

Shifting Dominance Within a Montane Vegetation Community: Results of a Climate-Warming Experiment



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deserves scholarly attention, ethical and moral concern, and governmental initiatives. In the longer term, masculinization of births will result in large cohorts of young unmarried males, posing social and cultural challenges in countries that are already undergoing rapid economic and political change. The trends we note are likely to complicate efforts to increase the social and economic status of women and their control over reproductive decisions.

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Shifting Dominance Within a Montane Vegetation Community: Results of a Climate-Warming Experiment

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In experimentally heated plots that each span a soil moisture gradient in a Rocky Mountain meadow, aboveground biomass of *Artemisia tridentata* (a sagebrush) increased in the drier habitat and that of *Pentstemon floricola* (a shrub cinquefoil) increased in the wetter habitat relative to control plots. In contrast, aboveground forb biomass decreased in the wet and dry habitats of the heated plots. These results, combined with evidence for enhanced sagebrush seedling establishment rates in the heated plots, suggest that the increased warming expected under an atmosphere with a concentration of carbon dioxide twice that of pre-industrial levels could change the dominant vegetation of a widespread meadow habitat.

Studies point to the likelihood of future changes in the composition of plant communities under climate change (1). In both montane and high-latitude ecosystems, such changes could be especially dramatic because of the sensitivity of regional climate to snow or ice cover (2) and the sensitivity of vegetation growth and nutrient availability to timing of snowmelt, length of growing season, soil and air temperatures, and midsummer soil drying (3, 4). In this report, we describe results from an in situ climate manipulation experiment designed to study the responses of montane meadow vegetation to climate warming.

Investigations of the ecological effects of climate change have included both controlled-climate laboratory studies (5) and field experiments with either plastic enclosures (6), snow fences (4), buried electric-resistance wires (7), or overhead radiators (8). We chose overhead radiators to simulate the increase in downward infrared radiation (IR) incident on vegetation and soil that is expected to occur under global warming (9).

Our study site was an ungrazed subalpine meadow at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, USA (38°53'N, 107°02'W; elevation, 2920 m). Typical of many montane regions, the area is characterized by a mosaic of habitats, and species composition varies over small spatial scales (10). Conifer and aspen stands are interspersed with both

wet and dry meadows that support diverse assemblages of forbs, graminoids, and shrubs. Within our study plots, there were approximately 100 angiosperm species, most of which were long-lived perennials (11). Sagebrush (*A. tridentata*) infiltrates in drier areas of the meadow because the site is at the upper elevational boundary of a tongue of Great Basin desert shrub habitat (Fig. 1A).

Annual precipitation at RMBL over the past decade has averaged 0.75 m, over 80% of that as snow. Total snowfall during the 1990 to 1991, 1991 to 1992, 1992 to 1993, and 1993 to 1994 winters was 0.69, 0.47, 0.99, and 0.68 m (water equivalent), respectively (12). Snowmelt (13) typically ends in May or early June (Table 1). Total precipitation from June through August was 0.10, 0.11, 0.05, and 0.04 m in 1991, 1992, 1993, and 1994, respectively. As a result of the low rainfall in 1993 and especially 1994, summer soil moistures were lowest in those years (Table 1), despite an exceptionally late melt in 1993 and an above normal snowfall during the 1992 to 1993 winter. Mean daily summer air temperature is about 10°C.

We established 10 3-m by 10-m experimental plots in 1990, each spanning an elevational, microclimatic, and vegetational gradient from a dry ridge downhill to a moist swale (Fig. 1, B and C). Electric heaters suspended 2.6 m above five of the plots provided a nearly uniform IR flux over those plots (14). At the onset of heating, 6 January 1991, we set the heater output at 15 W/m² incident on the soil surface; on 24 May 1993, we raised it to 22 W/m² (15). We monitored soil temperature and mois-

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ture at 2-hour intervals at depths of 5, 12, and 25 cm using thermocouples and gypsum blocks wired to multiplexers and data loggers (16). Temperature and moisture probes were located in the upper (drier) and lower (wetter) zones of each plot, as well as on the slope between them (Fig. 1C and Table 1).

Although nearly all vegetation at the site is perennial, the aboveground biomass (AGB) of forbs is essentially zero at snowmelt because the previous summer's aboveground growth senesces to litter over the autumn and winter. For shrubs and graminoids, we only measured AGB that was added during the growing season because some leaves, the woody parts of the shrubs, and some clumped dead grasses remained aboveground over the winter. Therefore, in all vegetation measurements, AGB refers to net aboveground leaf and stem biomass added in the current year. Because the seasonal succession of dominant forbs occurred from

snowmelt until mid or late August, forb AGB considerably underestimated total cumulative forb production in each plot.

We estimated AGB by four methods: (i) direct measurement of the dry weight of clipped vegetation in selected quadrats (17) and indirect measurement of (ii) leaf area indices (LAI) (18), (iii) areal coverage (19), and for shrubs only, (iv) incremental vegetative shoot length (20). We converted results of the three indirect measurements to AGB estimates by regressing directly measured AGB against simultaneously measured LAI, areal coverage, and shoot length (21).

Throughout the 1993 and 1994 growing seasons, for which we have the most extensive data, forb AGB was lower in the heated than in the control plots, shrub AGB was higher, and graminoid AGB was nearly equal (Fig. 2 and Table 2). Both forb and shrub response to the heating were greater in the dry zone than in the wet zone. Forb AGB in the heated plots decreased despite starting forb production 2 weeks earlier because of earlier snowmelt induced by the heating. In control and heated plots, shrub AGB increased at similar rates during the growing season, but the earlier start in the heated plots led to consistently higher shrub AGB levels in July and August. In only the dry zone of the heated plots did shrub AGB surpass forb AGB by mid or late summer in both years.

In the unusually wet growing season of 1992, for which we have only end-of-season vegetation data, shrub AGB was enhanced in the heated plots, whereas forb and graminoid AGB were relatively unaffected (Table 2). In 1991, the end-of-season graminoid AGB was enhanced in the heated plots of the wet zone and depressed in the heated

plots of the dry zone; the sum of forb plus shrub AGB was unaffected by heating in the dry zone and was enhanced in the wet zone (Table 2).

To determine the significance of the heating on AGB and to gain some understanding of the mechanism by which the heating influenced vegetation, we used analysis of covariance, with treatment as a categorical variable and three covariates: seasonal mean soil temperature, seasonal mean soil moisture, and time interval between completion of snowmelt and date of AGB measurement. These three covariates were previously shown to depend significantly on treatment (8). The three vegetation types were analyzed separately for each combination of zone (to avoid lumping different species), year, and sampling date (to avoid lumping nonindependent data).

This analysis indicated that heating had a significant effect on shrub AGB in the dry zone in 1993 ($P = 0.015$) and 1994 ($P = 0.001$) and in the wet zone in 1992 ($P = 0.036$). Shrub AGB was also significantly advanced by earlier snowmelt in the dry zone in 1992 ($P = 0.022$). Moreover, forb AGB was significantly depressed by earlier snowmelt in the dry zone in 1993 ($P = 0.001$) and 1994 ($P = 0.004$). Neither the type of treatment nor timing of snowmelt significantly influenced graminoid AGB. The analysis also showed that forb AGB was enhanced by high soil moisture and shrub and graminoid AGB were enhanced by cool, dry conditions. Thus, if heating directly (rather than indirectly by the reduced competition with forbs) enhanced shrub AGB, it is likely that it was through its effect on moisture, not temperature.

A potential difficulty with our analysis is that it cannot distinguish between a microclimate effect on vegetation biomass and a vegetation effect on microclimate. Because of shading, plots with especially dense vegetation are likely to have cooler soils than plots with sparse vegetation, and this, rather than an actual effect of microclimate on growth, could explain our results. To circumvent this, we measured elongation rates of individual shrub shoots over the 1992, 1993, and 1994 growing seasons. Elongation rates of individual shoots in the heated plots exceeded those in the control plots in all cases except in the dry zone in the driest year (1994), when heated and control plot elongation rates were nearly equal. This suggests that shrubs generally grew faster and were not simply more abundant in the heated plots. Hence, our qualitative results are not likely to be confounded by the effects of vegetation density on soil microclimate. Moreover, our observation of enhanced shrub AGB in the heated plots is qualitatively consistent with a study that

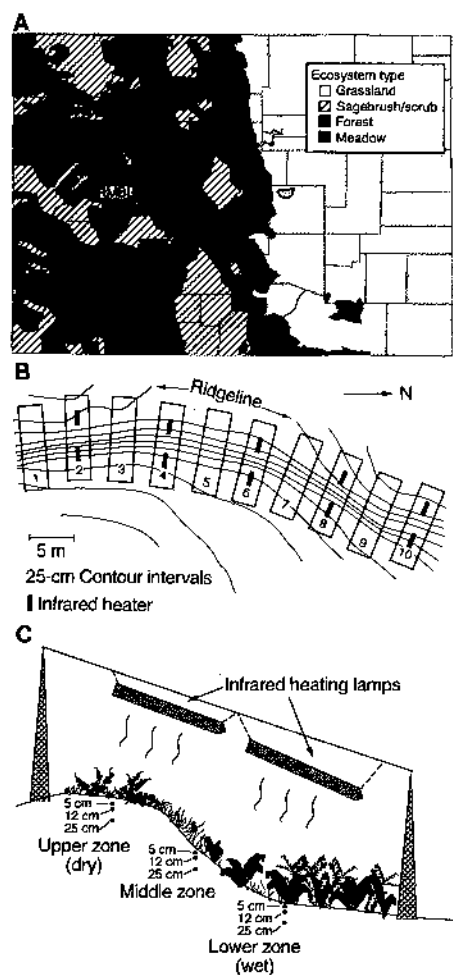


Fig. 1. Site and experimental design. (A) Vegetation communities of Colorado (adapted from classifications in [10]), with RMBL site indicated. (B) Arrangement of the plots. (C) Typical heated-plot profile (not to scale); control plots are similar but lack the heaters.

Table 1. Site characterization. Soil temperature and moisture values are averages of measurements taken every 2 hours over three depths (5, 12, and 25 cm), day and night, over the period from the end of snowmelt (13) to mid-August (8).

Year	Dry zone		Wet zone	
	Control plots	Heated plots	Control plots	Heated plots
<i>Soil temperature (°C)</i>				
1991	13.8	14.7	13.0	13.0
1992	12.6	13.5	12.1	12.2
1993	13.7	15.1	12.8	12.8
1994	15.0	16.6	13.9	14.0
<i>Soil moisture (percent by weight)</i>				
1991	20.7	18.1	33.7	32.1
1992	28.4	25.7	38.0	36.4
1993	18.8	17.3	29.3	28.6
1994	17.3	15.7	24.0	22.0
<i>Date of snowmelt (Julian day)</i>				
1991	135	131	142	133
1992	118	112	119	113
1993	145	132	150	135
1994	133	122	137	130

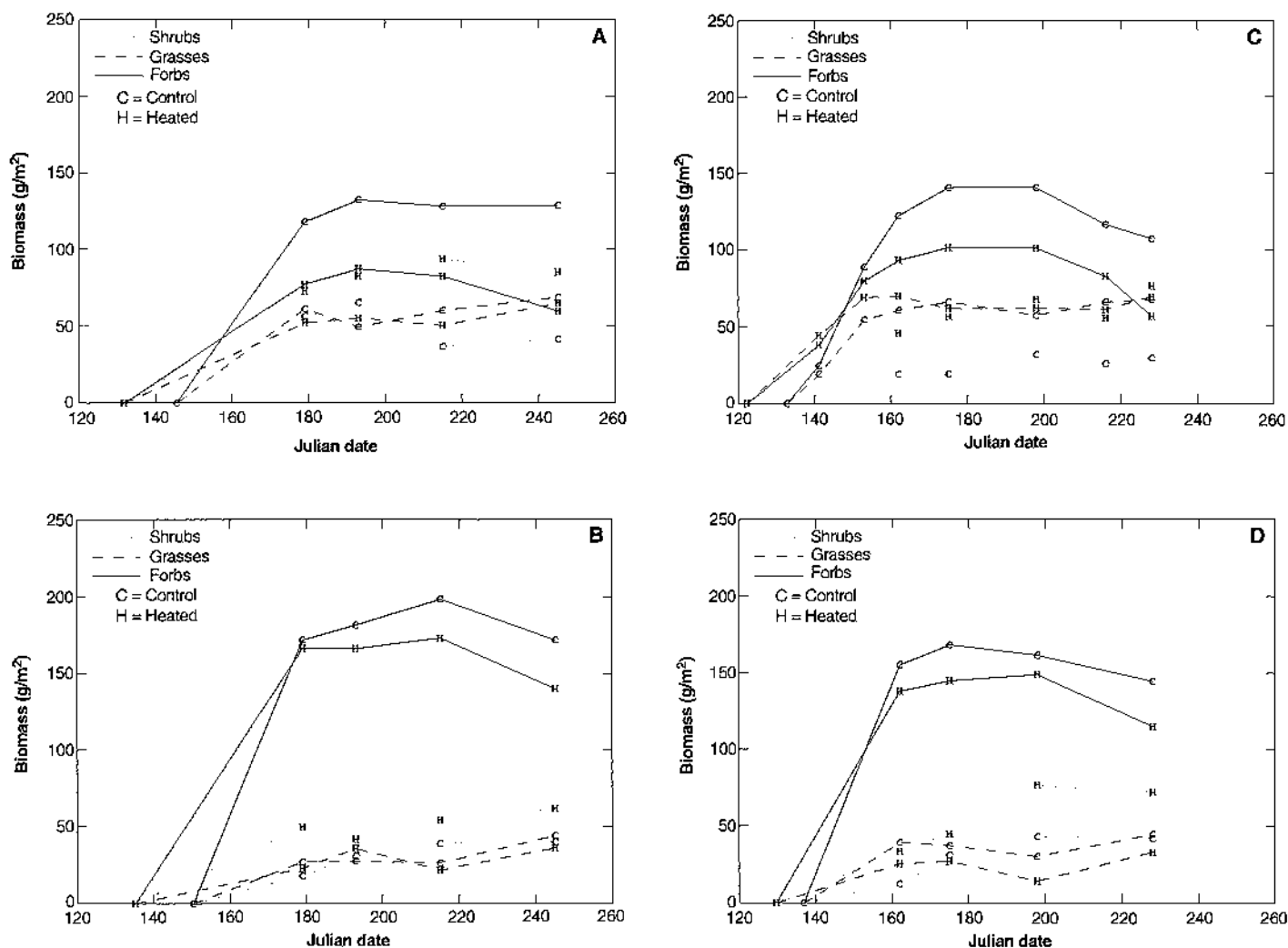


Fig. 2. Aboveground biomass of forbs, graminoids, and shrubs in heated and control plots. Biomass values are set to zero at the treatment-averaged date of snowmelt, as defined in (13). (A) Dry zone, 1993; (B) wet zone, 1993; (C) dry

zone, 1994; (D) wet zone, 1994. All data are from areal coverage estimates (19, 21).

attributed poor shrub growth under a deep snowpack to the detrimental effect of prolonged saturation of the root zone (4).

Within each zone-year combination, the peak value of the sum of forb, graminoid, and shrub AGB was generally independent of treatment, and the only sizable treatment difference occurred in 1992 (the wettest year) in the wet zone (heated plots: total AGB = 296.3 ± 53.1 g/m²; control plots: total AGB = 160.1 ± 17.4 g/m²). The positive effect of heating on shrub AGB dominated that difference. In other year-zone combinations, the treatment differences were negligible because the heating effect on forb and shrub AGB nearly canceled one another. Averaging over zone and treatment, the sum of shrub, forb, and graminoid AGB in 1991, 1992, 1993, and 1994 was 271, 207, 245, and 230 g/m², respectively, indicating little interannual variation in total AGB. These results are in agreement with research on tundra, which

showed that annual production of individual species varied greatly from year to year but total production exhibited interannual constancy (22). The duration of our study is not yet sufficient to detect a lagged correlation between total AGB in one year and soil microclimatic conditions in the previous year, in contrast to a recent long-term study (23), which found evidence for such a lagged effect.

The dominance of long-lived perennials in many montane meadows suggests that over several decades at least, the effects reported here of soil microclimate modification on the AGB of mature plants could greatly influence community structure. Nevertheless, a treatment-induced enhancement in shrub AGB and a decline in forb AGB do not necessarily mean shrubs will ultimately replace forbs in the meadow under global warming. Over the longer term, the effects of climate change on species-specific rates of germi-

nation and seedling establishment and growth will determine community structure to a great extent (24). To gain more insight into possible long-term consequences of heating on community structure, we measured seedling establishment of *A. tridentata* in 1994 by censusing surviving *A. tridentata* seedlings within the age class 0 to 3 years in a 1.7-m² transect in the drier zone of each plot. The mean number of surviving seedlings in the transects of the heated plots (3.60 ± 1.36) was significantly greater ($P < 0.05$; *t* test) than that in the control plots (0.40 ± 0.24), suggesting that warming enhances seedling establishment and not just the AGB of the sagebrush.

The Quaternary pollen record suggests that the effects of climate on the distribution of montane vegetation in the western United States are complex and depend on factors such as topography and dispersal characteristics of taxa as well as on mean

Table 2. Aboveground biomass of graminoids, forbs, and shrubs (in grams per square meter). Data for 1991 and 1992 are from harvested biomass (17); those for 1993 and 1994 are based on areal coverage measurements (19, 21) and are seasonal averages over Julian days 179, 193, 215, and 245 in 1993 and days 162, 175, 198, and 228 in 1994. The standard errors (in parentheses) are computed from the values of seasonally averaged data for each plot within a treatment group ($N = 5$).

Vegetation	Dry zone		Wet zone	
	Control plots	Heated plots	Control plots	Heated plots
1991				
Graminoids	122.9 (10.4)	95.4 (13.0)	70.9 (23.9)	122.9 (57.2)
Forbs and shrubs	146.2 (46.7)	148.2 (45.5)	167.2 (15.0)	209.0 (11.7)
1992				
Graminoids	71.5 (19.8)	58.1 (8.2)	29.8 (8.4)	42.5 (8.6)
Forbs	84.2 (7.8)	89.9 (10.6)	102.0 (12.6)	116.7 (15.0)
Shrubs	22.0 (7.6)	47.7 (18.4)	28.3 (12.8)	137.1 (41.2)
1993				
Graminoids	58.5 (17.5)	55.5 (15.9)	31.5 (10.6)	30.7 (8.3)
Forbs	127.0 (25.6)	78.2 (17.3)	181.4 (27.5)	161.8 (22.6)
Shrubs	49.9 (20.3)	85.3 (61.2)	33.6 (33.2)	50.8 (37.7)
1994				
Graminoids	61.0 (17.1)	62.0 (15.2)	36.7 (7.4)	26.4 (6.3)
Forbs	127.7 (22.7)	90.8 (15.4)	156.9 (25.3)	139.3 (20.1)
Shrubs	26.0 (10.9)	60.5 (36.8)	37.1 (34.7)	60.2 (33.7)

temperature and effective precipitation (25). Nevertheless, available pollen records over the past 10,000 years show intervals of increased abundance of *Artemisia* associated with periods of high tree line, which isotope data suggest are best interpreted as brief warm intervals (25, 26). There is therefore evidence that increased abundance of *Artemisia* may have been associated with climate warming in the past.

The existing mosaic of intermingled herbaceous- and shrub-dominated montane habitat implies that dispersal should not be a major barrier to a transition from dominant herbaceous to dominant shrub-steppe vegetation. The dramatic effect of warming we observed on the ratio of aboveground shrub cover to forb cover implies that the competitive status of shrubs is enhanced relative to forbs. The observed increase in *Artemisia* seedling establishment implies enhanced recruitment of sagebrush under warming. The data on shoot elongation rates, which show that shrub growth rates as distinct from cover density are enhanced by warming, are again indicative of enhanced competitive status of shrubs. The pollen record, although sketchy, supports all of these implications.

Greater understanding of the pace and pattern of this potential transition from forb to shrub dominated meadow awaits reliable forecasts of interannual climatic variability (27) and further information about effects of climate change on individual plant species (28), on plant reproduction and recruitment (24), on belowground plant growth, and on nutrient availability (22). Taken together, however, the evidence presented here suggests that the global warming associated with a doubling of the atmospheric concentration of carbon dioxide is

likely to result in the increasing dominance of *Artemisia* in the widespread montane meadow habitat now dominated by forbs.

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9. Soil heating under global warming results from both the direct effect of increased downward IR and the conduction of heat from a warmer atmosphere. Only the first of these is simulated by our manipulation. We chose not to manipulate precipitation at the site because of the large uncertainty in the magnitude and even the sign of impending changes in regional precipitation rates. Moreover, because the heaters advance the time of snowmelt and increase evapotranspiration rates, they allow us to investigate ecological effects of altered soil moisture without such manipulation. Our heaters do not detectably raise the temperature of the canopy air, but previous research has suggested that soil temperature is a more important factor than air temperature in controlling the growth of high-elevation plants; see, for example, L. C. Bliss, *Annu. Rev. Ecol. Syst.* **2**, 405 (1971).
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11. In the dry zone, typical vegetation species include *A. tridentata*, *Mertensia fusiformis*, *Helianthella quinquerivis*, *Delphinium nelsonii*, *Vicia americana*, *Lathyrus leucanthus*, and *Festuca thurberi*. In the wet zone, typical species include *Pentstemon floricola*, *Potentilla fruticosa* of various authors, *Claytonia lanceolata*, *Erythrocraea triflora*, *Veratrum tenuipetalum*, *Rhodiola integrifolia*, and *Melica spectabilis*. The only shrubs at the site are *A. tridentata* and *P. floricola*.
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13. The time of snowmelt in our experimental plots is defined as the time at which the soil temperature at a depth of 5 cm first reaches +1°C.
14. The 1.6-m-long heaters were purchased from Kalgio (Lehigh, PA); reflectors behind the heating elements were modified to provide a uniform radiation flux over the plots and to ensure negligible flux to adjacent plots (8). The heaters produce no visible radiation and less than one-millionth of the solar input in the far red (700 to 800 nm) spectral region. Two heaters per plot were used to achieve 15 W/m² and three per plot to achieve 22 W/m². The applied flux represents roughly a 3% increase over total average ambient downward radiation.
15. The effect of heating on soil temperature was proportional to the applied heat flux. Although an enhanced downward infrared flux of 22 W/m² exceeds the upper limit predicted from general circulation models for an atmosphere with twice the pre-industrial concentration of carbon dioxide, even with water vapor feedback (V. Ramanathan, *J. Atmos. Sci.* **38**, 918 (1981)), our flux was selected to compensate for the absence of air-warming in our manipulation (8). The heat flux was chosen to simulate the surface heating expected under a doubled-CO₂ atmosphere.
16. Campbell Scientific, CR10 data loggers.
17. In 1991, we randomly selected four 0.25 m by 0.25 m quadrats in both the wet (lower third) and the dry (upper third) zones of each plot. In 1992, we selected one 0.25 m by 2 m quadrat, centrally located and oriented parallel to the long dimension of the plots, in both zones of each plot. We clipped vegetation, dried it in an oven at 60°C to constant weight, and weighed it. We clipped vegetation on Julian days 224 to 226 in both years. In 1992, we separated forbs, graminoids, and shrubs for this analysis, but in 1991, we lumped forbs and shrubs. In 1993, dry weights were measured only for purposes of calibrating the indirect measures of AGB (20).
18. We estimated LAI separately for forbs, shrubs, and graminoids in 0.75 m by 0.75 m quadrats (centered around the soil microclimate probes) in the dry and in the wet zone of each plot on Julian days 195, 215, and 245 of 1993 and approximately every 10 days throughout the growing season in 1994. We used the point-intercept method, with 20 to 40 needle drops randomly selected within each quadrat on a grid ruled with 225 0.05 m by 0.05 m squares.
19. We estimated areal coverages of shrubs, forbs, graminoids, bare soil, gopher mound, litter, and rock in the same 0.75 m by 0.75 m quadrats and grid used for LAI measurement (18). Correlations among plots of the results of the LAI and areal coverage methods always yielded $R^2 > 0.7$ for each zone and year combination.
20. The lengths of five tagged shrub shoots in the dry and wet zones of each plot were measured at weekly intervals from the end of snowmelt through August in 1992, 1993, and 1994. Secondary growth on the

- previous year's shrub shoots is not included in our estimates.
21. For forbs, $AGB = LAI \times (49.94 \pm 4.76) \text{ g/m}^2$ ($N = 10$) and $AGB = (\text{percent of areal coverage}) \times 2.79 \text{ g/m}^2$ ($N = 10$). For graminoids, $AGB = LAI \times (26.20 \pm 2.34) \text{ g/m}^2$ ($N = 10$) and $AGB = (\text{percent of areal coverage}) \times (2.19 \pm 0.23) \text{ g/m}^2$ ($N = 10$). For shrubs, incremental $AGB = (\text{incremental shoot length in centimeters per square meter}) \times (0.028 \pm 0.005) \text{ g/m}^2$ ($N = 19$), and incremental shoot length = $(\text{percent of areal coverage}) \times (171.8 \pm 11.3) \text{ cm/m}^2$ ($N = 10$). Regressions of LAI or shoot length against the direct measure of AGB carried out separately for each zone and for each treatment showed no significant dependence of regression coefficients on zone or treatment.
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27. The importance of reliable forecasts of interannual climatic variability is underscored by our observation that the magnitude of the effect of heating on AGB varied with summer soil moisture levels; see also (23) and N. L. Stephenson, *Am. Nat.* **135**, 649 (1990).
28. Investigation of climate controls on growth of tundra species shows that within the broad grouping of forbs or shrubs, species at a particular site can differ

markedly in their responses to environmental influences (22).

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Effects of Competition, Colonization, and Extinction on Rodent Species Diversity

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Analyses of long-term experimental data from the Chihuahuan desert revealed that species diversity of other rodents was higher on plots from which kangaroo rats (*Dipodomys* spp.) had been removed. The difference was due to consistently higher colonization and lower extinction probabilities of small granivorous rodents in the absence of competitively dominant kangaroo rats. The results of this ecosystem experiment demonstrate the importance of both competitive exclusion and metapopulation dynamics for biological diversity in a natural community.

Theoretical and laboratory studies suggest that the number of species that coexist in a community is influenced by several processes, including competition, predation, mutualism, disturbance, and physical stress (1–6). Although there is evidence that each of these factors can affect the relative abundance of species in a natural community, there are few examples of how, either singly or in combination, they affect the number of coexisting species. Further, in order for these processes to alter species diversity rather than just relative abundance, they must affect metapopulation dynamics; that is, the probabilities of local colonization and extinction (6–8).

Mathematical models predict, and laboratory experiments have demonstrated, competitive exclusion—the capacity of a competitor to cause the local extinction of another species (1, 9). Evidence for competitive exclusion from field studies is more equivocal (4, 10–13). Examples of extinction of species native to islands and other isolated habitats are difficult to explain solely by competition from invading exotics, because such extinctions almost always coin-

cide with increased human influence (14).

Here we demonstrate the effect of competition on species diversity in a community of rodents in the Chihuahuan desert. The removal of seed-eating kangaroo rats (*Dipodomys* spp.) from small experimental plots increased the number of small granivorous rodent species. These increases in diversity resulted from higher probabilities of colonization or lower probabilities of extinction, or both.

In 1977, experimental plots (50 by 50 m) were established on a 20-ha site of relatively homogeneous Chihuahuan desert scrub vegetation near Portal, Arizona. Each plot was surrounded by wire mesh topped with aluminum flashing to control access by rodents. Plots were assigned various experimental treatments that included exclusion of different rodent species on the basis of body size. Equal access (or control) plots had 16 large (3.7 by 5.7 cm) gates in the wire mesh, which allowed access to all rodents. Plots from which kangaroo rats were removed had 16 small (1.9 by 1.9 cm) gates in the wire mesh, which allowed access by all small-bodied rodents but prevented the larger-bodied kangaroo rats (*Dipodomys spectabilis*, *D. merriami*, and *D. ordii*) from entering. From 1977 to 1987, there were 14 equal access and 4 kangaroo rat removal plots. In 1988, some equal access plots were converted into new kangaroo rat removal plots by changing their

gate size. Thus, from 1988 to the present (March 1994), there were eight equal access plots, four old kangaroo rat removal plots (*Dipodomys* excluded continuously since 1977), and four new kangaroo rat removal plots (*Dipodomys* excluded continuously since 1988).

Approximately each month since 1977, rodents on all plots have been censused. For one night, 49 Sherman live traps were placed on each plot and baited with millet. During each census, all gates were closed so that only resident individuals were caught. All individuals captured were identified, measured, uniquely marked, and released (13).

Kangaroo rats compete strongly with other rodents (15) and have large effects on vegetation (16, 17). Within 1 to 2 years of removal of kangaroo rats from experimental plots, densities of small seed-eating rodents increased more than twofold (13, 15); 8 to 10 years after kangaroo rat removal, annual and perennial grass density increased more than threefold (16, 17).

Species diversity of the other nocturnal rodents changed in response to experimental removal of kangaroo rats. During the past 17 years, a total of 14 such species have been recorded. Kangaroo rat removal plots usually supported more species of other rodents than did equal access plots (Fig. 1).

From 1977 to 1981, there was no difference in the number of non-*Dipodomys* species caught per month between equal access and kangaroo rat removal plots (Table 1). From 1982 to 1987, and again from 1988 to 1994, however, there were more rodent species per month on kangaroo rat removal plots than on equal access plots (Table 1). The increasing trend in species diversity can be attributed, in part, to the indirect effect of kangaroo rats on rodents through vegetation (18, 19), as well as to the direct effect of the relaxation of competition.

From 1982 to 1994, approximately one additional species per month was found on plots from which kangaroo rats had been removed. This difference represents only a snapshot of species diversity. Because the

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