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Northern Pocket Gopher (*Thomomys talpoides*) Control of Alpine Plant Community Structure

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Abstract

We evaluated the importance of the northern pocket gopher (*Thomomys talpoides*) in controlling plant species composition and richness in two alpine tundra plant communities. We hypothesized that forb diversity and relative abundance is modified by gopher mounding activities in moist meadows of Niwot Ridge, Colorado, U.S.A., where both the pocket gopher and forbs are most concentrated. We tested this hypothesis with simulated gopher mounds. Forbs recovered faster following burial than graminoids or cushion plants, demonstrating a resilience that we propose confers a competitive advantage over other growth forms and favors forb dominance in moist meadows. Gopher effects on species richness varied according to spatial scale of measurement and community type. For one decade we monitored the responses of a sedge-dominated community to gopher activity in 1.5 m² plots that included both gopher mounds and intermound spaces and found that species richness was significantly positively correlated with recent disturbance. Species richness on the simulated gopher mounds (0.2 m²) immediately declined significantly after burial but recovered within a year. When evaluated in conjunction with studies of gopher diet preferences and effects on ecosystem biogeochemistry, our findings suggest that the northern pocket gopher is instrumental in constructing a locally diverse alpine plant community.

Introduction

The importance of disturbance in controlling species diversity and plant community composition has been recognized across a variety of ecosystems and temporal and spatial scales (Grubb, 1977; Huston, 1979; Pickett and White, 1985). Disturbances imposed by burrowing animals such as pocket gophers, although small-scale, can influence plant community structure (e.g., Ellison and Aldous, 1952; Reichman et al., 1993; Hobbs and Mooney, 1995). During excavation of subterranean burrow systems, gophers deposit large quantities of well-mixed soil (Thorn, 1978; Burns, 1979) on the soil surface in heaps, or “gopher mounds.” Mound soils are physically, biogeochemically, and vegetatively distinct from the surrounding soil matrix (Inouye et al., 1987; Huntly and Inouye, 1988; Sherrod and Seastedt, 2001), provide open habitat for plant establishment, and reduce competition for surviving plants (Hobbs and Mooney, 1985; Chambers et al., 1990). Gopher modifications of the ecosystem therefore also may be manifest in the characteristics of colonizing and/or recovering vegetation. Many studies show that gopher disturbances increase species diversity at least for the short term (e.g., Tilman, 1983; Inouye et al., 1987; Chambers, 1993). Gopher disturbance can also alter plant species composition and growth form, usually with preferred dietary species decreasing in disturbed areas (Ellison and Aldous, 1952; Laycock and Richardson, 1975; Foster and Stubbendieck, 1980).

The present study focused on soil mounds created by the burrowing activities of the northern pocket gopher (*Thomomys talpoides*) in the alpine tundra of Niwot Ridge, Colorado, U.S.A. We evaluated plant species composition and richness of two Niwot Ridge plant community types—the moist meadow and a drier *Carex elynoides* community—in the context of these small, frequent disturbances to better understand the role of gophers in this ecosystem.

Niwot’s major plant community types, which occur in patches across the tundra landscape (Komárková and Webber, 1978), are

determined by alpine landscape position via topographic controls over snowpack and soil moisture (Billings, 1973; Walker et al., 1993). These community types, listed roughly in order of their water budget, include fellfield, dry meadow, moist meadow, snowbed, shrub tundra, wet meadow, and barren patches (Walker et al., 1993). Although pocket gophers and forbs are found in most of these community types (Thorn, 1982; Halfpenny et al., 1984), each exhibits highest densities in moist meadows (May and Webber, 1982; Thorn, 1982; Walker et al., 1993), which are intermediate along the moisture gradient. We hypothesized that gopher activities enhance the proliferation of alpine forbs in moist meadows via some inherent resilience, i.e., the ability of forbs to recover from a stressful impact such as gopher mound burial (e.g., Holling, 1973).

The large belowground biomass and energy content of alpine forbs (Webber and May, 1977; Jaeger and Monson, 1992; Steltzer and Bowman, 1998) and their widespread distribution make them ideal forage for belowground herbivory, supported by identification of multiple forb species roots in gopher food caches both at Niwot Ridge (Seastedt, personal observation) and elsewhere (Aldous, 1951; Laycock and Richardson, 1975). Because gopher activities are subterranean, however, it is difficult to quantify its use of any particular plant species. We chose instead to focus on whether alpine forbs are modified by pocket gopher mounding activities. Chambers et al. (1990) and Chambers (1993) have examined the potential of *Acomastylis rossii* seedling establishment on disturbed substrate, but to our knowledge there are no published studies of any alpine forb’s ability to survive following burial of aboveground structures.

Excluding a hypothesized keystone species from an ecosystem for an extended duration is the classic approach to determining its role (e.g., Brown and Heske, 1990). The extremely rocky substrate of Niwot Ridge makes underground fencing virtually impossible, however. Moreover, alpine tundra vegetation has slow growth rates and constrained responses to ecosystem manipulation (Diggle, 1997;

Meloche and Diggle, 2001), making a short-term, relatively small-scale study a prerequisite to larger scale evaluations. Our approach was a simulation of pocket gopher mounds in alpine moist meadows to evaluate the short-term responses of species and growth forms (forbs, graminoids, and cushion plants) to burial. We also monitored plant species richness.

In addition to the alpine moist meadows, we examined the influence of pocket gopher mounds on species richness in a community dominated by the sedge *Carex elynoides*. Along the southern Rockies, these plant communities are associated with substantial pocket gopher activity (Willard, 1960; Bamberg, 1961), suggesting that the rodent may be instrumental in maintaining their vegetative characteristics. Restricted to fairly steep, south-facing exposures (*Caricetum elynoidis* Association in Komárková and Webber, 1978), *C. elynoides* community types are not common at Niwot Ridge, but one such community monitored for over 10 years at the site has experienced repeated pocket gopher activity, presenting an opportunity for a long-term gopher study.

Materials and Methods

STUDY SITES

Niwot Ridge (40°03'N, 105°35'W), oriented from west to east in the Rocky Mountain Front Range, is about 35 km west of Boulder, Colorado. At ~3500 m above sea level (a.s.l.), Niwot Ridge is the alpine representative of the NSF's Long-Term Ecological Research (LTER) Program. The mean annual temperature at a long-term monitoring station ~200 m above the study sites is -3.7°C, and annual precipitation, predominantly snow, averages 930 mm (Greenland, 1989).

In a short-term study, we created artificial gopher mounds in moist meadows, a community type characterized by a substantial winter snowpack that normally persists until early summer (Burns, 1980). Moist meadows are dominated by the forb *A. rossii* and the grass *Deschampsia caespitosa* (May and Webber, 1982; Theodose et al., 1996), and plant productivity is intermediate for Niwot Ridge, averaging 410 g/m² (Fisk et al., 1998). Soil characteristics of moist meadows are described in Sherrod and Seastedt (2001). All areas of the alpine moist meadows are assumed to reflect their history of patchy gopher use in their species abundance patterns, as these communities do not change significantly over time (Turner, 2001; Forbis et al., 2004).

We monitored species richness at a long-term study site on the south slope of Niwot Ridge (3400 m a.s.l.). The dominant plant species at this site is the sedge *C. elynoides*. In 1987, twenty-five 2 × 1.5 m plots were established across an area approximately 36 × 16 m. No active gopher mounds were observed at the time of plot establishment, but gophers invaded the same year. Further geomorphic and pedological details of the site can be found in Litaor et al. (1996).

SAMPLES

Simulated Gopher Mounds

For the short-term study we created a total of 60 artificial pocket gopher mounds just after snowmelt in early July of 1997 and 1998. Each year, fifteen 0.5 m (diameter) mounds were created on the north and south slopes of Niwot Ridge, their locations chosen randomly within the moist meadow community type. We quantified pretreatment vegetation by counting individual forb species and estimating the percent cover of cushion plant and graminoid species. We then buried the surveyed area with soil from fresh gopher mounds, pouring the soil to a height of ~10 cm and reproducing the characteristics of natural gopher mounds. We quantified the recovering vegetation monthly (August and September) until snowfall; recovering vegetation was

defined as plants growing through the mound soil from the original tundra surface and not from plant propagule establishment or other recruitment. Recruitment of new individuals was negligible. Quantification methods were the same as those used before burial. We did not count the vegetation within 2.5 cm of the perimeter as this was negligibly impacted by the disturbance. Vegetation on mounds created in 1997 was quantified again in August 1998, 13 months after vegetation burial.

Four target forbs were considered explicitly in species-level analysis: alpine avens (*A. rossii*), Rocky Mountain sage (*Artemisia scopulorum*), American bistort (*Bistorta bistortoides*), and Parry clover (*Trifolium parryi*). All of these species are most common in the alpine moist meadow (May and Webber, 1982) and are believed to be part of the pocket gopher diet (Seastedt, personal observation). For each sampling date, the percent recovery of each species on each mound was calculated and these data were arcsin-transformed. For statistical analysis, species that recovered to >100% were assigned the same arcsin-transformed values as those that recovered to 100%. Repeated-measures ANOVA tested for differences in recovery of the four forbs between slopes, years, and species with sample date as the within-subjects factor. Only data from August and September were used for this analysis because data from the one-year time interval were unavailable for the 1998 treatment. A second repeated-measures ANOVA was used for the 1997 treatment only and included the one-year time interval. Because recovery data are percentages of pre-treatment vegetation, they inherently include baseline control values. Additionally, all species were categorized according to growth form, and species richness was also calculated for each simulated gopher mound. Data were analyzed as above.

Long-term Observations

We determined plant species composition in the long-term plots in the summers of 1988–1992 and 1996–1997 using a point-quadrat method. Unvegetated points, including gopher mound substrate, were recorded as rock or soil. The points representing fresh gopher mounds, i.e., those created during the same season as measurement, were summed within each plot for a measure of freshly disturbed area.

For data analysis we divided each 3 m² plot into two 1 × 1.5 m subplots to better reflect mound-vegetation relationships. Concerns about spatial autocorrelation are resolved with erosion data showing that the impacts of gopher mounds on adjacent areas are minimal, even on steep terrain (Sherrod and Seastedt, 2001).

In July 1998 we measured the soil organic matter (SOM) within each subplot as an index of soil fertility (Seastedt, 2001) to evaluate its relationship with community diversity. Three 10 cm soil cores were sampled with a 1.5 cm (diameter) auger and composited. The soils were sieved (2 mm), air-dried, and measured for SOM using loss on ignition. Pearson correlation was calculated between species richness (no. species per plot) and the number of points representing fresh mounds, and between richness and SOM.

Results

The simulated mounds of the short-term study exhibited weathering characteristics typical of naturally produced pocket gopher mounds, including a progressively larger representation of coarse particles on the mound surface with time, but retention of mound height and boundaries. Relatively flat local terrain prevented shifts in mound position between sampling.

Forbs exhibited greater recovery from burial than the other growth forms both within the season of burial and after one year (Table 1a; Fig. 1). Cushion plants showed no recovery within the season of burial. Greater percent recovery of graminoids and forbs in 1998 than 1997

TABLE 1

F values of repeated-measures ANOVA testing the effects of slope, sample date, and year of treatment on plant recovery after burial with simulated mounds. Sample date is the within-subjects factor. 1997-only data include second-season sampling for a total of three sampling dates; 1997 and 1998 data analyzed two sampling dates only, August and September. (a) Growth form analysis. (b) Species-level analysis is of *A. rossii*, *A. scopulorum*, *B. bistortoides*, and *T. parryi*.

Source	1997 only	1997 & 1998
(a) Growth form		
<i>Between subjects</i>		
Year		6.0*
Slope	0.1	0.0
Growth form	6.8**	3.5*
Growth form × Slope	0.3	0.2
Growth form × Year		0.2
Slope × Year		0.5
Growth form × Slope × Year		0.3
<i>Within subjects</i>		
Date	24.0***	0.3
Date × Slope	0.7	0.1
Date × Year		0.2
Date × Growth form	2.7*	1.4
Date × Slope × Growth form	0.2	0.3
Date × Year × Growth form		0.5
Date × Year × Slope		0.9
Date × Year × Slope × Growth form		0.2
(b) Species		
<i>Between subjects</i>		
Year		4.4*
Slope	0.4	0.0
Species	25.7***	5.6**
Species × Slope	0.3	0.1
Species × Year		1.6
Slope × Year		0.0
Species × Slope × Year		0.1
<i>Within subjects</i>		
Date	27.5***	1.4
Date × Slope	0.4	0.4
Date × Year		0.6
Date × Species	12.8***	3.9*
Date × Slope × Species	0.3	1.0
Date × Year × Species		1.4
Date × Year × Slope		3.6
Date × Year × Slope × Species		1.8

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

resulted in significant differences between treatment years (Table 1a), but statistical relationships among the growth forms (Fig. 1) were consistent.

Among the four target forbs, recovery of individual species differed significantly (Table 1b; Fig. 2). By the second season, the number of *B. bistortoides* on simulated mounds was no different than before burial ($t = 0.06$; $p = 1.0$). *Acomastylis rossii* had not recovered to its original numbers by the second season ($t = -6.4$; $p < 0.001$), but its second-season recovery was significantly greater than that of *T. parryi* or of *A. scopulorum* (Fig. 2, top); the latter was consistently the least resilient of the four species. Greater percent recovery of all species but *A. scopulorum* in 1998 resulted in significant differences between treatment years (Table 1b).

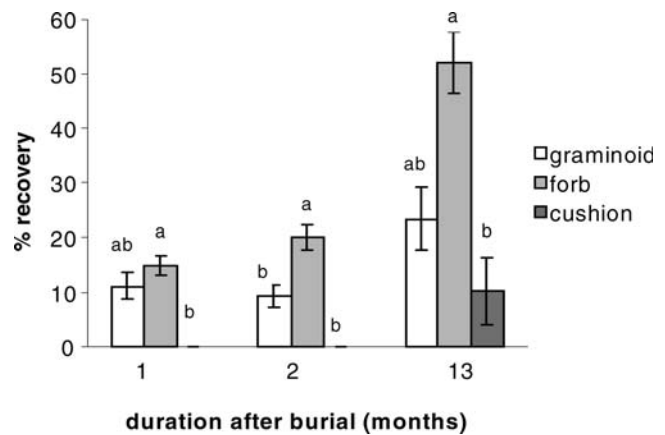


FIGURE 1. Average percent (± 1 SE) recovery of three growth forms buried by simulated gopher mounds. Data are pooled over 1997 and 1998. Cushion plants showed no recovery until 13 months. Different letters within a cluster indicate significant ($p < 0.05$) differences among growth forms for that sample date.

Species richness decreased immediately after burial on the simulated mounds and increased significantly by the second season (Fig. 3a; Table 2). By 13 months following burial on the north slope, species richness recovered to levels not significantly different than pre-treatment richness, but on the south slope was still significantly lower than pre-treatment levels. Greater species counts by an average of 1.5 species in 1998 resulted in significant between-year differences (Table 2), but statistical relationships among sample dates were consistent (Fig. 3a).

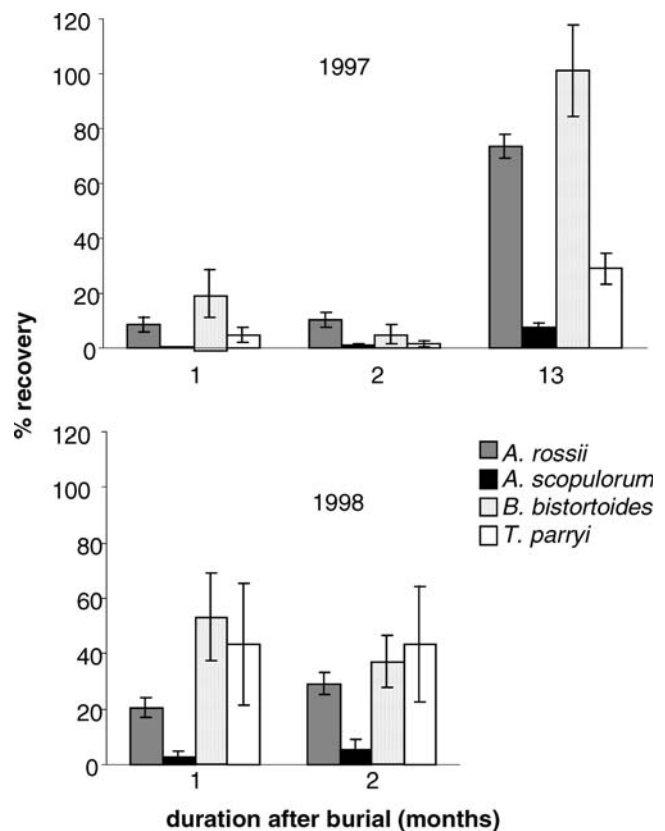


FIGURE 2. Mean (± 1 SE) percent recovery of *Acomastylis rossii*, *Artemisia scopulorum*, *Bistorta bistortoides*, and *Trifolium parryi* after burial by simulated gopher mounds.

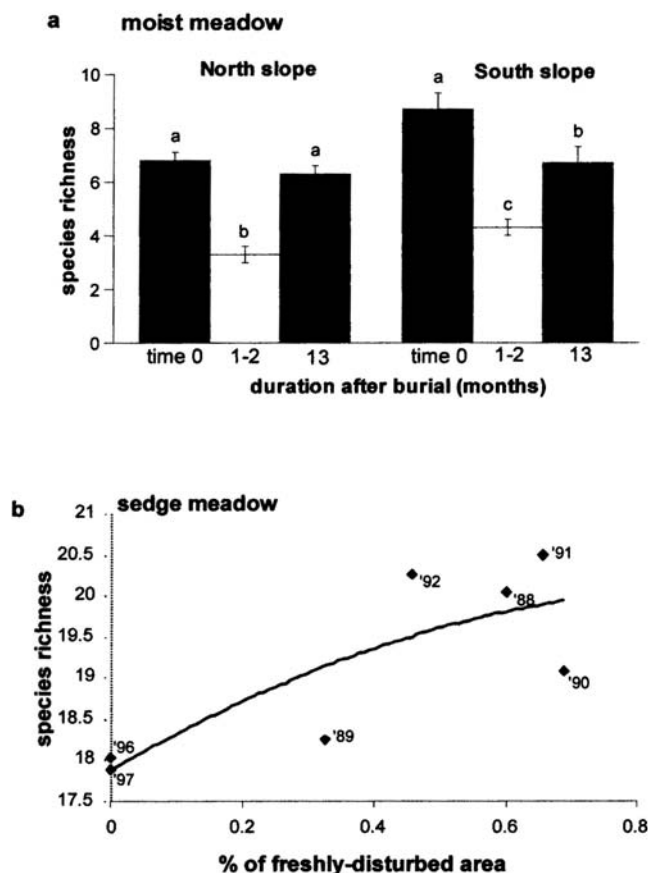


FIGURE 3. Comparison of species richness in response to gopher mounding activities at two scales of measurement. (a) Simulated mounds (short-term study). Species richness before (“time 0”) and after burial within the 0.2 m² mounds. Data are pooled between 1997 and 1998 treatments. Different letters within clusters indicate significant ($p < 0.05$) differences among dates on each slope. (b) Long-term study plots. Relationship between species richness and the number of freshly disturbed points (those disturbed during the same season as measurement) in the sedge meadow (1.5 m² plots). Points are labeled by year. $R^2 = 0.81$ ($p = 0.03$); $y = -2.45x^2 + 4.69x + 17.8$.

In contrast to the simulated mounds, species richness in the long-term study plots of the sedge meadow was significantly positively correlated with the number of points representing fresh disturbances ($r = 0.81$; $p = 0.03$; Fig. 3b). In addition, species richness on the long-term plots was significantly negatively correlated with SOM ($r = -0.48$; $p < 0.001$).

Discussion

Alpine forbs are less impacted by gopher mound burial than are graminoid and cushion plant species. The forbs even appear to benefit in the short term from gopher mound burial via the suppression of other growth forms in the moist meadows of Niwot Ridge. Our observations of short-term forb resilience following aboveground disturbance and their associated dominance (Fig. 1) are consistent with gopher studies in other ecosystems (Foster and Stubbendieck, 1980; Inouye et al., 1987; Martinsen et al., 1990). Although this study did not evaluate other components of pocket gopher activities and impacts such as herbivory, this evaluation of its aboveground disturbances to plant communities via burial lends insight into the mechanisms of plant community controls in this alpine tundra.

TABLE 2

F-values from repeated-measures ANOVA testing the effects of year of treatment and slope on species richness on simulated mounds. Sample date was the within-subjects factor. 1997-only data include second-season sampling for a total of four sampling dates (July [Time 0], August and September 1997, and August 1998); 1997 and 1998 data analyzed the first three sampling dates only (Time 0, August, and September).

	1997 only	1997 and 1998
<i>Between subjects</i>		
Year		38.4***
Slope	1.5	15.7***
Year \times Slope		6.9*
<i>Within subjects</i>		
Date	62.3***	118.6***
Date \times Year		3.9*
Date \times Slope	0.8	1.1
Date \times Year \times Slope		7.3**

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

Williams et al. (1986) and Hobbs et al. (1988) attributed the greater abundance of forbs in gopher-disturbed areas to “an increased ability to survive burial” and to the prevention of grass dominance, respectively, explanations that are consistent with our observations at Niwot Ridge. The rapid recovery of forbs following burial can be attributed to their appreciable carbon storage in belowground structures (Webber and May, 1977; Jaeger and Monson, 1992; Steltzer and Bowman, 1998). In years and community types with a more persistent snowpack and an abbreviated growing period, plants with belowground storage organs are at a competitive advantage over those with lower root:shoot ratios such as graminoids (Webber and May, 1977). This belowground structure also confers an advantage to other aboveground obstructions such as pocket gopher mounds (Fig. 1).

Although this alpine tundra is dominated by perennial graminoids across its cumulative community types, it distinguishes itself from other grasslands in two important ways. First, activities of the northern pocket gopher in alpine moist meadows, by inhibiting graminoids and cushion plants, may contribute to processes resulting in a forb-dominated, rather than a grass-dominated, ecosystem. Second, varying growth form responses to added nitrogen (N) among different grassland ecosystems support the idea of alpine forb dependence on belowground energy stores when aboveground biomass is obstructed. In tallgrass prairie (Seastedt et al., 1991) and shortgrass steppe (Vinton and Burke, 1995), patches of artificially increased N are normally colonized by weedy forbs, but such patches are colonized by graminoids in alpine tundra (Bowman et al., 1993). Conceivably, the four-year preformation constraint of alpine forbs (Diggle, 1997; Meloche and Diggle, 2001) prevents them from taking advantage of spatial variation in surplus nutrients; as such, there are no recognized “weedy” forbs in alpine tundra. Because fresh pocket gopher mounds are microsites of higher inorganic N relative to intermound spaces (Sherrod and Seastedt, 2001), we should expect higher graminoid representation on gopher mounds than other growth forms (Bowman et al., 1993). The fact that they are not as well represented as forbs supports the idea that the mechanisms of forb resilience include their diversion of energy use to belowground stores in addition to their ability to withstand the mechanical impact of soil burial.

The observations that forbs appear to respond positively to gopher mounding activities in the short term and that gophers depend on forbs for nourishment (Aldous, 1951; Ward and Keith, 1962; Laycock and

Richardson, 1975) support propositions that the gopher effectively cultivates alpine forbs (Cortinas and Seastedt, 1996) and that the taxa share an interdependent relationship. Such a relationship, by extension, would predispose the entire moist meadow community to a degree of interdependence with the pocket gopher. As the dominant growth form, forbs may afford the alpine moist meadows a community-wide resilience that is greater than that of plant communities with lower relative forb cover such as alpine dry meadows or snowbeds (Webber and May, 1977; May and Webber, 1982). Thus, the impacts of relatively high pocket gopher concentrations in alpine moist meadows (Burns, 1979; Thorn, 1982) may be sustained by community-level resilience; in turn, gopher activities contribute to the maintenance of characteristics typical of the alpine moist meadows which are marked by forb dominance.

The strong short-term recoveries of *A. rossii* and *B. bistortoides* are integral to the greater resilience observed among forbs rather than among graminoids or cushion plants (Figs. 1, 2). *Bistorta bistortoides*, with its relatively tall stature and large belowground storage capacity (Jaeger and Monson, 1992), showed the strongest resilience following burial, recovering to 100% within a year (Fig. 2). *Acomastylis rossii* is also fairly resilient, recovering 73% of its original abundance one year following burial (Fig. 2).

Gopher effects on species richness varied according to spatial scale of measurement and community type. In the long-term study plots of the sedge meadow, fresh mounds and species richness were positively correlated (Fig. 3b). This could be due to the heterogeneity of the substrate (Tilman, 1982), as our plots (1.5 m²) included both gopher mounds and intermound spaces. Alternatively, this positive disturbance-richness relationship may be via the reduction of SOM in gopher mounds (Sherrod and Seastedt, 2001), as species richness was also significantly negatively correlated with SOM. A negative SOM-richness relationship was also demonstrated in alpine wet meadows (Theodose and Bowman, 1997). Although our single collection of soil for SOM measurements does not represent the entire decade as an index of soil fertility, mounding activities within the long-term study plots were minimal during 1993–1998, and we reason that SOM, for at least the latter part of the sequence, is adequately represented by our single measurement.

Although not directly comparable to the long-term study plots of the sedge meadow, species richness within the simulated pocket gopher mounds (0.2 m²) declined in the short term, although recovery was rapid (Fig. 3a). The opposite response on simulated mounds on Texas coastal prairie (Williams et al., 1986) confirms that pocket gopher effects are site-specific, which can be said of other keystone species (Paine, 1995; Power et al., 1996).

Only a subset of studies measuring gopher impacts have shown significant impacts on plant community composition (e.g., Ellison and Aldous, 1952; Laycock and Richardson, 1975; Hobbs and Mooney, 1985) or species diversity (Tilman, 1983; Williams et al., 1986; Martinsen et al., 1990). In the extreme environment of the Niwot Ridge tundra, pocket gophers have repeatedly been shown, at multiple spatial scales, to significantly impact vegetative structure, nutrient cycling, and ecosystem processes (Cortinas and Seastedt, 1996; Litaor et al., 1996; Sherrod and Seastedt, 2001). Our research further indicates that gophers perform a unique function in this system through their impacts on forb species composition and species richness.

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