dominated community on a sandy clay loam soil that predominates along the foothills of the Los Piños Mountains (Soil Survey of Socorro County Area 1988). This location may receive slightly more rainfall (ca. 10%) compared with the other locations (Gosz et al. 1995).

At each single species dominated location, ten 3 × 4 m plots were selected that met dominance criteria based on visual estimates (>50% of total canopy cover); half were randomly assigned to removal and half to control plots. At the two ecotones, fifteen 3 × 4 m plots were selected that contained similar cover of the two dominant species (10–25%). Five plots were randomly assigned to each of three plot types: removal of one dominant species, removal of second dominant species, or control (no removals).

Removal plots were created by removing aboveground material with a shovel of all plants of one dominant species within a plot boundary;

removals were repeated annually as necessary. For grasses, plant material including crowns was removed with a shovel just below the soil surface with minimal disruption of deeper soil layers. Main trunks of *L. tridentata* shrubs were severed by clipping just below the soil surface. Although surface soils were slightly disturbed at the time of removals, no evidence of a soil disturbance was observed at the time of sampling. Resprouts from the trunk were removed annually, and the plants were dead with no further sprouts within 3 years after the start of the study.

Prior to conducting removals in the first year (1995), canopy cover by species was visually estimated in each of 12 1-m<sup>2</sup> sub-plots; values were then averaged for a plot-level estimate. For analyses, sub-dominant species were aggregated into functional types based on growth form and lifespan (perennial grasses, perennial forbs, shrubs, annuals) to represent traits that can influence recovery in perennial grasslands and shrublands (Peters 2002a, Munson and Lauenroth 2009).

Prior to the start of treatments, each foundation species overwhelmingly dominated its community of dominance with >80% of cover on control and removal plots (Table 1). Within each community, functional types had similar cover

and species composition (based on simplified Morisita Index of Similarity) on control compared with removal plots (Table 1). Canopy cover by species was estimated using the 12 1-m<sup>2</sup> sub-plots, and values were then averaged for a plot-level estimate in each subsequent year (1996 or 1999 through 2010) following removal of regrowth by the dominant species. Cover measurements were obtained in September or October near the time of peak growth following calibration of estimates among personnel.

### Statistical analyses

Initial (1995) community similarity between the control and a removal treatment at each of the five locations (except location BG-1) was examined using simplified Morisita Index of Similarity (Horn 1966 cited in Krebs 1999). In 1995, percentage covers were measured for the three dominant species (*B. gracilis*, *B. eriopoda*, *L. tridentata*) and seven sub-dominant functional types (annual forb, annual grass, perennial forb, perennial grass, shrub, cactus, and yucca); the similarity index was calculated using percentage covers of these 10 categories. Because the occurrence of cacti and yucca were very low, for simplicity we did not include these two categories into total plant cover for any other analyses. At location BG-1 (started in 1998), initial community similarity between control and removal plots was not examined because cover of the dominant species *B. gracilis* was not recorded before removal.

At each location, long-term average cover and standard error of each dominant species and sub-dominant functional types were calculated across 5 plots of the same treatment. For location BG-1, averages and standard errors were calculated during 1998–2010 (N = 13) for the control plots, and during 1999–2010 (N = 12) for the removal plots. For the remaining five locations, averages and standard errors were calculated during 1995–2010 for control plots (N = 16), and during 1996–2010 (N = 15) for removal plots. The means of total plant cover of control plots (or removal plots) across the 6 locations (or 8 combinations of location × removal treatment) were compared using analysis of variance (ANOVA) for nested classification, with location (or location × removal treatment) as the fixed effect, and plot nested within each location (or location × removal

treatment) (SAS, PROC MIXED). Pairwise comparisons between any two locations (or location × treatment combinations) were tested with the least-square means statement within the PROC MIXED procedure. Total plant cover was either log-transformed (for control plots) or square-root transformed (for removal plots) to meet the assumptions of ANOVA. A significance level of 0.05 was used for all statistical tests.

Temporal trends in covers of dominant species or functional types within treatment at a location were examined using simple linear regression, with mean cover across 5 plots in a year as response variable and year as explanatory variable (SAS, PROC REG). Covers between treatments at a site were compared using repeated-measure ANOVA, with plot as the subject of repeated measures (over time) (SAS, PROC MIXED). When the interaction between treatment and time was significant, average covers between control and a removal treatment were compared within every single year using the SLICE option within the PROC MIXED procedure. When needed, data were log- or square-root transformed to meet the assumptions of ANOVA.

## RESULTS

### Long-term dominance and functional type composition

For control plots, each foundation species (*B. gracilis*, *B. eriopoda*, *L. tridentata*) contributed 61–87% of total cover (averaged over the time span of the study) in the communities of single-species dominance, and two dominant species together contributed 66–86% of total cover in the communities of co-dominance (Fig. 3A). Other perennial grasses had higher average contributions to cover at the grassland-shrubland ecotone (19% of total cover) and the shrubland location (14% of total cover), compared to the four grassland locations (2–6% of total cover). Perennial forbs were more important at BG-1 (10% of total cover) than at the other five locations (2–5% of total cover). Contributions of other shrubs and annual plants (grasses and forbs) to total cover were low in all locations (other shrubs: 0–8%, annuals: 2–7% of total cover). *Bouteloua eriopoda* had similar cover (14% and 15%) and relative contributions (33% and 30% of total cover) for



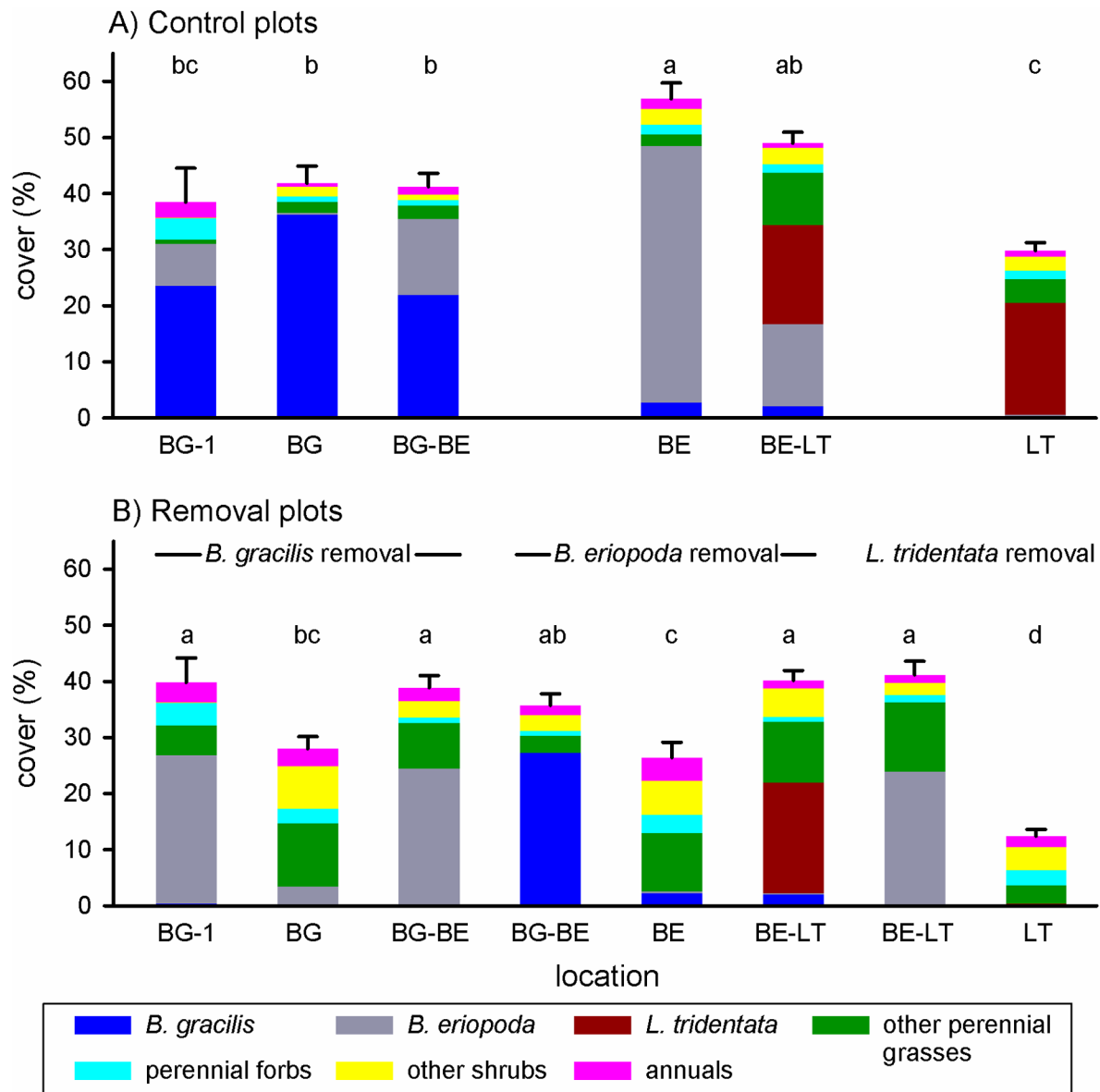


Fig. 3. Long-term average cover ( $\pm$  one standard error for total plant cover, excluding cacti and yucca) of three foundation species (*B. gracilis*, *B. eriopoda*, *L. tridentata*) and four functional types for communities dominated or codominated by the foundation species on: (A) control and (B) removal plots (see Fig. 2 for location names and abbreviations). Letters indicate significantly different means of total plant cover across locations within each treatment type. Covers in the control plots were averaged across 13 years (1998–2010) at location BG-1, and 16 years (1995–2010) at the other five locations. Covers in the removal plots were averaged across the same periods as the controls but excluding the first year in the period.

both ecotonal communities. The co-dominant *B. gracilis* had 22% average cover (53% of total cover) at the grassland ecotone (BG-BE), and the co-dominant *L. tridentata* had 18% average cover

(36% of total cover) at the grassland-shrubland ecotone (BE-LT). Largest total cover occurred in the *B. eriopoda* grassland (BE), and smallest total cover was found in the shrubland (LT). Similar

total cover was found at all four remaining communities (Fig. 3A).

For removal plots, long-term average responses differed for communities dominated by one compared with two foundation species. In communities with one foundation species, other than the location (BG-1) where initial shrub presence (0.2% of total cover) was extremely low, its loss resulted in a long-term average shift in dominance to a mixed functional type community based on cover as a proportion of the total (Fig. 3B). Following removals, the two grassland locations (BG and BE) were co-dominated by perennial grasses (BG: 40%, BE: 39% of total cover) and other shrubs (BG: 26%, BE: 23% of total cover), and the *L. tridentata* shrubland (LT) was co-dominated by other shrubs (32% of total cover), other perennial grasses (26% of total cover) and perennial forbs (22% of total cover). At ecotonal communities (BG-BE, BE-LT), the resident co-dominant species dominated cover averaged over time. *B. eriopoda* dominated following removal of *B. gracilis* or *L. tridentata*, and either *B. gracilis* or *L. tridentata* dominated following the loss of *B. eriopoda*. Largest total cover occurred at the two ecotone locations where the other co-dominant species were present, and at the *B. gracilis* location (BG-1) where the initial *B. eriopoda* cover was high (Fig. 3B). Total plant covers at the other locations with only one dominant species (BG, BE, and LT) were lower, with the lowest cover occurring at the shrubland location (LT) (Fig. 3B).

#### Response of co-dominant species through time

The Chihuahuan Desert grassland foundation species, *B. eriopoda*, increased in cover following the removal of *B. gracilis* at both the *B. gracilis* communities (locations BG-1 and BG) and the grassland ecotone (location BG-BE) (Fig. 4A–C): *B. eriopoda* covers in removal plots increased over time, and became statistically higher than those in control plots in almost all years (BG-1) or in later years (BG and BG-BE). By contrast, at the grassland-shrubland ecotone (BE-LT), *B. eriopoda* did not respond to *L. tridentata* removal (Fig. 4E). *B. eriopoda* recruitment has not occurred in the shrubland community dominated by *L. tridentata* where this grass species was not found at the start of the study (Fig. 4F).

The Shortgrass Steppe foundation species, *B.*

*gracilis*, did not respond to the removal of *B. eriopoda* at the grassland ecotone ( $p = 0.17$ , Fig. 5C), yet *B. gracilis* dominated this community by maintaining high initial cover through time (Fig. 3B). At locations where *B. gracilis* covers were very low, *B. eriopoda* community (BE) and the grassland-shrubland ecotone (BE-LT), *B. gracilis* did not respond to the removal of dominant species, either ( $p = 0.90$  and  $0.35$ , respectively; Fig. 5D, E). *B. gracilis* was unable to recruit following removals in communities where it was not found at the start of the study (Fig. 5F).

Similar to *B. gracilis*, the Chihuahuan Desert shrub, *L. tridentata* did not respond following removal of *B. eriopoda* at the grassland-shrubland ecotone ( $p = 0.39$ , Fig. 6E). *L. tridentata* dominance resulted from higher initial cover through time than other groups rather than a positive response to grass removals (Fig. 3B). This shrub species was unable to recruit into removal (or control) plots in any of the grassland communities where it did not occur at the beginning of the study (Fig. 6A–D). At the *L. tridentata* community (location LT), *L. tridentata* cover in control plots decreased over time (Fig. 6F).

#### Response of total plant cover through time

There was no trend in total plant cover over time in any plots, control or removal ( $p$ -value ranging from 0.12 to 0.92; Fig. 7). When *B. gracilis* was removed, total plant covers after removal were the same as those in control plots in most years (Fig. 7A–C). When *B. eriopoda* was removed at the *B. eriopoda* community (location BE), total plant cover after removal was lower than those in control plots in all years after removal (Fig. 7D). When *L. tridentata* was removed from the *L. tridentata* community (location LT), total plant covers after removal were lower than those in control plots in all years after removal with an exception of one year (Fig. 7F). At the two ecotonal communities (locations BG-BE and BG-LT), total plant covers after the removal of *B. eriopoda* or *L. tridentata* were the same as control plots (Fig. 7C, E).

#### Response by functional types through time

Other perennial grasses (excluding *B. gracilis* and *B. eriopoda*) responded positively to removal of *B. eriopoda* in its community of dominance within the first year following removal (Fig. 8D),



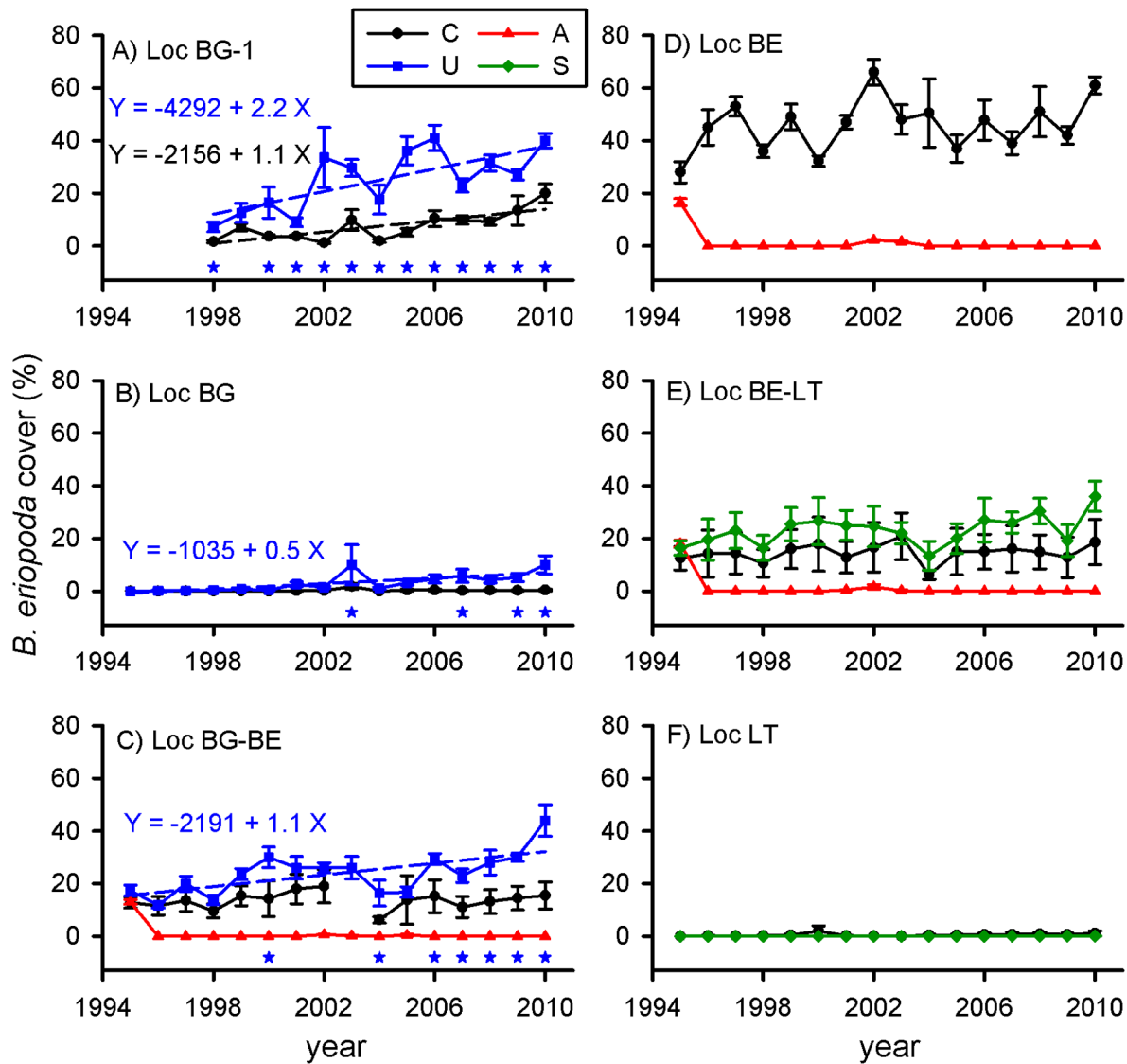


Fig. 4. Cover of *B. eriopoda* (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Treatments: C: control; U: *B. gracilis* removal; A: *B. eriopoda* removal; and S: *L. tridentata* removal. A dashed straight line indicates a significant temporal trend. An asterisk right above the X-axis indicates significant difference between a removal treatment and the control within a year. The color code of the straight line, regression equation, and the asterisk is the same as the one in the legend box. The p-value and  $R^2$  value for the significant temporal trends are as follows: (A) C: 0.002, 0.60; U: 0.005, 0.53; (B) U: 0.0009, 0.56; and (C) U: 0.005, 0.44.

and within two years following removal of *B. gracilis* regardless of location (Fig. 8A–C). However, this functional type did not respond to removal of *B. eriopoda* at the grass ecotone ( $p = 0.47$ ; Fig. 8C) or removal of either co-dominant species at the grassland-shrubland ecotone ( $p = 0.78$ ; Fig. 8E), or following removal of *L. tridentata* at the shrubland location ( $p = 0.40$ ;

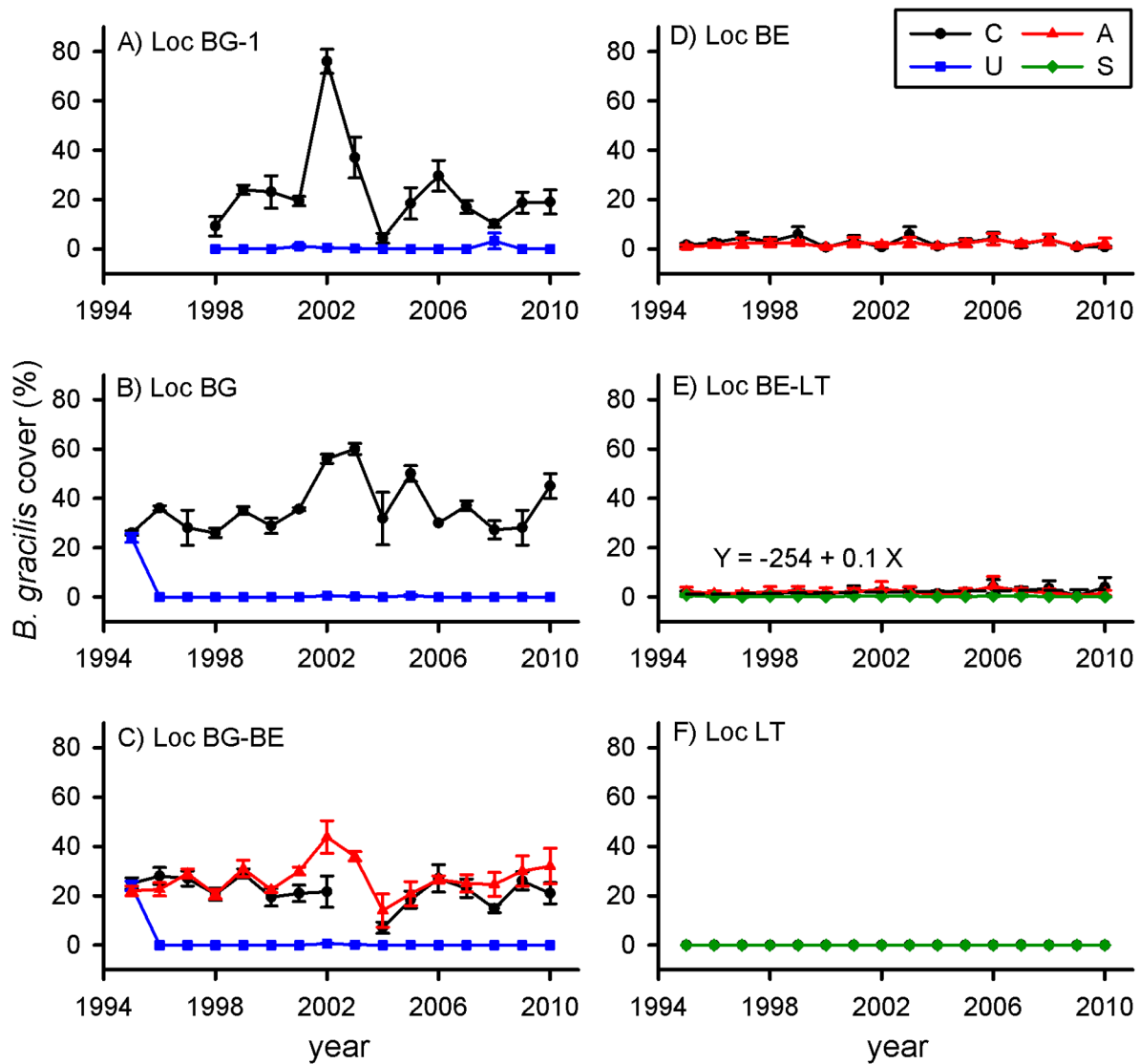


Fig. 5. Cover of *B. gracilis* (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4. The p-value and  $R^2$  value for the significant temporal trend are as follows: (E) C: 0.026, 0.30.

Fig. 8F). Cover of this functional type increased over time at the control plots in *L. tridentata* community (Fig. 8F).

Perennial forb cover was variable through time, and in general, was greater in most years following removal of *B. gracilis* and *B. eriopoda* in mono-species dominated communities (Fig. 9B, D), but cover was not affected by removal of

either species at the two ecotones ( $p = 0.85$  and  $0.59$ , respectively; Fig. 9C, E), of *B. gracilis* at the foothills location ( $p = 0.90$ ; Fig. 9A), or *L. tridentata* at the shrubland location ( $p = 0.21$ ; Fig. 9F).

Cover of other shrubs (excluding *L. tridentata*) gradually increased with time following the removal of *B. gracilis* or *B. eriopoda* at the

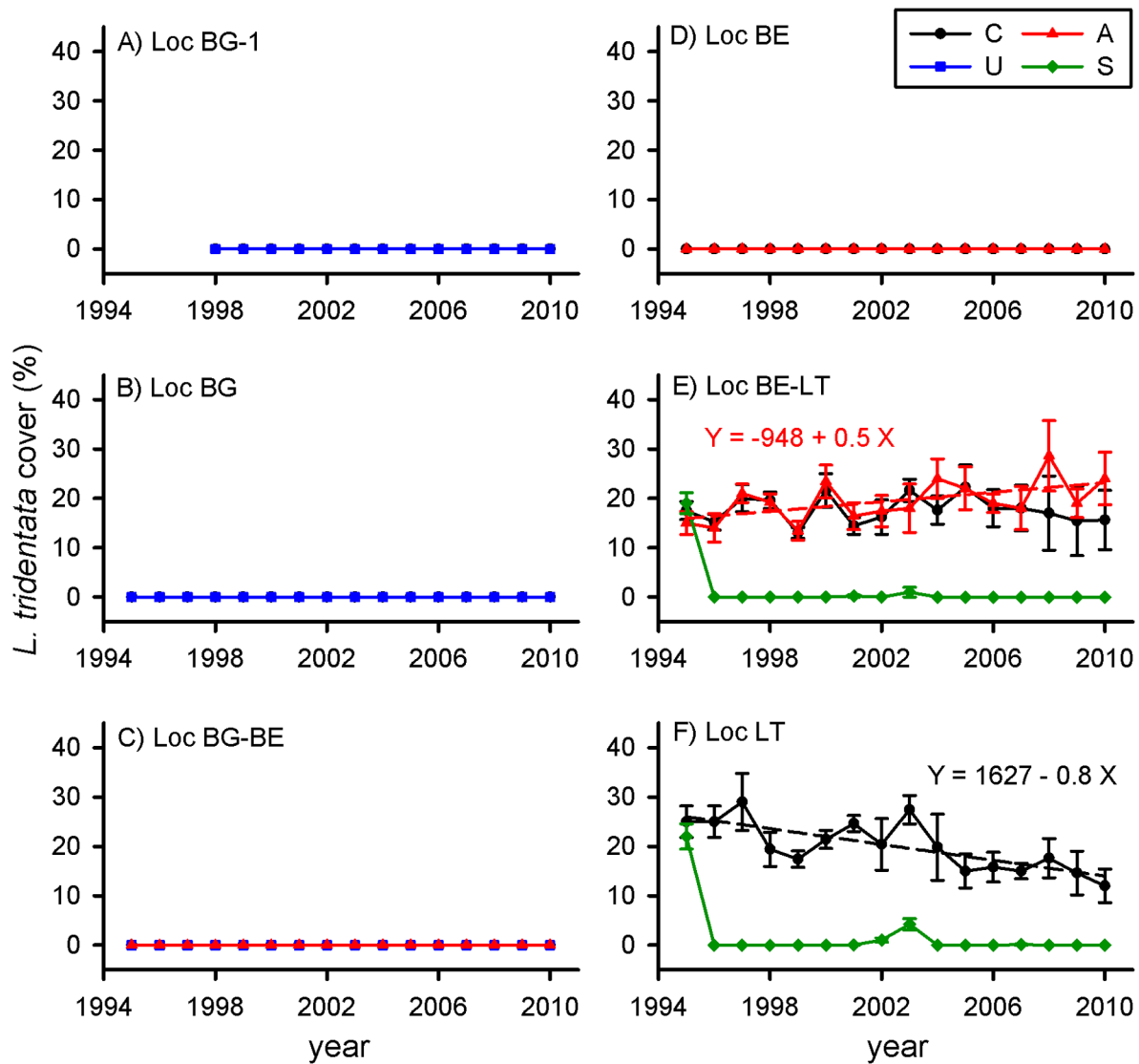


Fig. 6. Cover of *L. tridentata* (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4. The p-value and  $R^2$  value for the significant temporal trend are as follows: (E) A: 0.024, 0.31 and (F) C: 0.0007, 0.57.

grassland locations (Fig. 10B–D), except at the foothills where long-term average cover was extremely low on removal (0.06%) and control plots (0.13%) for most years (Figs. 3, 10A). At the grassland-shrubland ecotone and the shrubland location these shrubs did not respond to removal of either *B. eriopoda* or *L. tridentata* ( $p = 0.15$  and 0.23 respectively; Fig. 10E, F). Cover of other

shrubs was mostly (>80%) one species, the native *Gutierrezia sarothrae* (broom snakeweed).

Annual grasses and forbs responded to removal of each of the three foundation species in the first year following removal, and occasionally in other years, but these years were not the same across community types and were not related to precipitation (Fig. 11). For example, cover of

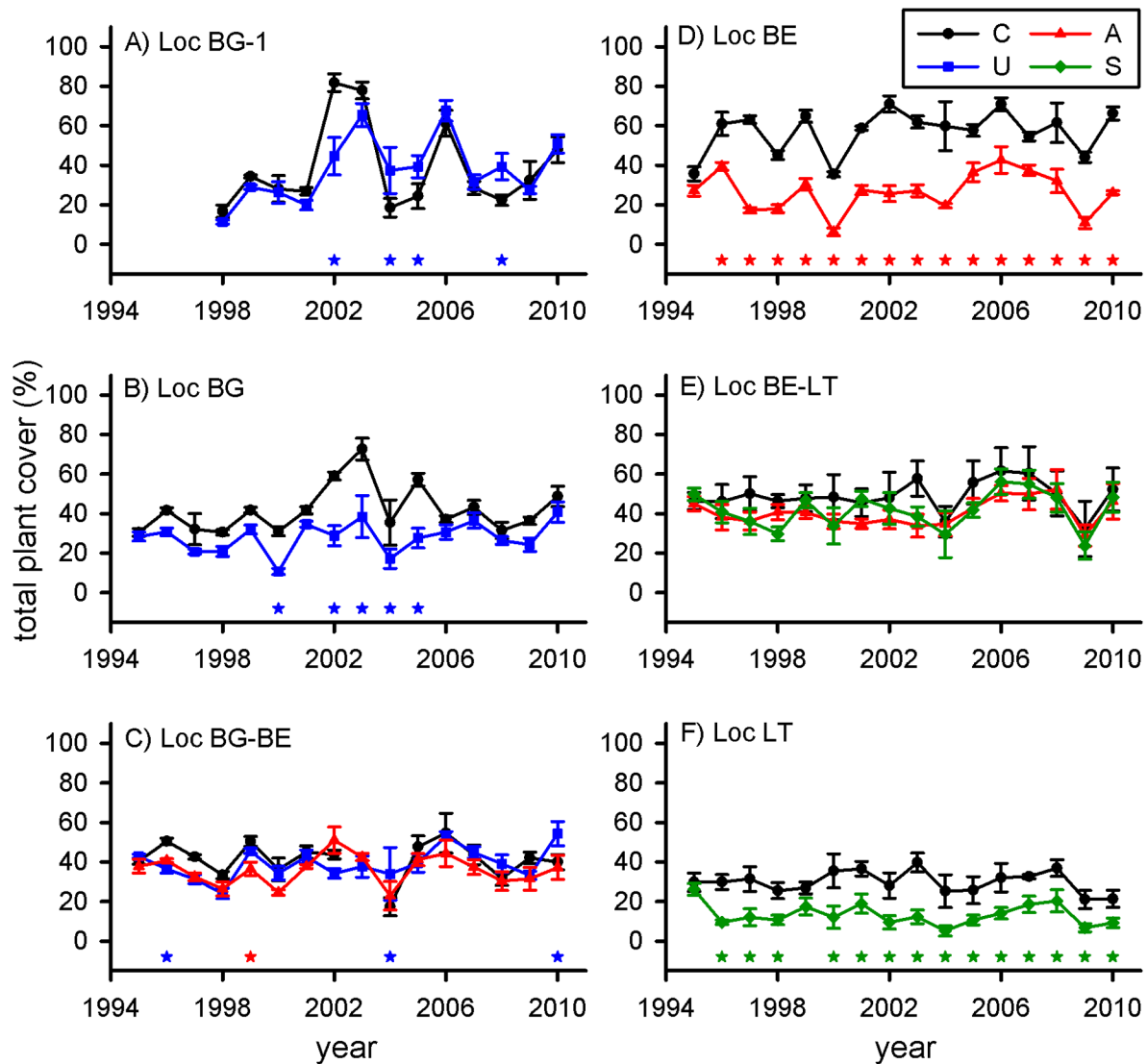


Fig. 7. Total cover (excluding cacti and yucca) (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4.

annuals was high in 1999 and 2002 for most communities, although these years had average precipitation amounts (Fig. 1).

## DISCUSSION

### Patterns in dominance and trends in cover through time

Ecotones at biome transition zones where species co-exist near their geographic limits are

among the most responsive communities to climate-induced mortality of dominant species (Allen and Breshears 1998, Davis and Shaw 2001, Peñuelas and Boada 2003). In the current study of arid-semiarid transition zones, the most consistent response regardless of species removed or community type was an increase in cover by the Chihuahuan Desert dominant grass, *B. eriopoda*, and by other perennial grasses. The rate of increase by *B. eriopoda* in grasslands depended

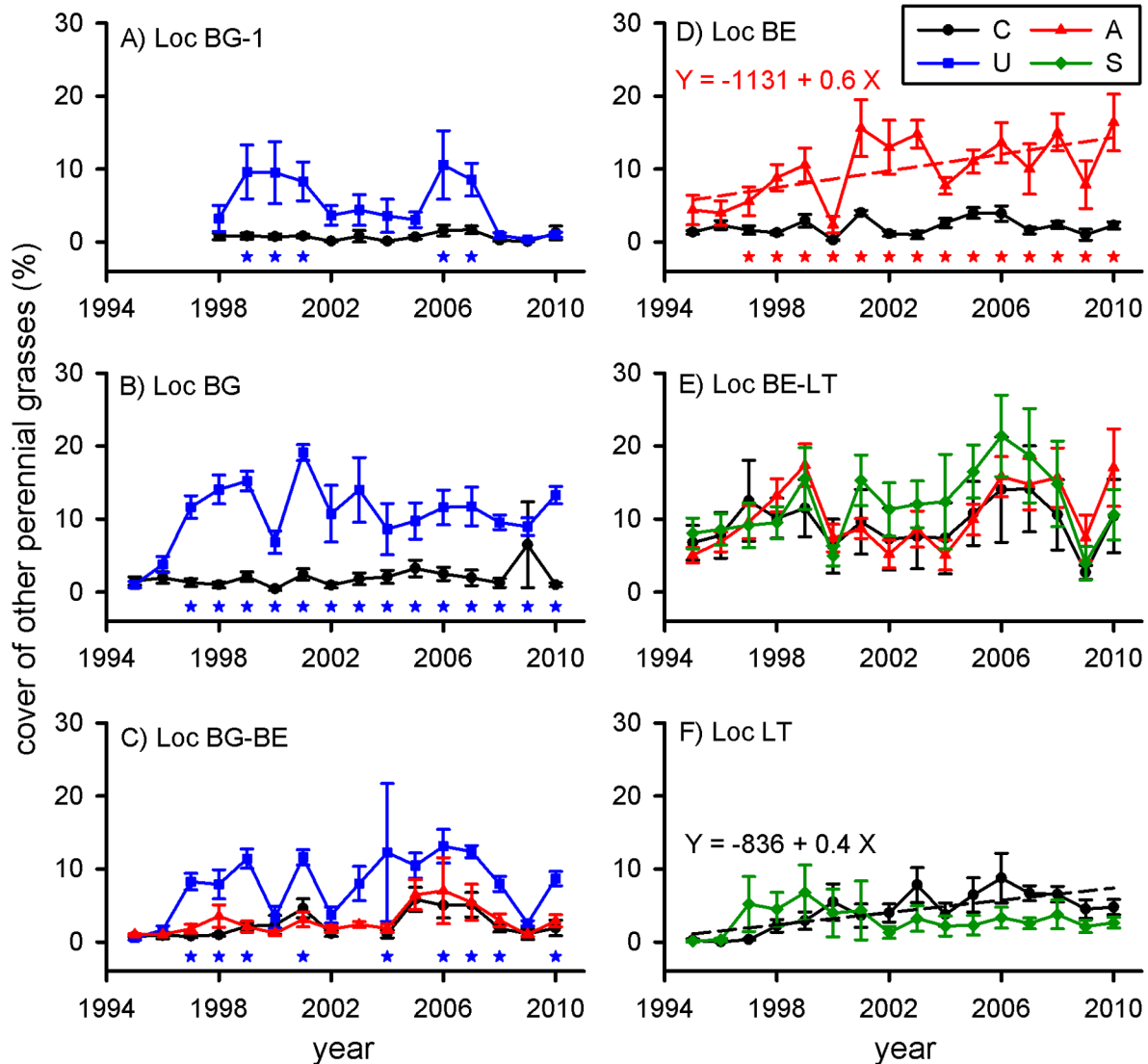


Fig. 8. Cover of sub-dominant perennial grasses (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4. The p-value and  $R^2$  value for the significant temporal trends are as follows: (D) A: 0.012, 0.37 and (F) C: 0.0008, 0.56.

on initial cover, and resulted from both vegetative growth and seedling recruitment from other locations. The lack of a response at the shrubland location may be due to changes in soil properties with shrub encroachment that reduced plant available water to result in very low cover and very low rates of seedling establishment by *B. eriopoda* (Buxbaum and Vanderbilt 2007, Peters et

al. 2010). Thus, a broad-scale loss of the Shortgrass Steppe foundation species, *B. gracilis*, or the Chihuahuan Desert dominant shrub, *L. tridentata*, from mixed grasslands and shrublands would result in *B. eriopoda*- or subdominant grass-covered landscapes that are expected to be more vulnerable to shrub invasion, drought, and livestock grazing than current landscapes that



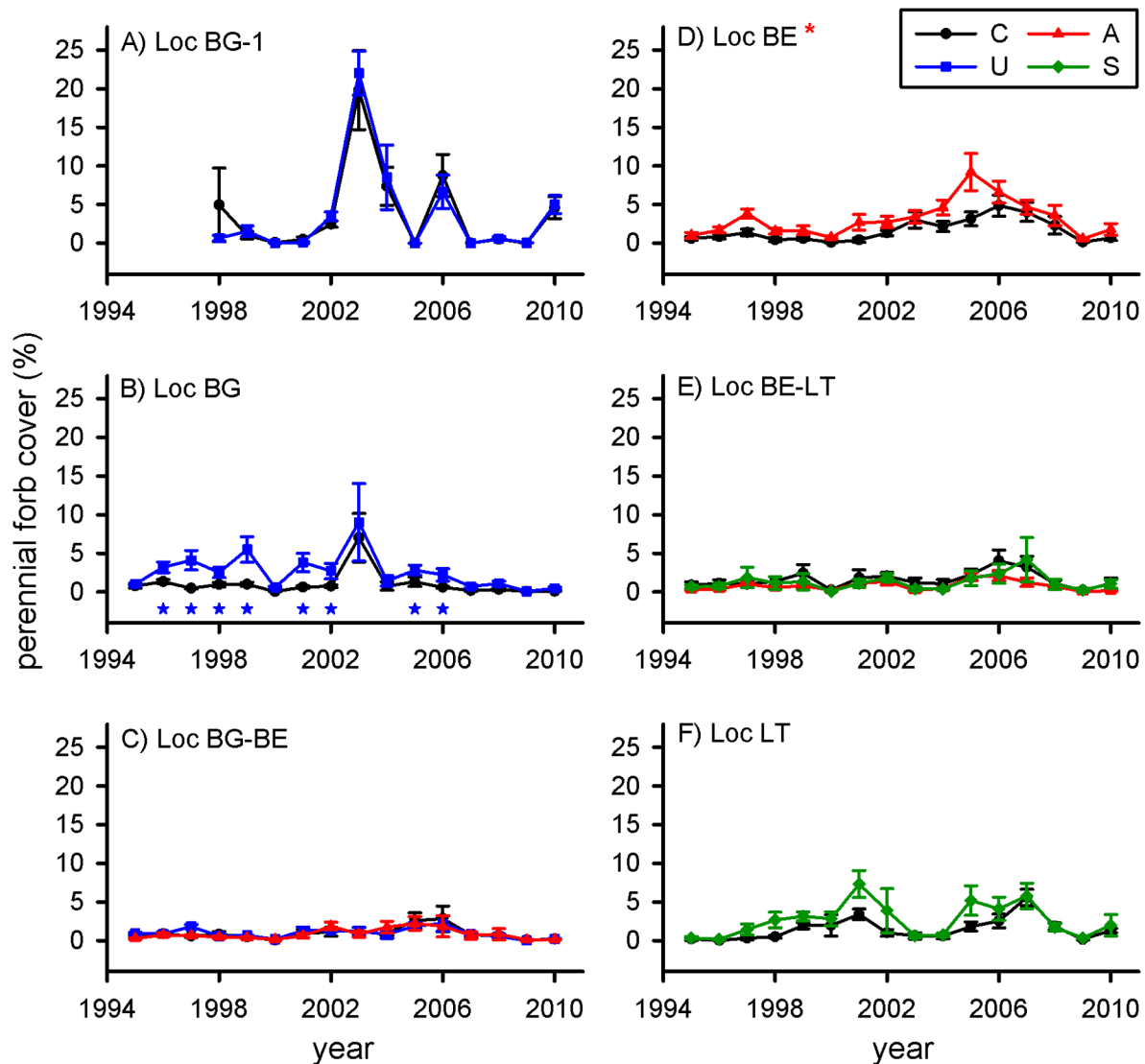


Fig. 9. Cover of perennial forbs (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4. The asterisk next to the location name (Loc BE) indicates overall significant difference between the removal treatment and the control.

contain all three species in various combinations (Humphrey 1958, Miller and Donart 1979, Lauenroth et al. 1994, Peters et al. 2009). By contrast, the lack of response of *B. gracilis* or *L. tridentata* to *B. eriopoda* removal suggests that these communities will change very little if environmental conditions result in broad-scale mortality of *B. eriopoda*.

An increase in cover by *B. eriopoda* through seedling establishment is in contrast to previous studies suggesting that this species is adapted to a historic climate such that current Chihuahuan Desert populations are relics with very low rates of recruitment by seedlings (Valentine 1970, Neilson 1986). Our results suggest that seedling establishment, growth, and survival can occur to

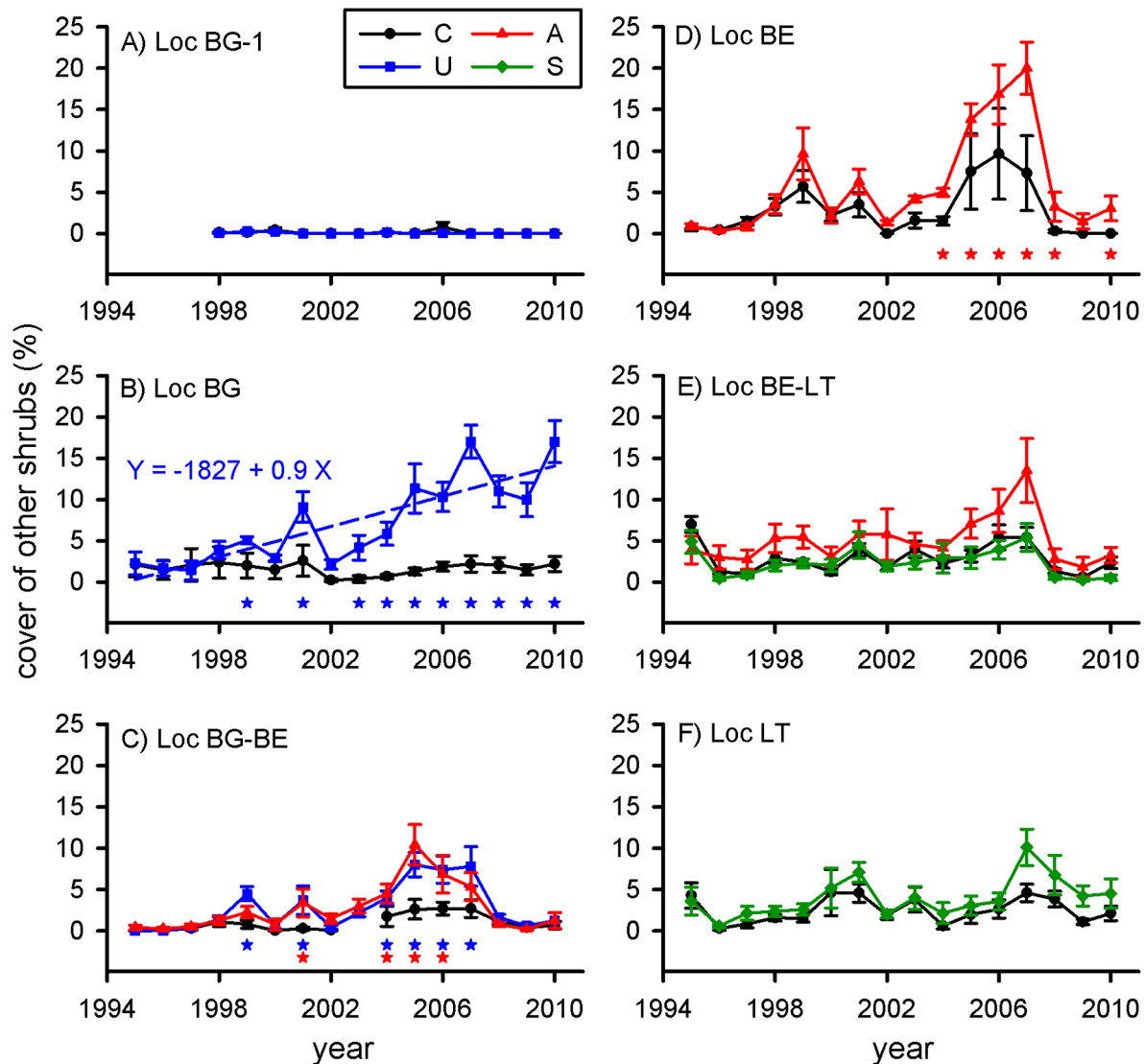


Fig. 10. Cover of sub-dominant shrubs (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4. The p-value and  $R^2$  value for the significant temporal trends are as follows: (B) U:  $< 0.0001$ , 0.71.

allow *B. eriopoda* to dominate grasslands within 8 years following species removals, even for communities with little or no initial cover of this species. These results are supported by simulation analyses showing that recruitment decreases geographically from the Shortgrass Steppe to the Chihuahuan Desert, but remains  $>0$  at this biome transition zone (Minnick and Coffin

1999). However, *B. eriopoda* may be a relic based on current land management practices that promote livestock grazing throughout the region on public and private land, except in protected areas such as the Sevilleta National Wildlife Refuge. Grazing of *B. eriopoda* decreases stolon and flowering culm densities that reduces the ability of plants to survive under variable

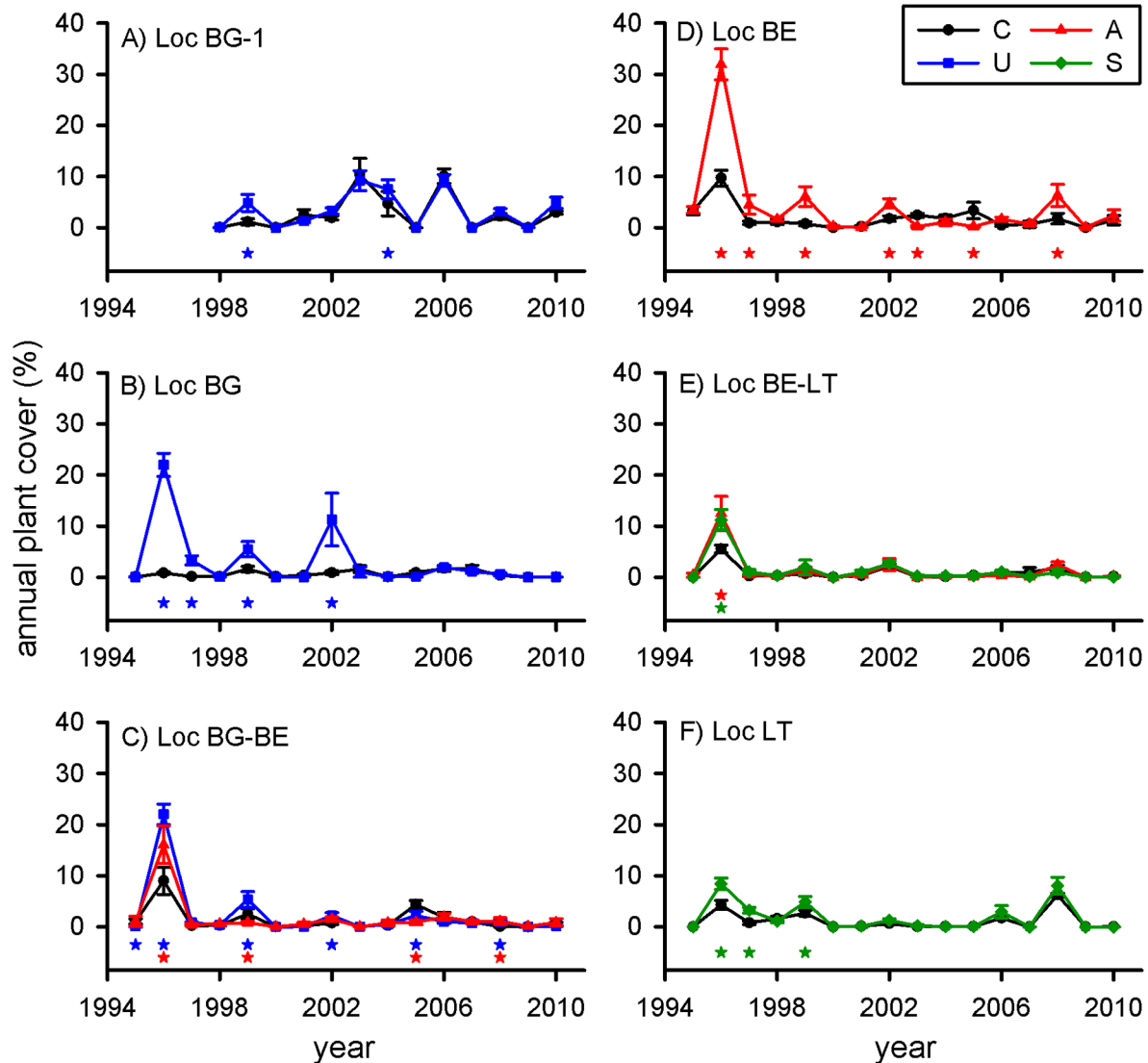


Fig. 11. Cover of annuals (grasses, forbs) (mean,  $\pm$  one standard error) through time on control and removal plots at six locations that include one *B. gracilis*-dominated community (A) BG-1, and locations that span two ecotones: Shortgrass Steppe to Chihuahuan Desert grasslands [(B) *B. gracilis*, (C) *B. gracilis*-*B. eriopoda*, (D) *B. eriopoda*] and Chihuahuan Desert grasslands to shrublands [(D) *B. eriopoda*, (E) *B. eriopoda*-*L. tridentata*, (F) *L. tridentata*] (see Fig. 2 for location names and abbreviations). Symbols are as in Fig. 4.

climatic conditions and to respond following disturbance (Valentine 1970, Miller and Donart 1979).

For most species and functional types, trends in cover through time were related to the remaining species assemblages rather than to variable climatic conditions. Cover of *B. gracilis* and *L. tridentata* remained sufficiently high following removals of the other co-dominant

species to maintain dominance at ecotones where they co-dominated, and cover of *B. eriopoda* increased through time or remained the same. Subdominant perennial grasses increased rapidly following removals in grassland locations, except after *B. eriopoda* removal at the ecotone. Subdominant shrubs increased through time following removal in grassland locations with an exception at BG-1, and were the only group that responded

similarly across locations to a series of wet years (2005–2007). Annuals and perennial forbs had variable cover values through time that were not clearly related to pulses in precipitation and were not synchronized across locations. The only consistent response was an increase in annual cover the first year following removals at all locations, similar to expectations from successional theory (Pickett et al. 2011).

#### *Key processes and constraints explaining responses*

Release from competition and environmental constraints on recruitment and growth are often determinants of community structure following plant mortality (Cavender-Bares et al. 2004, Myers and Harms 2009, 2011). These processes had different levels of importance for the ecotonal and mono-dominated communities studied here. Compensatory increases in cover by *B. eriopoda* following the removal of *B. gracilis* are likely a result of the release of belowground resources, the most frequently limiting resources in arid and semiarid regions (Noy-Meir 1973). The ability of *B. eriopoda* to respond to these resources may be related to its flexible rooting structure and production of stolons that allow rapid recovery following disturbance (Valentine 1970, Fields et al. 1999). By contrast, an increase in cover by the same lifeform, subdominant perennial grasses in grasslands, following species loss in mono-dominated communities indicates overlap in rooting distributions and strong competition that limits their abundance in the presence of a foundation species (Hooper and Vitousek 1997). The release of resources with foundation species mortality would allow these sub-dominant species to increase (Bret-Harte et al. 2008).

The inability of *B. gracilis* or *L. tridentata* to increase in cover following removal of *B. eriopoda* indicates that these species interactions are asymmetric, but the mechanisms for the two species may be different. *B. gracilis* has a relatively inflexible rooting morphology related to the crown structure of a bunchgrass (Coffin and Lauenroth 1991), and has very low rates of seedling establishment that limit its ability to recover following disturbance (Lauenroth et al. 1994, Peters 2000, 2002b). Similarly, the shrub *L. tridentata* does not spread clonally in the Chi-

huahuan Desert, although seed production occurs frequently (Peters et al. 2006b). Because recruitment events were not observed during the time frame of this study, all responses by this species were the result of vegetative increases in shrub canopy cover. Recruitment events may occur in the future for both species that would increase their cover locally to result in their expansion across landscapes through time. The lack of response to-date in our study suggests that adult plants of these dominant species were unable to access water and nutrients made available by the mortality of *B. eriopoda*, and that seed dispersal and recruitment from nearby locations did not occur in the time frame of this study.

The very slow responses of a potential, alternative dominant species in mono-dominated communities, i.e., *B. eriopoda* in locations BG and LT, *B. gracilis* in location BE, and *L. tridentata* in location BE, were likely a result of variation in micro-environmental conditions of soil properties and elevation that affected recruitment and survival (Kröel-Dulay et al. 2004, Buxbaum and Vanderbilt 2007). Seed availability of these species is not expected to be a limiting factor across this relatively small landscape. Both *Bouteloua* species have flowering plants and germinable seeds found in variable abundance throughout the landscape, except in the shrubland community that was not sampled (Peters 2000, 2002a). Because seeds of these grass species are widely dispersed by wind, and the shrubland is within 50 m of communities dominated by these species, seeds are expected to be available to this shrubland community, but soil water is insufficient for establishment on these soils (Peters et al. 2010). Similarly, *L. tridentata* recruits and plants are widely distributed across this landscape at varying densities (Peters et al. 2006b). Plants of this shrub species can produce viable seeds year-round that would be available to all communities studied here.

Biotic and abiotic legacies were less important than other processes to patterns in dominance and composition because of the variable responses to loss of the same species in different community types (i.e., mono- vs co-dominated). Although characteristics of the recovering species relative to site-specific conditions governed dynamics across these ecotones, legacies may be

important for shorter time scales or finer spatial scales than studied here. For example, plant-soil microbial feedbacks play important roles in carbon and nitrogen availability following short-term pulses of precipitation (Collins et al. 2008). Plant-fungal interactions in desert species provide important insights to fine-scale patterns in seedling establishment and initial growth (e.g., Barrow et al. 2008). More detailed studies are needed to determine how these fine-scale processes scale to the community, and if these processes can explain variability in responses for these different communities.

#### *Consequences of fine-scale responses to community and landscape dynamics*

A shift from co-dominance to dominance by one species may alter dynamics at broader-scales in response to drivers such as disturbance, invasive species or climate. At the Shortgrass Steppe–Chihuahuan Desert transition zone, a widespread loss of *B. gracilis* would have serious consequences for landscape dynamics. Because *B. gracilis* communities are resistant to invasion by *L. tridentata*, this shrub species has not expanded to dominate these landscapes under current conditions (Peters et al. 2006a, b). However, changes in climate or land use that result in broad-scale *B. gracilis* mortality, and a subsequent shift in dominance to *B. eriopoda* or other perennial grasses, are expected to lead to broad-scale encroachment by *L. tridentata*, similar to broad-scale conversion throughout the Chihuahuan Desert over the past 150 years (Gibbens et al. 2005). These transformations from grasslands to shrublands are part of the desertification process that includes increases in erosional losses of water, soil, and nutrients, and changes in plant and animal populations that feed back to maintain shrublands through time (Schlesinger et al. 1990, Kieft et al. 1998, Sanchez and Parmenter 2002, Hochstrasser and Peters 2004, D’Odorico et al. 2007, Kurc and Small 2007, Ravi et al. 2010).

*Bouteloua eriopoda* has decreased in cover, abundance, and dominance throughout the American Southwest over the past several centuries as a result of livestock overgrazing during periods of extended, severe drought (Dick-Peddie et al. 1999). The loss of this species at this biome transition zone would eventually

result in a landscape with communities dominated by one of two grazing-tolerant species, *B. gracilis* or *L. tridentata*, that are very stable under current conditions. However, *B. gracilis* recovers very slowly or not at all following disturbance that kills plants (Coffin et al. 1996); thus these communities would become vulnerable in the long-term to effects of intense soil disturbance, such as prairie dog colony activity. A shift from grasslands to *L. tridentata* communities would result in desertified shrublands (Schlesinger et al. 1990).

*Larrea tridentata* populations at this transition zone are near their physiological limits to cold temperatures (Martinez-Vilalta and Pockman 2002); thus a change in climate to more extreme temperatures would result in widespread shrub mortality. This loss of *L. tridentata* would lead to grassland communities dominated or co-dominated by the two *Bouteloua* species, each with different sensitivities to soil disturbance, climate, and invasive species. These grasslands dominated landscapes throughout the Shortgrass Steppe–Chihuahuan Desert transition zone prior to widespread encroachment by *L. tridentata* beginning in the late 1800s.

In mono-dominated communities, a shift to species that are currently sub-dominants is expected to result in greater invasibility by exotic grasses (e.g., *Pennisetum ciliare* [buffelgrass], *Eragrostis lehmanniana* [Lehmann lovegrass]) and forbs (e.g., *Centaurea repens* [Russian knapweed], *C. solstitialis* [yellow star thistle], *Peganum harmala* [African rue]) that are increasing regionally with global warming and changes in precipitation regimes (Anable et al. 1992, Cox et al. 1988, Williams and Baruch 2000, Arriaga et al. 2004, Bradley 2009). Invasive, exotic species can have a myriad of effects on community structure with direct and indirect effects on ecosystem services (Mooney and Cleland 2001, Pejchar and Mooney 2009).

## CONCLUSIONS

Transition zones between the Shortgrass Steppe and Chihuahuan Desert have been persistent in the American Southwest over the past several centuries. As environmental drivers continue to change, often in nonlinear and unpredictable ways that go beyond the range of



historic variability (IPCC 2007), species distributions will also be affected (Williams et al. 2007, Jackson et al. 2009) to influence the vulnerability of these arid and semiarid landscapes to future drivers. This study showed that trends in cover through time following loss of the current dominant species were related to the remaining species assemblages rather than to variable climatic conditions. In ecotonal communities, resident co-dominant species increased to dominance following the loss of a foundation species with little change in community composition. In mono-dominated communities, dominant species loss resulted in a shift to species that are currently sub-dominants of the same functional type as the species that was removed.

The most common response regardless of the identity of the species removed or the community type was an increase in cover by sub-dominant grasses and by the arid grass species (*Bouteloua eriopoda*). The rate of increase by *B. eriopoda* depended on initial cover, and resulted from both vegetative growth and seedling recruitment from other locations. Seed dispersal and seedling recruitment from other locations were not found for the semiarid grass, *Bouteloua gracilis* or the arid shrub, *Larrea tridentata*. Because *B. eriopoda* is more susceptible to shrub invasion, drought, and livestock grazing than the other two foundation species, widespread loss of either of the other species and subsequent increase in *B. eriopoda* is expected to result in an increase in landscape-scale vulnerability to these environmental drivers. The extent and magnitude of these consequences will depend on the plant-scale processes associated with the ability of species to respond, either as adults or recruits, relative to the micro-environmental conditions of the site rather than climatic variability or legacies associated with the mortality of different species.

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