

On the role of small mammals in mediating climatically driven vegetation change

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Abstract

Biotic and abiotic processes jointly influence natural systems, yet opportunities to integrate studies of both processes are uncommon. For two decades we have excluded different subsets of the small mammal community from a series of plots near a grassland-desert ecotone in the northern Chihuahuan Desert. These studies spanned a period of historically high winter rainfall, allowing us to distinguish the effects of climate and small mammals on the composition and patch structure of vegetation. Removal of only kangaroo rats (*Dipodomys*) or of all small mammals led to increased cover of large herbaceous vegetation. The size of vegetative patches increased in all plots but this increase was three times greater where all rodents were removed. Thus, the activity of small mammals that forage under and near shrub canopies appear to significantly inhibit the expansion of existing vegetative patches, and may have a stronger influence on habitat structure than previously recognized.

Keywords

Abiotic factors, biotic factors, Chihuahuan Desert, climate change, small mammals.

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INTRODUCTION

The structure and dynamics of arid ecosystems have been attributed to a variety of biotic and abiotic factors ranging from geological processes (Bowers & Lowe 1986; McAuliffe 1994; Schlesinger *et al.* 1996) and the distribution of abiotic soil resources (Noy-Meir 1973; Crawford & Gosz 1982; Schlesinger *et al.* 1990), to the activities of biotic organisms (e.g. Brown & Heske 1990; Chew & Whitford 1992; Hawkins & Nicoletto 1992; Heske *et al.* 1993) and the influence of climate (Walter 1973; Brown *et al.* 1997; Swetnam & Betancourt 1998). These processes clearly do not operate independently, and the effects of both abiotic and biotic factors generally act in concert with other processes to organize ecological systems (Andrewartha & Birch 1954; Chapin *et al.* 1997; Polis 1999).

In the American South-west shrub cover has been increasing over the past century (Hastings & Turner 1965; Humphrey 1987; Bahre 1991; Dick-Peddie 1993), and while numerous factors have been invoked to explain this pattern, recent changes in the precipitation regime appear to be the most likely candidate, at least in the northern Chihuahuan Desert (Brown *et al.* 1997; Swetnam & Betancourt 1998). Against this backdrop of abiotic-

induced changes, we have been tracking small mammal and plant dynamics in experimental plots as a model system for examining the interaction of intrinsic (to the community) biotic process such as granivory, and extrinsic abiotic processes such as climate. Here we integrate studies of desert small mammal community structure (e.g. Brown *et al.* 1986; Brown 1998) with decadal changes in rainfall patterns (Betancourt 1996; Brown *et al.* 1997) in order to compare and contrast the relative effects of abiotic (precipitation) and biotic (granivory by small mammals) factors on the patch dynamics and vegetative composition of a Chihuahuan Desert/arid grassland ecotone. Specifically, we ask: (1) How has this grassland/shrubland system changed over the past two decades?; and (2) How have rodents (largely granivorous) altered the spatial structure and vegetation composition of this grassland/shrubland system?

MATERIALS AND METHODS

Our study site is located 6.5 km E, 2 km N of Portal, in Cochise Co., Arizona, at an elevation of 1330 m. In 1977 a 20-ha site was fenced to exclude cattle. Within this area, 24 50 × 50 m plots were established with wire mesh fencing containing holes of varying sizes to selectively exclude

different sizes of granivorous rodents (Munger & Brown 1981; Brown *et al.* 1986; Brown 1998). Treatments used in the present study include removal of all rodents (no holes in fences, hereafter designated as -R, $N = 4$ plots), removal of kangaroo rats (*Dipodomys* sp.; -D, $N = 4$ plots), and control plots with complete access by all rodents (C, $N = 4$ plots). Treatment plots probably also partially exclude collared peccary (*Pecari tajacu*; Linnaeus 1758), but they have not greatly influenced movements of rabbits (*Sylvilagus bachmani*; Waterhouse 1839) and hares (*Lepus californicus*; Gray 1837). During the 20 years that these treatments have been in place, periodic El Niño Southern Oscillation events (ENSO) have caused changes in precipitation, especially in winter (Fig. 1; Betancourt 1996; Brown *et al.* 1997). In the present study we examine the distribution of ground cover in 1979 and

1995, and we evaluate the interaction between three major variables – time, rodent removal and ground cover. We interpret differences in community and landscape structure (e.g. in patterns of ground cover) across rodent treatments (C, -D, -R) as responses to biotic interactions (e.g. granivory, herbivory). Changes in structure between 1979 and 1995 are less clearly attributed to a single cause. Although several mechanisms (e.g. changes in climate, ongoing release from over-grazing and consequent soil depletion and alteration of seasonal fire regimes) might influence long-term dynamics at this site, there is good evidence that the most recent shift in vegetation is primarily in response to changes in rainfall and not to grazing or drought (Brown *et al.* 1997).

Patterns of ground cover

Low elevation (30 m) high resolution photographs (Fig. 2) were taken of the study area in the winters of 1979 (2 years after the study was initiated) and 1995 (18 years after initiation). These years bracket the wettest recorded period of this century, with historically high winter rains (Fig. 1; Brown *et al.* 1997). Aerial photographs were scanned into an Apple Macintosh computer, and a supervised classification (the grey-scale was set to characterize certain microhabitat types) was conducted using Adobe Photoshop (Frey & Curtin 1997). This classification reflected four principal cover types at our site: large shrubs (primarily in the genera *Acacia*, *Ephedra*, *Flourensia*, and *Prosopis*), tall herbaceous vegetation (primarily large-seeded winter annuals), low herbaceous cover (primarily grasses), and bare ground (Fig. 2). The scanned images were then transferred into the National Institutes of Health (NIH) shareware program Image (available through NIH) in order to measure the proportion of the different cover types, the distance between patches, and the size of habitat patches (see Young & Kostel-Hughes 1995). We define patches as contiguous cover by vegetation at the scale of meters, an appropriate scale of analysis for habitat selection by small mammals (e.g. Rosenzweig 1973; Kotler & Brown 1988); of course, these rodents use their environment at finer spatial scales as well. Aerial images were ground-truthed by two means. First, within weeks of the 1995 flight we measured on the ground the size and density of the shrub and grass patches depicted in our 1995 aerial image to validate our measurements from the aerial image. Second, we compared cover estimates of the different functional groups taken from aerial photographs with measures of plant species composition taken in the field in the spring of 1995 (for a detailed explanation of these methods, see Guo *et al.* 1995).

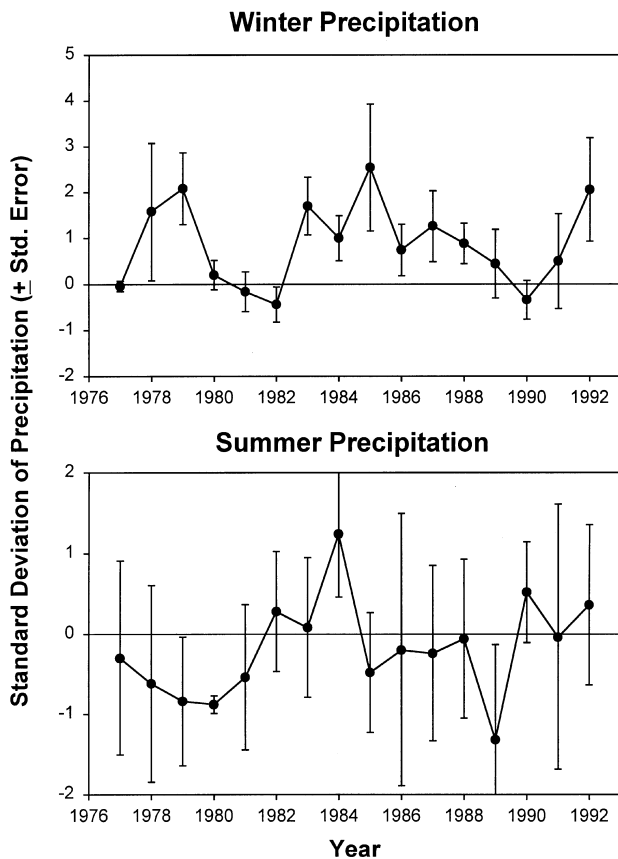


Figure 1 Yearly differences (measured in standard deviations) in regional precipitation from long-term averages (set equal to zero) for Douglas, Arizona (from 1903), Jornada, New Mexico (from 1914), Safford, Arizona (from 1898), Tombstone, Arizona (from 1889), and Tucson, Arizona (from 1867) (all data from Brown *et al.* 1997). At all stations 1977–92 winter precipitation was significantly higher than prior years (Mann–Whitney U -tests, all $P < 0.01$; see Brown *et al.* 1997). Regional summer precipitation did not deviate significantly from average.

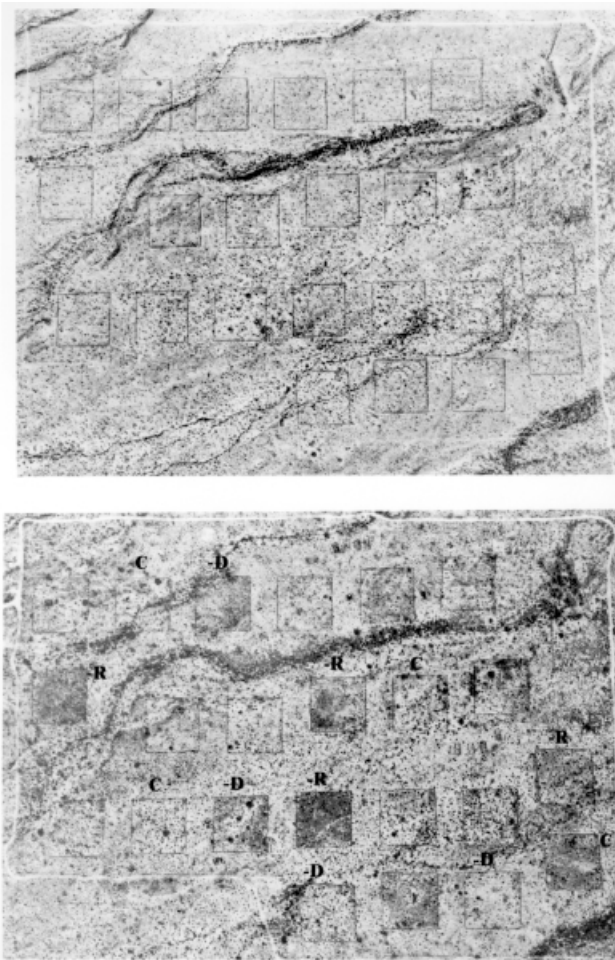


Figure 2 Low-elevation, high resolution aerial photographs illustrate changes in vegetation composition at our site between 1979 and 1995. Rodent treatments are coded as C (control), -D (*Dipodomys* exclusion), and -R (all rodents removed).

Statistical analysis

Ground cover

Overall change in ground cover was initially examined with a multivariate analysis of variance (MANOVA), with three of the four cover classes as dependent variables (only three were used as the four categories always summed to 100%; we excluded bare ground from this analysis), and PLOT(RODENT TRT), TIME, and RODENT TRT*TIME as independent variables. The error term for RODENT TRT was PLOT(RODENT TRT), and for TIME and RODENT TRT*TIME we used TIME*PLOT(RODENT TRT). The metric employed was the number of pixels on a computer screen that were classified in each of the four cover categories; all plots were magnified evenly so that the number of pixels remained constant across plots and across time.



A comparison of a 1977 (top photo) and 1994 image (lower photo) illustrates how the site has shifted from an arid grassland in the 1970s, to predominantly a shrubland by the mid-1990s. These changes are thought to have been the result of changes in rainfall patterns, with these patterns even more extensive within rodent removal plots.

The MANOVA indicated that ground cover did not vary statistically across rodent treatments (over two time periods, three rodent treatments, and three cover categories) but that both TIME and the TIME*RODENT TRT interaction were significantly variable. We therefore followed this with separate univariate analyses of variance (ANOVAs) on each dependent variable in order to evaluate which of these were responsible for the significant main effects in the MANOVA. Each ANOVA was a two factor model (RODENT TRT and TIME) with nested (PLOT(RODENT TRT)) and interaction (RODENT TRT*TIME) effects. Scheffe's a posteriori multiple comparisons test was used to discriminate which treatments differed when ANOVA reported statistical significance (Day & Quinn 1989).

Table 1 Results of multivariate analysis of variance to evaluate overall variation in variables measuring ground cover over time and across rodent treatments, as well as the interaction between these

Source	Error term	Wilk's lambda	<i>F</i>	d.f. (numerator/denominator)	<i>P</i>
Rodent Trt	Plot(Rodent Trt)	0.6136	0.6455	6/14	0.6933
Time	Time × Plot(Rodent Trt)	0.0280	81.0594	3/7	0.0001
Time × Rodent Trt	Time × Plot(Rodent Trt)	0.1456	3.7818	6/14	0.0001

Source	d.f.	MS	<i>F</i>	<i>P</i>
<i>Bare ground cover</i>				
Model	14	14420316	1.75	0.2015
Rodent Trt	2	17228878	1.67	0.2417
Plot(Rodent Trt)	9	10320404	1.25	0.3723
Time	1	15278508	1.85	0.2067
Time × Rodent Trt	2	29632259	3.59	0.0714
Error	9	8253184		
<i>Low herbaceous vegetation</i>				
Model	14	34389647	15.98	0.0001
Rodent Trt	2	4812730	0.47	0.6381
Plot(Rodent Trt)	9	10185302	4.73	0.0150
Time	1	371149350	172.43	0.0001
Time × Rodent Trt	2	4506275	2.09	0.1792
Error	9	2152470		
<i>Tall herbaceous vegetation</i>				
Model	14	21106232	8.21	0.0016
Rodent Trt	2	22251483	1.64	0.2471
Plot(Rodent Trt)	9	13574021	5.28	0.0104
Time	1	72387740	28.17	0.0005
Time × Rodent Trt	2	28215172	10.98	0.0039
Error	9	2570044		
<i>Shrubs</i>				
Model	14	6721638	2.87	0.0581
Rodent Trt	2	2287478	0.56	0.5891
Plot(Rodent Trt)	9	4074327	1.74	0.2107
Time	1	48906150	20.90	0.0013
Time × Rodent Trt	2	1976441	0.84	0.4612
Error	9	2340189		

Table 2 Results of a three-factor analysis of variance on the number of pixels representing four plant cover classes as functions of rodent treatments and time, with interaction. Presented are separate univariate ANOVA tables for each response variable. The error term for Rodent treatment was Plot(Rodent Trt)**Table 3** Results of multivariate analysis of variance to evaluate overall variation in patch size and distribution over time and across rodent treatments, as well as the interaction between these

Source	Error Term	Wilk's lambda	<i>F</i>	d.f. (numerator/denominator)	<i>P</i>
Rodent Trt	Plot(Rodent Trt)	0.1075	8.2007	4/16	0.0009
Time	Time × Plot(Rodent Trt)	0.0547	69.1575	2/8	0.0001
Time × Rodent Trt	Time × Plot(Rodent Trt)	0.3310	2.9521	4/16	0.0528

Patch size and interpatch distance

Mean patch size and distance were derived from four measurements per plot (area of bare ground, low and tall herbaceous vegetation, and shrubs) using NIH Image

(Young & Kostel-Hughes 1995; Frey & Curtin 1997). Size and distance were analysed separately with univariate ANOVAs with RODENT TRT, TIME, and RODENT TRT*TIME as independent variables.

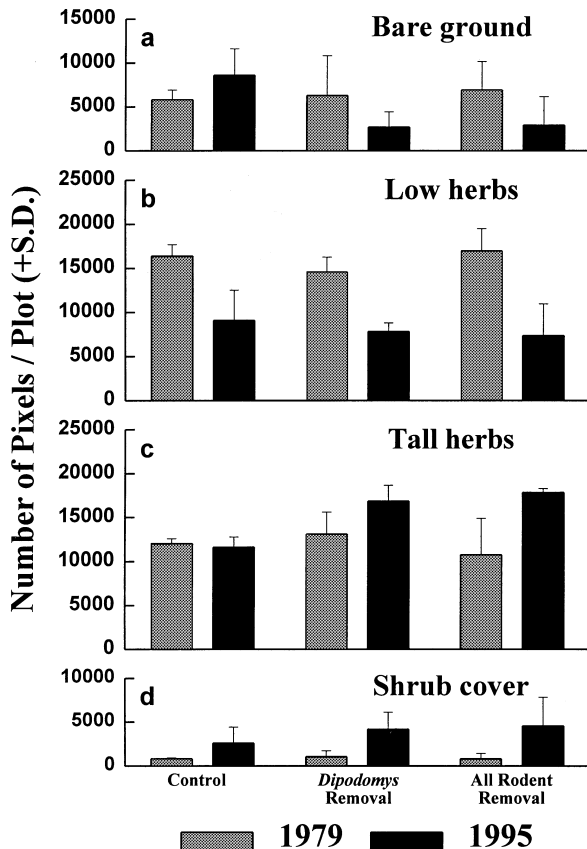


Figure 3 Bar diagram of ground cover (derived from pixel counts of habitat types within our 12 study plots) by shrubs, tall herbaceous vegetation, low herbaceous vegetation, and bare ground, in three rodent treatments in 1979 and 1995.



A fence-line contrast of one of the mammal exclusion plots, taken at the time of our second aerial image in March 1995, illustrates the extreme differences in vegetation composition as a result of small mammal herbivory.

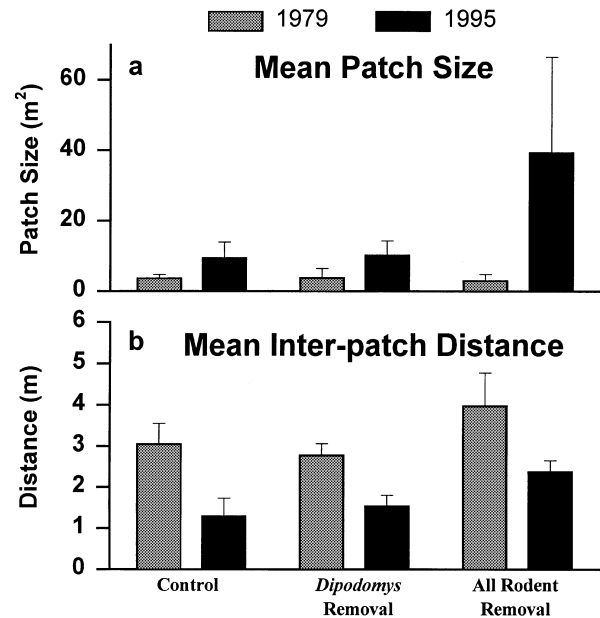


Figure 4 Bar diagram of mean distance between vegetation patches and mean patch size for plots in three rodent treatments in 1979 and 1995.

RESULTS

Ground cover

As noted above, coverage by three plant cover types did not differ across RODENT TRT, but they did change over TIME, and a significant RODENT TRT*TIME interaction was observed (Table 1). Thus, we proceeded with univariate ANOVAS on each dependent cover variable (Table 2). Bare ground cover did not vary across TIME or RODENT TRT, although the RODENT TRT*TIME interaction approached statistical significance ($P \approx 0.07$), reflecting modest temporal declines in bare ground cover in both rodent treatments (-D, -R) but increases in control plots (Fig. 3a). All three plant cover categories changed over TIME, with shrub and tall herbaceous cover increasing, and low herbs decreasing (Table 2). Significant variation was observed within treatments for both herbaceous cover categories (PLOT(RODENT TRT)), but only tall herbaceous vegetation exhibited a significant RODENT TRT*TIME interaction; this vegetation class remained similar over time in control plots, but increased in both rodent removal treatments (Table 3, Fig. 3c).

Patch size and interpatch distance

The spatial distribution of vegetation changed significantly during this study. A MANOVA on patch size and interpatch distances demonstrated significant variation across RODENT TREATMENT and TIME (Table 3). The interaction effect was marginally significant ($P \approx 0.05$),

Source	d.f.	MS	F	P
Inter-patch distances				
Model	14	1.60	8.76	0.0013
Rodent Trt	2	2.80	10.57	0.0043
Plot(Rodent Trt)	9	0.24	1.45	0.2929
Time	2	14.11	77.41	0.0001
Rodent Trt × Time	2	0.13	0.72	0.5117
Error	9	0.18		
Scheffe's a posteriori tests:				
Rodent Trt	C	-D	-R	Time
	<u>2.15</u>	<u>2.15</u>	<u>3.18</u>	1979
				<u>1995</u>
				<u>3.258</u>
				<u>1.725</u>
Patch sizes				
Model	14	373.84	3.15	0.0446
Rodent Trt	2	554.83	3.79	0.0640
Plot(Rodent Trt)	9	146.47	1.23	0.3804
Time	2	1576.26	13.26	0.0054
Rodent Trt × Time	2	614.82	5.17	0.0320
Error	9	118.86		
Scheffe's a posteriori test:				
	Time	1979	1995	
		<u>3.333</u>	<u>19.542</u>	
Patch size – analyses by year				
1979				
Model	2	0.79	0.19	0.8283
Rodent Trt	2	0.79	0.19	0.8283
Error	9	4.11		
1995				
Model	2	1168.85	4.47	0.0448
Rodent Trt	2	1168.85	4.47	0.0448
Error	9	261.22		

Table 4 Results of a two-factor analysis of variance on the distance between shrub patches, and on the mean size of shrub patches, as functions of rodent treatments and time, with interaction. The error term for RODENT TRT WAS PLOT(RODENT TRT). For Scheffé a posteriori tests the value of the metric is given, and values joined by underlining are not statistically different from each other

and so was retained in subsequent univariate ANOVAS on these variables.

Both the sizes of individual patches of vegetation, and the distances between them, differed across TIME (Table 4), reflecting increases in the former and declines in the latter (Fig. 4). The large increase in mean patch size in -R treatments was responsible for the significant interaction effect. Patch size did not differ among rodent treatments in 1979, but was marginally significant in 1995 (Fig. 4a), with smaller patches tending to occur in control plots and larger patches in -R plots. Higher initial interpatch distances in -R plots evidently led to higher final distances as well, resulting in a significant RODENT TRT effect for this variable (Table 4b).

To summarize, overall ground cover did not change over time, but the composition of existing vegetative cover did change. Low herbs decreased, and shrubs and tall herbs increased; all herbaceous vegetation varied significantly within RODENT TRT, but only tall herbs exhibited a significant RODENT TRT*TIME interaction, reflecting increases only on -R and -D plots. Vegetation patch size and interpatch distances underwent reciprocal

changes over time, with the former increasing and the latter decreasing; a significant RODENT TRT*TIME interaction in patch size reflected particularly large increases in patch size in rodent removal plots.

DISCUSSION

The only patterns that were consistent across all treatments were a temporal increase in shrub cover and a concomitant decline in low herbaceous vegetation. Increases in shrub cover have been observed throughout the south-west (e.g. Hastings & Turner 1965; Humphrey 1987; Bahre 1991; Dick-Peddie 1993), and, at least in the region of the San Simon valley where this study was conducted, have been closely linked to a shift in precipitation in the past two decades (Brown *et al.* 1997). Brown *et al.* (1997) demonstrated that a substantial ecosystem reorganization at the north-western extent of the Chihuahuan Desert appeared to be caused by a shift in regional climate since the late 1970s. Increased precipitation, especially during winter months, appears to have been directly or indirectly responsible for

changes in woody shrub density, local extinction of previously common animals, and concomitant increases in numbers of previously rare species. While our treatments (consisting of fences ≈ 40 cm tall) may have inhibited access by peccary and by rabbits and hares, subsequent studies indicate these effects were not significant (Curtin & Brown 1999). Additionally, the general temporal patterns observed are identical to those documented throughout the region (Brown *et al.* 1997), suggesting a more regional causality. Here, we extend the results of Brown *et al.* by evaluating the role that small mammals play in directing the distribution and structure of plant communities within the broader climatically driven vegetative changes.

Although we observed significant changes in cover of the three vegetation categories studied, the nonsignificant TIME effect for bare ground cover (Table 2) indicates that increases in the spatial distribution of one cover category were roughly matched by decreases in other categories. The aggregation of resources in the system, however, as reflected in the number and size of vegetation patches, changed significantly over the 16-year study period, with larger patches of vegetation located closer together (Table 4, Fig. 4). While shrub cover increased across all plots, the most notable pattern may be the decrease in bare ground cover where rodents were removed (-R, -D; Table 2, Fig. 3a). In the face of significantly different changes in vegetation patches (Fig. 4), temporal changes in cover by vegetative categories were similar in both removal treatments (Fig. 3). This suggests that the consumption or redistribution of seeds by granivorous rodents, including but not limited to the larger kangaroo rats, plays an important role in mediating climatic variation by dampening the spatio-temporal variation in resources that we observed (e.g. cover by tall herbs, size of vegetative patches). In the presence of kangaroo rats (C), tall herbaceous vegetation did not change over the course of the study (Fig. 3c), and in the presence of the smallest species (C and -D), changes in vegetative patch size were greatly diminished (Fig. 4a).

Although removal of kangaroo rats (-D) and of all rodents (-R) produced similar effects on vegetation cover types, they differentially affected the vegetation matrix on the landscape, with removal of all rodents having a three-fold greater effect on mean patch size than removal of kangaroo rats alone (Fig. 4a). Given the similar total coverage of all three vegetative cover categories (Table 2, Fig. 3) this suggests that relative to control and *Dipodomys* removal plots, all rodent removal plots had many fewer but larger vegetation patches. Thus, in rodent removal plots the increase in shrub and tall herbaceous cover evidently resulted from a coalescence of existing vegetation patches (thereby reducing the number of patches but not greatly altering the total vegetative cover or the mean

distances between remaining patches). This suggests that different rodents exert qualitatively different impacts on the environment. Removal of kangaroo rats at this site has been shown to result in increased leaf litter accumulation, reduced soil surface disturbance, increases in tall perennial and annual grasses, decreased foraging by granivorous birds, and differential colonization by other rodent species (see Brown & Harney 1993). Removal of all rodents, however, appears to lead to even greater structural changes in plant communities, although the impact of this on total cover by different plant classes is not greatly different from that observed when only kangaroo rats are excluded (Fig. 3). Pocket mice (*Chaetodipus*, *Perognathus*) forage more extensively under shrub cover than *Dipodomys*, which forage more in open microhabitats (Reichman & Price 1993), and pocket mice may significantly impact seed survival and the probability of successful recruitment by plants under and along the edges of shrub patches. Seed banks in desert environments typically are greater under shrubs, with gradual declines towards the edges of shrub canopies (Guo *et al.* 1998), and seedling growth may be optimal along canopy edges where water availability remains relatively high but insolation allows for rapid growth. If this is true then the presence of shrub-foraging granivores (or graminivores; Kerley *et al.* 1997) may have a much stronger impact on the generation of structure in arid zone ecosystems than has been believed.

Several recent authors have documented interactions between herbivores and their environment. Milchunas & Lauenroth (1993) concluded that above-ground net primary productivity influenced the impact of grazing on local species composition. Frank *et al.* (1998) documented functional similarities between Serengeti and the Yellowstone ecosystems, and similar patterns have been documented for Kansas prairies (Knapp *et al.* 1999) dominated by bison, and temperate savannas colonized by prairie dogs (Weltzin *et al.* 1997). These patterns may reflect emergent consequences of long-term interactions of herbivores with their environment (Milchunas *et al.* 1988).

Our results complement previous studies by underscoring the possible role of small mammals in mitigating the effects of other influences (e.g. climate, grazing) in arid ecosystems. Although the most apparent effect was on tall herbaceous vegetation (Fig. 3c), perhaps the most interesting result is the increase in vegetative patch size that was observed only when all rodents were removed (Table 4, Fig. 4a). The compensatory changes in abundance of pocket mice in response to kangaroo rat removal (Valone & Brown 1995) and the demonstration of strong responses by the plant community to -R and -D treatments, suggest that the "keystone granivore guild" (Brown & Heske 1990) has a broader membership than only kangaroo rats. Understanding the activities of small mammals in these

habitats is likely to be important to understanding vegetative responses to long-term changes in climate.

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REFERENCES

- Andrewartha, H.G. & Birch, L.C. (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, Illinois.
- Bahre, C.J. (1991). *A Legacy of Change: Historic Human Impact on Vegetation of the Arizona Borderlands*. University of Arizona Press, Tucson.
- Betancourt, J.L. (1996). Long- and short-term climate influences on southwestern shrublands. In: *Proceedings: Shrubland Ecosystem Dynamics in a Changing Environment* (eds Barrow J.R., McArthur E.D., Sosebee R.E. and Tausch R.J.). General Technical Report INT-GtR-338. U.S. Forest Service, Ogden, Utah, USA.
- Bowers, M.A. & Lowe, C.H. (1986). Plant-form gradients on Sonoran Desert bajadas. *Oikos*, 46, 284–291.
- Brown, J.H. (1998). The desert granivory experiments at Portal. In: *Issues and Perspectives in Experimental Ecology* (eds Reseratis, W.L. Jr & Bernardo, J.), Oxford University Press, Oxford.
- Brown, J.H. & Harney, B.A. (1993). Population and community ecology of heteromyid rodents in temperate habitats. In: *Biology of the Heteromyidae* (eds Genoways, H.H. & Brown, J.H.). Special Publications, 10, American Society of Mammalogists.
- Brown, J.H. & Heske, E.J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, 250, 1705–1707.
- Brown, J.H., Davidson, D.W., Munger, J.C. & Inouye, R.S. (1986). Experimental community ecology: the desert granivore system. In: *Community Ecology* (eds Diamond, J.M. & Case, T.J.). Harper & Row, New York.
- Brown, J.H., Valone, T.J. & Curtin, C.G. (1997). Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl. Academy*, 94, 9729–9733.
- Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. (1997). Biotic control over the functioning of ecosystems. *Science*, 277, 500–504.
- Chew, R.M. & Whitford, W.G. (1992). A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosote bushes (*Larrea tridentata*). *J. Arid Environments*, 22, 375–386.
- Crawford, C.S. & Gosz, J.R. (1982). Desert ecosystems: their resources in space and time. *Environ. Conservation*, 9, 181–195.
- Curtin, C.G. & Brown, J.H. (1999). Climate and herbivory in structuring the vegetation of the Malpai borderlands. In: *Changing Plant Life of la Frontera: Observations of Vegetation in the United States/Mexico Borderlands* (eds Bahre, C.J. & Webster, G.). University of New Mexico Press, Albuquerque, New Mexico.
- Day, R.W. & Quinn, G.P. (1989). Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monographs*, 59, 433–463.
- Dick-Peddie, W.A. (1993). *New Mexico Vegetation: Past Present Future*. University of New Mexico Press, Albuquerque.
- Frank, D.A., McNaughton, S.J. & Tracy, B.J. (1998). The ecology of the earth's grazing ecosystems. *Bioscience*, 48, 513–521.
- Frey, T.C. & Curtin, C.G. (1997). A low-tech technique for aerial photograph analysis. *Ecol. Bull.*, 78, 203–204.
- Guo, Q., Rundel, P.W. & Goodal, D.W. (1998). Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. *J. Arid Environments*, 38, 465–478.
- Guo, Q., Thompson, D.B., Valone, T.J. & Brown, J.H. (1995). The effects of vertebrate granivores and folivores on plant community structure in the Chihuahuan Desert. *Oikos*, 73, 251–259.
- Hastings, J.R. & Turner, R.M. (1965). *The Changing Mile*. University of Arizona Press, Tucson.
- Hawkins, L.K. & Nicoletto, P.F. (1992). Kangaroo rat burrows structure the spatial organization of ground dwelling animals in a semiarid grassland. *J. Arid Environments*, 23, 199–208.
- Heske, E.J., Brown, J.H. & Guo, Q. (1993). Effects of kangaroo rat exclusion on the vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia*, 95, 520–524.
- Humphrey, R.R. (1987). *90 Years and 535 Miles: Vegetation Changes Along the Mexican Border*. University of New Mexico Press, Albuquerque.
- Kerley, G.I.H., Whitford, W.G. & Kay, F.R. (1997). Mechanisms for the keystone status of kangaroo rats: granivory rather than granivory? *Oecologia*, 111, 422–428.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C. & Towne, E.G. (1999). The keystone role of bison in North American tallgrass prairie. *Bioscience*, 49, 39–49.
- Kotler, B.P. & Brown, J.S. (1988). Environmental heterogeneity and the coexistence of desert rodents. *Annu. Rev. Ecol. Syst.*, 19, 281–307.
- McAuliffe, J.R. (1994). Landscape evolution, soil formation, and ecological patterns and processes in Sonoran desert bajadas. *Ecol. Monographs*, 64, 111–148.
- Milchunas, D.G. & Lauenroth, W.K. (1993). Quantitative effects of grazing on vegetation and soil over global range of environments. *Ecol. Monographs*, 63, 327–366.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Naturalist*, 132, 87–106.
- Munger, J.C. & Brown, J.H. (1981). Competition in desert rodents: an experiment with semipermeable enclosures. *Science*, 211, 510–512.
- Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annu. Rev. Ecol. Syst.*, 4, 25–51.
- Polis, G.A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, 86, 3–15.
- Reichman, O.J. & Price, M.V. (1993). Ecological aspects of heteromyid foraging. In: *Biology of the Heteromyidae* (eds Genoways, H.H. & J.H. Brown), pp. 539–574. Special Publications, 10, American Society of Mammalogists.
- Rosenzweig, M.L. (1973). Habitat selection experiments with a pair of coexisting heteromyid rodent species. *Ecology*, 62, 327–335.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huen-

- neke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990). Biological feedbacks in global desertification. *Science*, 247, 1043–1048.
- Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 77, 364–374.
- Swetnam, T.W. & Betancourt, J.L. (1998). Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Climate*, 11, 3128–3147.
- Valone, T.J. & Brown, J.H. (1995). Effects of competition, colonization, and extinction on rodent species-diversity. *Science*, 267, 880–883.
- Walter, H. (1973). *Vegetation of the Earth in Relation to Climate and Eco-Physical Conditions*. Springer, New York.
- Weltzin, J.F., Archer, S. & Heitschmidt, R.K. (1997). Small mammal regulation of vegetation structure in a temperate savanna. *Ecology*, 78, 751–763.
- Young, T.P. & Kostel-Hughes, F. (1995). NIH Image: free software for image analysis. *Bull. Ecol. Soc. Am.*, 76, 39–40.

BIOSKETCH

Douglas Kelt studies the ecology and biogeography of small mammals, focusing primarily on arid systems. Current research also addresses the ecology and evolution of granivory in arid regions.

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