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Effects of bannertail kangaroo rat mounds on small-scale plant community structure

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Abstract The effects of bannertail kangaroo rat (*Dipodomys spectabilis*) mounds and associated soil-surface disturbance on plant species composition and diversity in the Chihuahuan Desert were examined with multivariate analysis. Kangaroo rat mounds created disturbance gaps and contributed to local species diversity by creating microhabitats that supported unique plant communities. These microhabitats supported populations of species that were relatively rare in surrounding areas. The diversity observed at the whole habitat level resulted from (1) local spatial heterogeneity, because the mounds offered microenvironments with distinctive nutrient, water, and light conditions; and (2) local patterning of disturbance, because the digging and traffic of the kangaroo rats maintained high levels of soil disturbance at and near the mounds. At a finer scale, species diversity was highest in the area immediately adjacent to active and inactive mounds, and was lower on both the highly disturbed soil of the mounds and in the relatively undisturbed area between mounds. Lowest species diversity occurred on inactive mounds. Annual plant biomass was much greater on mounds than in inter-mound areas. The results support the predictions that intermediate levels of disturbance and small-scale environmental heterogeneity contribute to supporting high species diversity.

Key words Kangaroo rat mound · Disturbance · Microhabitat · Diversity · Intermediate disturbance hypothesis (IDH)

Introduction

Environmental heterogeneity and disturbance (especially at moderate levels), among others, have been considered as major factors that can promote and support high species diversity (MacArthur et al. 1966; Rosenzweig and Winakur 1969; Cody 1975; Abugov 1982; Sousa 1984). It is still not well understood, however, how and at what scale environmental heterogeneity and disturbance affect species diversity in a particular habitat (Huston 1979). For the plant community, the mosaic of disturbance patches of different biotic and abiotic conditions may be simultaneously a source of mortality of individuals for some species in some microsites and a source of establishment microsites for others, thus permitting more species to coexist in the overall habitat (Denslow 1980). Differences in disturbance level by kangaroo rats on the mounds versus inter-mound areas provide a remarkable degree of small-scale (within meters) environmental heterogeneity and may be important in maintaining species diversity in arid landscapes (Hawkins and Nicoletto 1992).

In the southwestern United States, kangaroo rat mounds are conspicuous features of some landscapes, and they form a mosaic of disturbance patches of distinctive environmental conditions (Schroder and Geluso 1975). Further, disturbance level (measured as the intensity of kangaroo rat activity and its disturbance on soils) decreases from mounds to inter-mound areas, although disturbance level might not be linearly correlated with the distances from the mounds. The gradient of decreasing disturbance from mounds to inter-mound areas provides a test of the intermediate disturbance hypothesis (IDH; Paine and Vadas 1969; Horn 1975; Connell 1978; Huston 1979; Abugov 1982; Miller 1982). This hypothesis predicts that an intermediate level of disturbance will produce highest species diversity (Paine and Vadas 1969; Horn 1975; Connell 1978; Miller 1982). At high levels of disturbance only fugitive species can survive and reproduce, and conversely, at low levels of disturbance only competitive species can persist. Consequently, highest

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diversity should be at an intermediate level of disturbance where both kinds of species coexist. The IDH would predict that the areas immediately surrounding mounds can be regarded as ecotones which should support highest species diversity.

Early attempts to investigate the effects of animal burrowing activity and associated mounds on vegetation compared two types of factors on and off mounds: (1) biomass in relation to soil condition (pocket gopher: Mielke 1977; Grant et al. 1980; Tilman 1983; Reichman and Smith 1985; Spencer et al. 1985; Huntly and Inouye 1988; prairie dogs: Agnew et al. 1986; kangaroo rat: Schroder and Geluso 1975; Mun and Whitford 1990) and (2) individual plant species coverage (e.g., Moroka et al. 1982; Reichman and Smith 1985; Moorhead et al. 1988; Mun and Whitford 1990). For example, previous results showed that, in comparison to the surrounding habitat, kangaroo rat mounds: (1) were dominated by different plant species; (2) supported more annual plant cover and biomass relative to inter-mound areas; and (3) exhibited higher soil nitrogen content and greater water loss after rainfall (Moorhead et al. 1988; Mun and Whitford 1990).

The banner-tailed kangaroo rat, *Dipodomys spectabilis*, is a large, bipedal, granivorous rodent in arid and semiarid regions of the southwestern United States and northern Mexico (Vorhies and Taylor 1922; Holdenreid 1957; Best et al. 1988; Brown and Heske 1990). These animals create large, conspicuous mounds (3–5 m in diameter and up to 1 m in height; Fig. 1) in which they not only live but also store large quantities of seeds (Best 1972; Kay and Whitford 1978; Best et al. 1988; Brown and Heske 1990; Mun and Whitford 1990; Brown and Harney 1993). Kangaroo rats affect other organisms and ecosystem processes in several ways. They may regulate their own and other rodent species' foraging intensity and pattern by intra- and interspecies aggression around mounds (Frye 1983; Bowers et al. 1987; Bowers and Brown 1992; Hawkins and Nicoletto 1992). They also create disturbed microhabitats and thereby alter structure, water availability, nutrient concentration, and organic matter content of the soil (Moorhead et al. 1988; Mun and Whitford 1990). Mounds provide favorable microhabitats for a large number of vertebrates, invertebrates, and microbial symbionts (Hawkins and Nicoletto 1992). Further, the disturbed microhabitats of occupied and abandoned mounds create a mosaic of successional microsites that serve as germination sites and "source" microhabitats for fugitive plant species (Kalisz and Stone 1984; McConnaughay and Bazzaz 1987) and therefore affect plant microspatial distribution (Guo 1994). Consequently, the presence of kangaroo rats creates a patchy landscape and increases fine-scale environmental heterogeneity, potentially promoting and maintaining plant species diversity.

Fig. 1 A typical active mound of *Dipodomys spectabilis* at the study site. Mounds usually have several entrances, tunnels, and chambers and can persist for decades being reused by many generations (photo from Brown and Harney 1993)

After a mound is abandoned, soil properties such as nitrogen content, moisture, and temperature undergo additional changes (Hawkins and Nicoletto 1992; Mun and Whitford 1990). Active mounds contain large caches of seeds and other plant materials, as well as urine and feces of the occupants (Monson 1943; Hawkins and Nicoletto 1992). There is also higher content of organic matter (especially living or standing dead plants) on inactive mounds, and these organic materials decompose, increasing the nitrogen content in the soils. In general, nitrate, total nitrogen, and N mineralization potential of the mound soils are higher than those of inter-mound soils (Greene and Reynard 1932; Moorhead et al. 1988; Mun and Whitford 1990). Since mound soils lose water faster than intermound soils through both runoff and infiltration, soil moisture is higher in inter-mound areas than in mound soils (Moorhead et al. 1988; Mun and Whitford 1990). Once abandoned by kangaroo rats, mounds collapse and undergo a successional process that begins the development of dense vegetation (Hawkins and Nicoletto 1992).

Even though earlier reports have shown significant differences between plant communities on the mounds and intermound areas, there was no attempt to investigate the mechanisms and variations in plant life-history traits associated with the successional processes after the mounds were created and abandoned. One predominant hypothesis in successional theories is that earlier species often have greater dispersal power (smaller seeds) and higher growth rates than later ones (Salisbury 1975; Huston and Smith 1987). In this study I use kangaroo rat mounds to examine the effects of kangaroo rat mounds on small-scale plant community structure and then to explain the functional roles of animal-produced disturbance gaps in promoting and maintaining local high plant species diversity. The goal is to test two hypotheses:

1. The presence of kangaroo rat mounds increases habitat heterogeneity and thus promotes higher species diversity.
2. Disturbance at an intermediate level results in highest species diversity at the edges of mounds.

Finally, rather than extensively examining all life history traits, I use available data to compare two potentially important traits, seed size and plant size (i.e., biomass) between earlier and later species (i.e., between species that dominate on mounds and intermound areas) to provide some insights on the successional mechanisms in arid ecosystems.

Methods

The study was conducted in the winter and summer of 1992 at a long-term study site in a northern portion of the Chihuahuan Desert near Portal, Arizona. Livestock have been excluded from this site since 1977 (Brown and Munger 1985). The region is relatively flat with alluvial soils, but there is substantial finer-scale variation, much of it associated with *D. spectabilis* mounds. The 20-ha study site was located in the transition zone between shrubland and grassland, and supports relatively high plant diversity: 44 species of winter annuals and perennials, 30 species of summer annuals and perennials were recorded during this study. The vegetation was dominated by shrubs (i.e., *Acacia constricta*, *Flourensia cernua*, *Ephedra trifurca*, *Gutierrezia sarothrae*) mixed with grasses (e.g., *Eragrostis*, *Aristida*). The most abundant annual plants were *Eriogonum abertianum* and *Haplopappus gracilis*. In correspondence to the bimodal distribution of annual precipitation, two distinct assemblages of annuals, winter and summer, occur with high predictability (Davidson et al. 1985). Of total annual precipitation (248 mm), 30–40% generally falls in the winter and 60–70% in the summer (Martin 1963; Davidson et al. 1985).

Winter annuals were censused in April and May of 1992, after the winter growing season. Summer annuals were censused in September 1992, after the onset of the fall dry season. Radiating out from each mound, a transect of five 0.25-m^2 plots was established along the disturbance gradient from mound center to maximum inter-mound distance. The transects were oriented in random directions but constrained to avoid the effects of other mounds. The plots along the transects centered on active mounds were referred to as A, B, C, D, and E and those on inactive mounds as a, b, c, d, and e. The distance from plot A to plot B was 1–1.5 m (from center to the edge of mound depending on the mound size), from B to C was 2 m, from C to D was 3 m, and from D to E was 4 m. The distances between plots were similar for inactive mounds. To measure population densities, plants were counted by species on each plot. To estimate biomass, 5–20 individuals for each species in each plot (depending on the abundance) were harvested, dried, and weighed. Then total biomass was calculated by multiplying mean biomass by the number of individuals of that species in each plot. A total of 28 active and 32 inactive mounds, were surveyed in the winter, and a random subset of these, 16 active and 16 inactive mounds, were surveyed in the summer. The smaller number of mounds surveyed in the summer was justified, because analysis of the winter data showed that this sample provided enough statistical power for the multivariate analysis.

To analyze the impact of kangaroo rat activity and their mounds on small-scale plant community structure and species diversity, the mounds were categorized as either active or inactive. It was easy to identify active or inactive mounds, based on signs of recent rodent activity. However, there was great variation within each class: active mounds exhibited different levels of disturbance, and inactive mounds had been abandoned for different lengths of time and were in different stages of succession. Time of abandonment, known in some but not all cases (some were surveyed on kangaroo rat exclusion plots where kangaroo rats have been excluded for different period of times), varied from 4 to 15 years (also see Schroder and Geluso 1975).

To determine whether disturbance at an intermediate level could support higher species diversity, I stratified study plots along a disturbance gradient that spanned a range of soil conditions from mounds to off-mound areas (the intensity of overall kangaroo rat activity decreases from mounds to off-mound areas). In cases where the mounds and the immediate vicinity were highly disturbed, B-plots were placed a little further away from the mounds, thereby increasing distances between A and B plots) to assure that the plots were in the ecotonal areas between highly disturbed areas and inter-mound areas.

Canonical discriminant analysis (CDA) was used to characterize describe plant community structure along the disturbance gradient by reducing the dimensionality of the species density data (SAS 1988). CDA is a technique related to principal component analysis that uses dummy variables to separate discrete categories of observations, in this case the five locations of plots (A to E) along the disturbance gradient. It also employs Mahalanobis squared distance (D^2), which can be used to detect the correlations between "treatment" variables. First, CDA analyses were performed on active or inactive mounds separately to investigate the changes in small-scale plant community structure from mounds to inter-mound area. Then, in order to describe the community dynamics (i.e., the changes in community structure after the mounds were abandoned), I combined the data from both active and inactive mounds to perform one CDA analysis to examine the trajectories of sample change in multivariate space. Plant density data for all species were log-transformed before performing CDA. Species diversity was measured by species richness.

Finally, in an effort to understand the mechanisms of microsuccession of plant communities when the mounds were created and abandoned, I compared characteristics (particularly seed size) of the pioneer (or fugitive) species, which first occupy the disturbed mounds, with other plants in the local habitat. The published seed size data from Samson et al. (1992) and measurements from the field collection during this study were used.

Table 1 Pairwise Mahalanobis distances (D^2) between groups of plots showing the similarities between plant communities on different plots along the disturbance gradient. Small D^2 indicates high degree of similarity. Values located above diagonals are for active mound and values located below the diagonal are for inactive mounds

Pairwise Mahalanobis distances (D^2)						
Winter						
	A	B	C	D	E	
a		7.97	17.69	18.26	15.37	A
b	17.03		9.94	11.39	10.61	B
c	24.89	8.55		1.77	4.23	C
d	25.19	10.36	3.19		3.51	D
e	32.08	13.98	6.24	2.91		E
	a	b	c	d	e	
Summer						
	A	B	C	D	E	
a		18.55	21.92	17.71	21.32	A
b	34.02		6.43	6.62	6.51	B
c	41.49	7.56		3.17	2.11	C
d	47.27	13.05	3.09		2.31	D
e	53.78	14.88	4.17	1.68		E
	a	b	c	d	e	

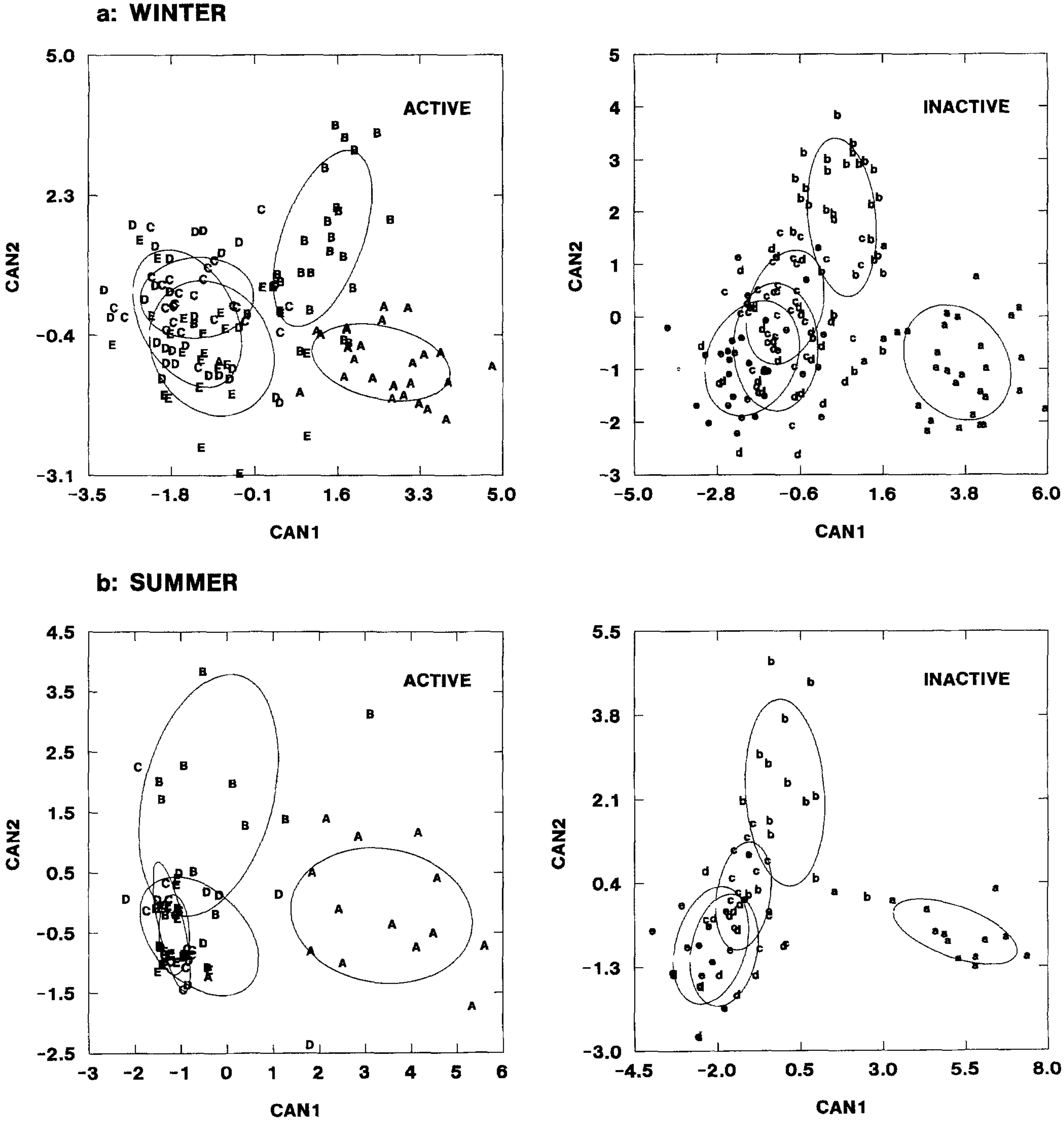

Fig. 2 Results of canonical discriminant analysis (CDA) showing separation of microhabitat communities along the disturbance gradient on kangaroo rat mounds from A-plots (on mounds; highly disturbed) to B-plots (adjacent to mounds; intermediately disturbed) and C, D, E plots (≥2 m away from mounds; least disturbed). B-plots can also be considered ecotone locations between communities on mounds and off mounds. *Ellipses* represent 95% bivariate confidence intervals for total samples within each microhabitat group (*CAN 1*, first canonical axis, *CAN 2*, second canonical axis)

Results

The first prediction, that the presence of kangaroo rat mounds increases habitat heterogeneity and thus promotes higher species diversity, was supported by the data. Canonical discriminant analysis indicated that kangaroo rat mounds (plots A, a) support a distinctive combination of plant species when compared with immediately surrounding areas, for example, the vegetation on active mounds after the winter growing season was clearly different from the vegetation in the less disturbed areas (Fig. 2). The first two canonical axes (CAN 1 and CAN

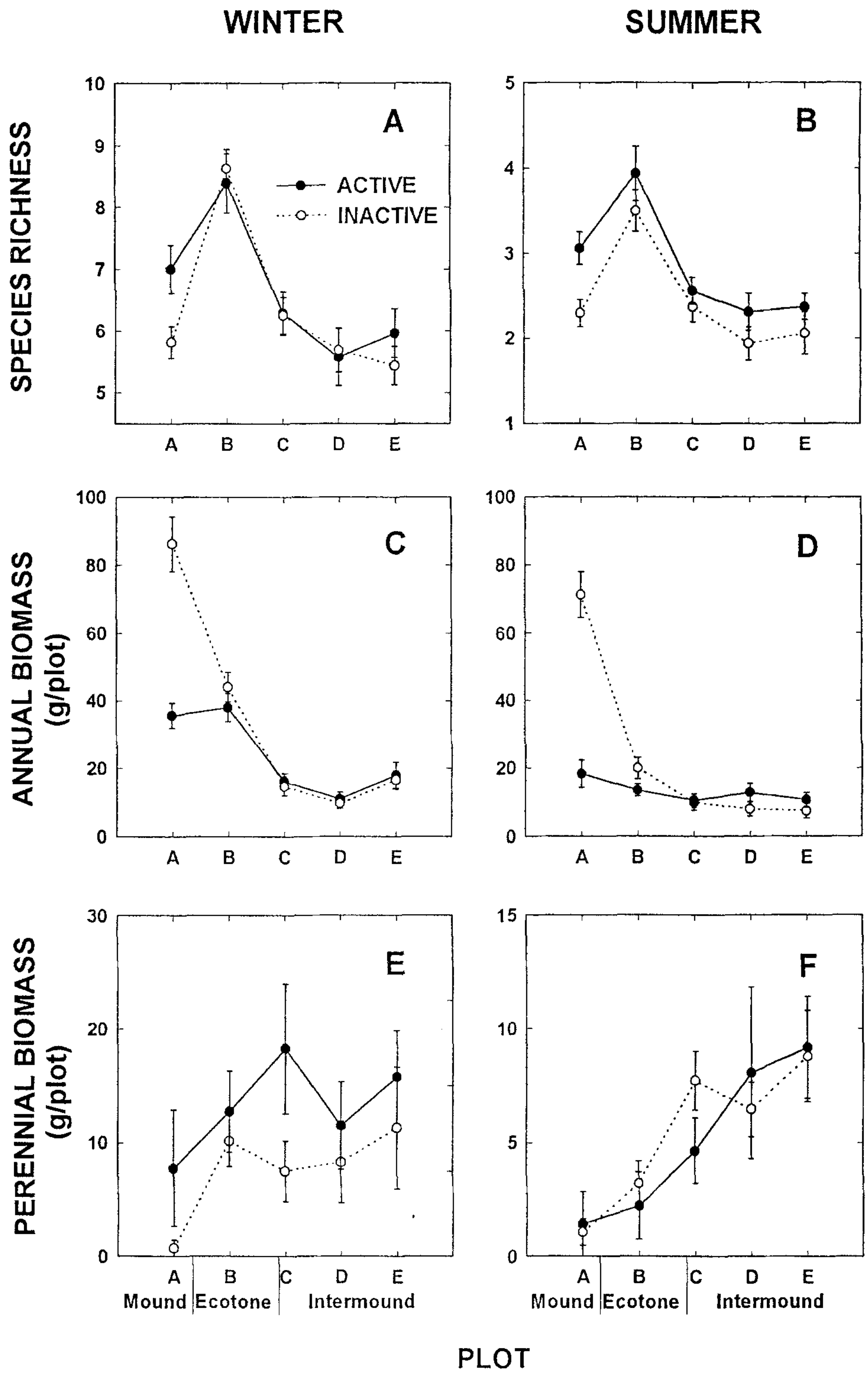

Fig. 3A–F Patterns of species diversity (±SE; **A** winter, **B** summer) and plant biomass (±SE; **C**, **D** annuals, **E**, **F** perennials) along the disturbance gradient from mound tops (A, a plots) to inter-mound areas (C, c, D, d, E, e plots)

2) accounted for 86% (68% and 18% for CAN 1 and CAN 2, respectively) of total variation for active mounds and 88% (70% and 18% for CAN 1 and CAN 2, respectively) for inactive mounds. Similar patterns were found in separate analyses of inactive mounds in winter and active and inactive mounds in summer (Fig. 2). The first two canonical axes accounted for 89% (70% and 19% for CAN 1 and CAN 2, respectively) of total variation for active mounds and 95% (80% and 15% for CAN 1 and CAN 2, respectively) for inactive mounds. In both winter and summer, the vegetation on inactive mounds appeared to be the most distinctive (Fig. 2). The species composition of plant communities at the edges of mounds (plots B and b) also separated clearly from those on the mounds and those in inter-mound areas (plots C, c, D, d, E, e). These unique mound-edge species assemblages reflected either intermediate disturbance regimes (on active mounds) or ecotones (between both active and

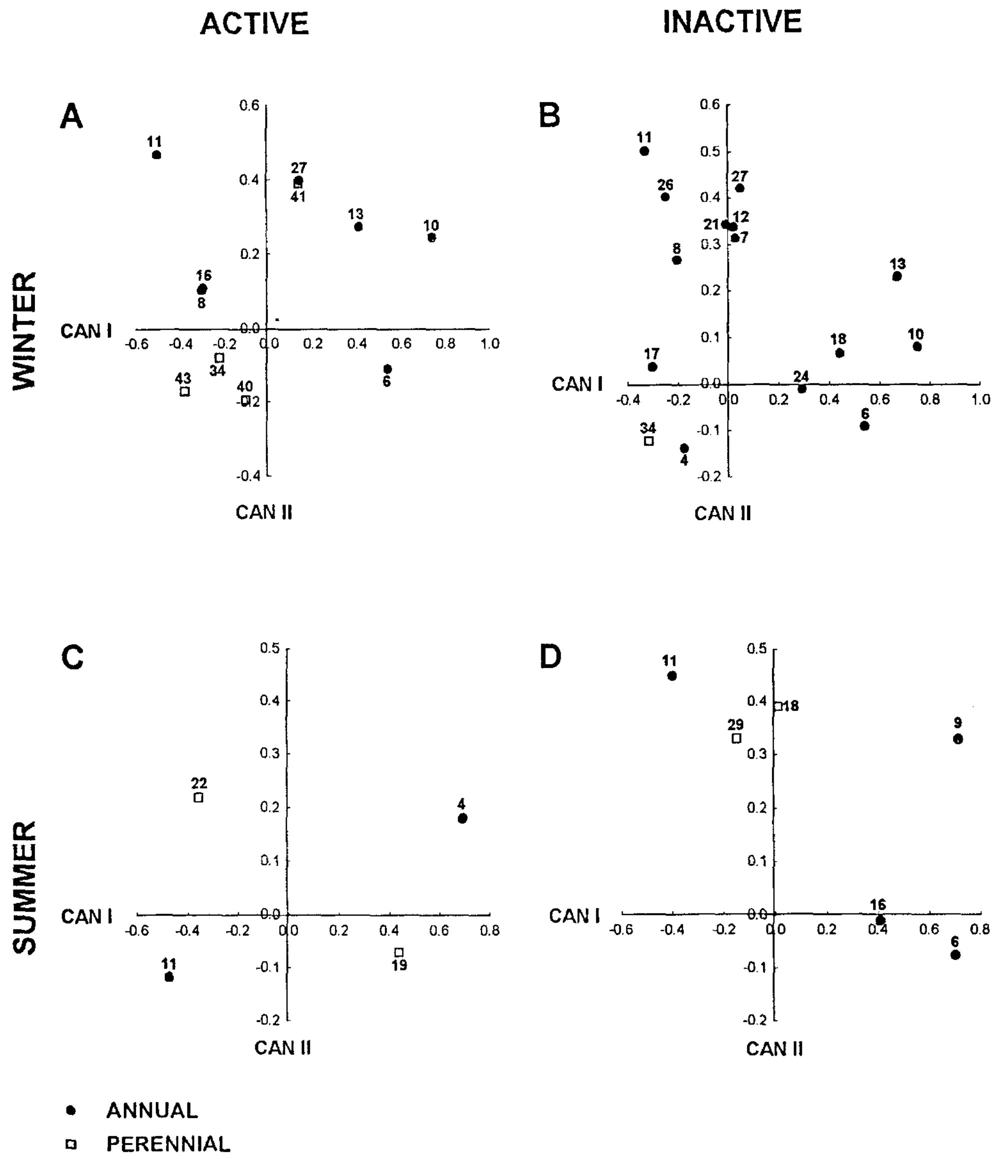

Fig. 4A–D Plots of total canonical structure for **A**,**B** winter plants (including perennials) and **C**,**D** summer plants (including perennials) from four separate analyses on both active and inactive mounds. Note that only the species that showed significant differences in abundance along the disturbance gradient are plotted and marked with *numbers* (identified in Table 2)

inactive mounds and inter-mound microhabitats). However, beyond this ecotonal area there was no detectable relationship between plant species and mound disturbance. Vegetation samples ≥2 m from the edge of the mound overlapped broadly in CDA space (Fig. 2).

Similarities among samples along the gradient were estimated by Mahalanobis distances (D^2; Table 1). On active mounds, in both winter and summer, plots at the mound edge (B) were more similar to those on the mound (A) than to those in the inter-mound areas (C, D, E; Table 1). In contrast, the vegetation in plots at the edge of inactive mounds (plot b) was more similar to the vegetation off the mounds (c, d, and e) than those on the abandoned mounds (a) (Table 1).

The second prediction, that an intermediate level of disturbance would produce highest species diversity, was also supported. Species diversity (measured as species richness) was highest in the area immediately adjacent to active and inactive mounds (plots B, b), and was lower on both the highly disturbed soil of the mounds (plots A, a) and in the much less disturbed area between mounds (plots C, c, D, d, E, e). Inactive mounds exhibited the lowest species diversity (Fig. 3a, b). Compared with inactive mounds, active mounds supported more annual plant species and lower biomass. The finding that both active and inactive mounds supported higher annual plant biomass than inter-mound areas corresponded with Moroka et al. (1988) and Moorhead et al. (1988). However, perennial biomass typically showed the reverse pattern (Fig. 3e, f; Moroka et al. 1988).

The relationships and patterns of the individual species summarized in Fig. 4 and Table 2 suggest that the responses of species to disturbance and microhabitat variation were highly individualistic. The species falling to the right on the first axis (CAN I) dominated the samples on mounds (active or inactive), whereas the species on left-hand side were most abundant in the inter-mound areas. In winter, *Eriogonum abertianum*, *Descurainia pinnata*, and *Chenopodium fremontii*, were more abundant on the mounds than in the intervening habitat, and

Table 2 Responses of winter and summer annuals to soil-surface disturbance by kangaroo rats (i.e., variance among plot positions along the transect from mounds to inter-mound areas; ***F*** test on density data) (*np* not present)

	Acitve mound	Inactive mounds
Winter		
Annual	*F* (*df*=135)	*F* (*df*=155)
1 *Astragalus allochrous*	0.25	1.44
2 *A. nuttalianus*	0.44	np†
3 *Baileya multiradiata*	1.34	1.50
4 *Calycoseris wrightii*	1.00	3.25
5 *Chaenactis stevioides*	0.79	0.16
6 *Chenopodium fremontii*	9.92***	12.67***
7 *Cryptantha crassisepala*	1.72	2.34
8 *C. micrantha*	2.96*	3.03*
9 *Delea brachystachys*	1.00	1.00
10 *Descurainia pinnata*	25.79***	33.08***
11 *Eriastrum diffusum*	13.28***	11.01***
12 *Erigeron divergens*	0.13	2.60*
13 *Eriogonum abertianum*	7.48***	25.07***
14 *Erodium cicutarium*	0.47	1.03
15 *Eschscholtzia mexicana*	1.51	0.60
16 *Gilia sinuata*	3.16*	1.61
17 *Haplopappus gracilis*	0.82	3.11*
18 *Lepidium lasiocarpum*	1.56	7.48***
19 *Lesquerella gordoni*	0.52	np
20 *Lipinus coccinus*	1.00	1.14
21 *Malacothrix fendleri*	1.82	2.74*
22 *Microseris linearifolia*	0.76	1.71
23 *Oenothera primiveris*	1.37	2.15
24 *Phacelia arizonica*	5.33***	3.83**
25 *Plantago purshii*	0.18	0.34
26 *Spermolepis echinata*	2.01	6.02***
27 *Stephanomeria exigua*	3.08*	7.95***
28 *Vulpia octoflora*	0.27	0.55
Perennial		
29 *Aristiada hamulosa*	1.00	1.00
30 *A. longiseta*	1.96	2.39
31 *Bahia absinthifolia*	0.60	1.45
32 *Cassia bauhinioides*	1.41	2.07
33 *Eragrostis lehmanniana*	0.75	np
34 *Gutierrezia sarothrae*	2.79*	4.46**
35 *Haplopappus spinulosus*	1.14	0.75
36 *H. tenuisectus*	0.50	0.73
37 *Hoffmanseggia densiflora*	0.36	0.87
38 *Perezia nana*	0.83	np
39 *Rumex augustifolia*	1.45	0.25
40 *Sida procumbens*	3.24*	0.75
41 *Solanum elaeagnifolium*	3.24*	0.28
42 *Sphaeralcea laxa*	0.79	np
43 *Tridens pulchellum*	4.69**	1.90
44 *Zinnia grandiflora*	np	1.00
Summer		
Annual	*F* (*df*=75)	*F* (*df*=75)
1 *Aristida adscensionis*	0.75	1.00
2 *Bahia biternata*	1.00	np
3 *Baileya multiradiata*	1.63	np
4 *Bouteloua aristidoides*	11.54***	0.75
5 *B. barbata*	1.07	np
6 *Chenopodium fremontii*	2.41	14.85***
7 *Dalea brachystachys*	0.75	np
8 *Erigeron divergens*	1.00	np
9 *Eriogonum abertianum*	0.81	20.68***
10 *Euphorbia serpyllifolia*	0.06	1.00
11 *Haplopappus gracilis*	4.03**	2.87*
12 *Machaeranthera tanacetifolia*	0.50	np
	Active mounds	Inactive mounds
Summer		
Annual	*F* (*df*=75)	*F* (*df*=75)
13 *Panicum arizonicum*	1.00	1.00
14 *Portulaca parviflora*	0.75	1.00
15 *Sida spinosa*	0.75	1.00
16 *Tidestromia lanuginosa*	1.98	3.26*
Perennial		
17 *Aristida hamulosa*	0.52	1.07
18 *A. longiseta*	1.00	2.14
19 *Atriplex acanthocarpa*	3.31*	0.94
20 *Cassia bauhinoidis*	0.50	1.09
21 *Croton corymbulosa*	0.52	np
22 *Gutierrezia sarothrae*	2.52*	1.63
23 *Haplopappus tenuisectus*	0.77	1.00
24 *Hoffmanseggia densiflora*	1.00	np
25 *Muhlenbergia porteri*	1.00	2.06
26 *Perezia nana*	1.00	np
27 *Sporobolus contractus*	np	0.79
28 *Talinum angustissimum*	0.96	1.00
29 *T. aurantiacum*	0.50	2.57*
30 *Tridens pulchellum*	1.33	1.54

* $0.01 < P < 0.05$, ** $0.001 < P < 0.01$, *** $P < 0.001$

also had much higher density on inactive mounds than on active mounds. *Lepidium lasiocarpum* dominated only inactive mounds. The species which loaded heavily on the second axis (CAN II) were mostly found in the ecotones at the edge of the mounds (plots B, b; Fig. 4). Most conspicuous species among those were the winter annuals *Eriastrum diffusum* and *Stephanomeria exigua* on active mounds and *E. diffusum*, *S. exigua*, *Spermolepis echinata*, *Cryptantha crassisepala*, *C. micrantha*, *Erigeron divergens*, and *Malacothrix fendleri* on inactive mounds.

In summer, an annual, *Bouteloua aristidoides*, and a perennial, *Atriplex acanthocarpa*, were significantly more abundant on active mounds. Several different species dominated inactive mounds in summer: *Chenopodium fremontii*, *Eriogonum abertianum*, and *Tidestromia lanuginosa*. *E. abertianum*, *Aristida longiseta*, *Talinum aurantissimum*, and *Gutierrezia sarothrae* were important components of the ecotonal vegetation at the edges of mounds.

No annual plants were found exclusively at any plot position along the gradient, but most perennial plants never occurred on the mounds. One exception was the summer perennial, *Atriplex acanthocarpa*, which was most abundant on active mounds (Fig. 4). Even though most small-seeded species also occurred off mounds, the species with significantly higher densities on mounds were exclusively small seeded. A GLM-ANOVA test on winter annuals showed that the dominant species on mounds (plots A, a) had significantly smaller seeds than those off mounds (plots C, c, D, d, E, e; $P = 0.0458$). Summer annuals did not show a significant difference in seed size in terms of their location ($P = 0.2246$), because nearly all summer annuals had small seeds (Fig. 5). Simi-

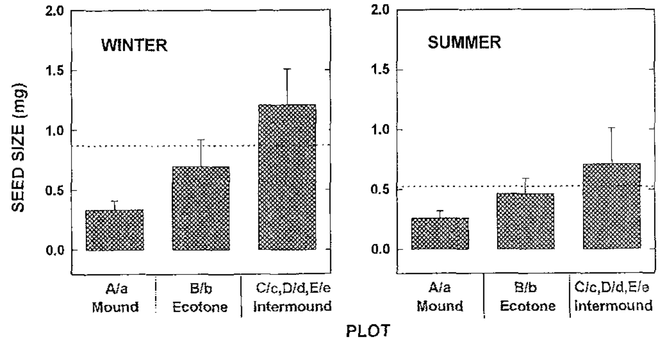

Fig. 5 Comparison of seed size (±SE) of the species that had significant responses to plot position along the disturbance gradient. The *dashed lines* represent mean seed size for winter and summer annuals respectively

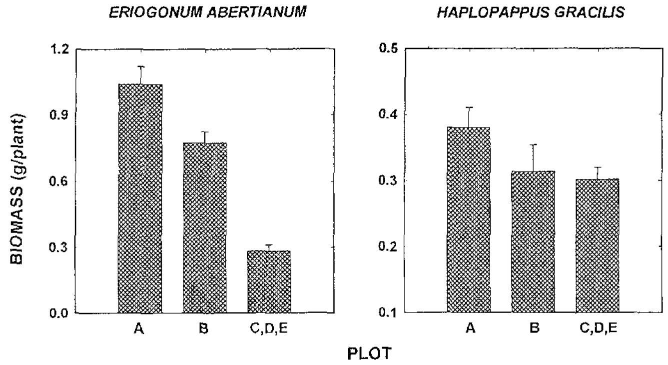

Fig. 6 Spatial variation in plant biomass (±SE) of two dominant biseasonal annuals along the transect from active mounds to intermound areas measured in summer 1992 (*left Eriogonum abertianum*, *right Haplopappus gracilis*)

lar tests, however, showed that plants of some species on the mounds were much larger than those of the same species off mounds (Fig. 6; $P < 0.001$; see also Inouye 1991; Gutierrez and Whitford 1987; Mun and Whitford 1990).

Discussion

The results summarized in Figs. 2, 3, 4 and Tables 1 and 2 demonstrated that kangaroo rat mounds had a major impact on both winter and summer annual plant communities in the northern Chihuahuan Desert. The observed patterns also supported the two proposed hypotheses; i.e., intermediate disturbance produced highest species diversity at the edges of mounds, and the presence of kangaroo rat mounds promoted higher regional plant species diversity. Kangaroo rat disturbance caused a net increase of nitrogen in the disturbed gaps (mounds) for early colonizers, and the mounds served as safe sites to support "source" populations of these "fugitive species"; as a consequence, local and regional coexistence of more species was ensured (Sousa 1984) and higher intraspecific variation was also produced (Fig. 6).

When there is a strong gradient from highly disturbed to relatively undisturbed areas, is it reasonable to regard the narrow zone of intermediate disturbance as an ecotone? The results presented here suggest the affirmative. Since highly disturbed areas on mounds and much less disturbed areas off mounds supported different species assemblages (Fig. 2), a high level of species diversity occurred where the two assemblages met at the edges of mounds (Fig. 3). This is also predicted by the intermediate disturbance hypothesis. However, as mentioned earlier, there are similar microsites with high species diversity at the edges of inactive mounds, but these must be owing to the effects of previous kangaroo rat activities on soil characteristics rather than to contemporary disturbance per se. Thus, ecotones with high species diversity at mound edges associated with intermediate levels of disturbance adjacent to active mounds, and intermediate soil conditions adjacent to inactive mounds also supported different species assemblages (Fig. 4). For example, the perennial *Solanum elaeagnifolium* was more abundant at the edges of active mounds but not at the edges of inactive mounds. In contrast, the winter annuals, *Erigeron divergens*, *Malacothrix fendleri*, and *Spermolepis echinata* were more abundant at the edges of inactive mounds but not at the edges of active mounds.

In the southwestern United States, the activities of rodents in creating and maintaining mounds and the environmental changes due to disturbance and abandonment of mounds produced highly predictable spatial and temporal patterns of small-scale plant community structure and dynamics as shown in Figs. 2 and 3 (Laycock 1958). Comparison of aerial photos taken in 1978 with the present distribution of mounds revealed high rates of mound creation and abandonment. Some mounds that have been abandoned for more than a decade (on the kangaroo rat removal plots; see Brown and Munger 1985) can still be easily recognized by noting their distinctive soil characteristics and plant species assemblages, especially the very high dominance by a few annual species. It probably takes several decades for abandoned mounds to return to a vegetation condition more characteristic of the surrounding habitats. Thus, the kangaroo rat mounds seem to be ideal for studying the effects of microhabitat heterogeneity on plant community structure and dynamics. They also provide opportunities to study microsuccessional processes during the mound creation and especially after mound abandonment (Denslow 1980).

The mounds of *D. spectabilis* provide disturbed space and distinctive microenvironments for several annual plant species, allowing them to germinate successfully, reproduce and coexist with disturbance-sensitive but competitively superior species. The cessation of kangaroo rat burrowing activities following abandonment of a mound causes a restructuring of small-scale plant communities (i.e., succession) within months (Hawkins and Nicoletto 1992). Thus, aside from their roles as seed predators (Brown et al. 1979; Brown et al. 1986), kangaroo rats affect species composition and diversity by causing small-scale disturbance and spatial heterogeneity.

Plant life history strategies and dispersal mechanisms vary among species and are likely to influence plant community composition and succession (Bazzaz 1990; Brown 1992). Species that were significantly more abundant on the mounds exhibited some evidence for being superior colonists as suggested by their producing smaller seeds (Fig. 5) and more seeds per plant. In winter dominant species on mounds had significantly smaller seeds than those off mounds; summer annuals did not show a significant difference in seed size in terms of their location, because nearly all summer annuals had small seeds. In general, smaller seeds may have the advantages of being easily dispersed because of their smaller mass (Salisbury 1975; Fenner 1985; Huston and Smith 1987; Van Andel et al. 1993) and are less likely to be consumed by kangaroo rats (Samson et al. 1992; Heske et al. 1993; Guo et al. 1995), so that small-seeded species can reach and colonize the disturbed gaps earlier than other species. This is supported by the field data at this study site where wind dispersal is the major driving force in seed redistribution (Inouye 1991). However, caution is needed when interpreting the functional roles of seed size in successional processes in different ecosystems. For example, Rydin and Borgegård (1991) reported that seed size was less important in successional processes of island systems where water dispersal was more dominant.

It is clear that species responded very differently to animal disturbance (Table 2; Fig. 4). Individual plants of the species that significantly increased in density on mounds appeared to germinate earlier and grow faster compared with those of the same species in inter-mound areas due to the high levels of nutrients, especially nitrogen, in the soil of mounds (Fig. 6; Gutierrez and Whitford 1987; Mun and Whitford 1990). Low levels of available nitrogen in the inter-mound soils apparently limited the growth of some desert annuals, even with higher water availability (Gutierrez and Whitford 1987; Moorhead et al. 1988; Mun and Whitford 1990; see also Tilman 1982, 1988). Thus, species (mostly annuals) that significantly increased their abundances on the mounds are positively associated with N concentration, and in contrast, those (mostly perennials) with decreased densities are positively correlated with water supply (Fig. 3; Moorhead et al. 1988; Mun and Whitford 1990). Nonetheless, it is also interesting to note that the species composition on active and inactive mounds was quite different, especially with respect to summer annuals (Fig. 4). While this study does not shed light directly on the mechanisms that produced the difference in community structure between active and inactive mounds, I presume that kangaroo rat burrowing and foraging activities as well as associated soil conditions could be responsible for generating these differences. The more similar community structure between edges of inactive mounds and intermound areas shown in Table 1 also seems to support this hypothesis, because both locations were less disturbed by kangaroo rats.

Finally, because most of the annual plant species favor, but do not exclusively occupy, the disturbed areas, they exhibited remarkable within-species life history variation along the transects in which disturbance level and soil conditions were very different (Fig. 6). Thus, soil-surface disturbance not only affected small-scale plant community structure, but also caused significant intraspecific variation in life history traits. The microhabitats created by kangaroo rats could be important for the maintenance of higher within-species genetic diversity because they could support different phenotypes or even genotypes of the same species in a small area (Q. Guo, unpublished work; see also Turkington and Aarssen 1984).

In conclusion, kangaroo rat burrowing activities play an important role in structuring small-scale communities and in promoting high species diversity of plants in southwestern deserts (Schroder and Geluso 1975; Moroka et al. 1982). The presence of kangaroo rat mounds in the desert created two levels of environmental heterogeneity: (1) at a microscale of meters by causing a gradient of disturbance and nitrogen and water availability from mound to inter-mound areas; (2) at a larger scale of hectares by creating a mosaic of unique isolated microhabitat patches within a matrix of relatively undisturbed habitat. Disturbance by rodents created "source" microsites for establishment (Mooney and Godron 1983; Pickett and White 1985) and maintenance of viable populations of fugitive species, allowing them to coexist with competitively superior species in the surrounding matrix.

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