

Plant Succession on Gopher Mounds in Western Cascade Meadows: Consequences for Species Diversity and Heterogeneity

CHAD C. JONES,^{1,3} CHARLES B. HALPERN^{1,4} AND JESSICA NIEDERER²

¹College of Forest Resources, Box 352100, University of Washington, Seattle, Washington 98195-2100

²College of Agriculture and Life Science, Cornell University, Ithaca, New York 14853

ABSTRACT.—Pocket gophers have the potential to alter the dynamics of grasslands by creating mounds that bury existing vegetation and locally reset succession. Gopher mounds may provide safe sites for less competitive species, potentially increasing both species diversity and vegetation heterogeneity (spatial variation in species composition). We compared species composition, diversity and heterogeneity among gopher mounds of different ages in three montane meadows in the Cascade Range of Oregon. Cover of graminoids and forbs increased with mound age, as did species richness. Contrary to many studies, we found no evidence that mounds provided safe sites for early successional species, despite their abundance in the soil seed bank, or that diversity peaked on intermediate-aged mounds. However, cover of forbs relative to that of graminoids was greater on mounds than in the adjacent meadow. Variation in species composition was also greater within and among mounds than in adjacent patches of undisturbed vegetation, suggesting that these small-scale disturbances increase heterogeneity within meadows.

INTRODUCTION

Pocket gophers (Geomyidae) play important roles in shaping grassland communities across North America (Huntly and Inouye, 1988). Gophers act as “ecosystem engineers” by bringing subsurface soils to the ground surface, burying existing plants and creating new sites for colonization. Mound formation can initiate succession at a local scale and, where mounding is common, it can influence the composition and diversity of grassland communities (Huntly and Inouye, 1988; Collins, 1989).

Succession on gopher mounds occurs as early colonists are replaced over time by the dominant competitive species and as total plant cover increases (Collins, 1989). This may lead to one of two different patterns of diversity (Peet, 1992). First, if species turnover is low and colonization is continuous, diversity may increase over time, peaking late in succession (Odum, 1969). Alternatively, diversity may peak at an intermediate stage, when both short-lived colonists and longer-lived, but disturbance-sensitive, species are present (*i.e.*, the intermediate disturbance hypothesis; Connell, 1978). Both types of patterns have been observed in studies of succession on gopher mounds: continuous increases (*e.g.*, Rogers *et al.*, 2001; Sherrod *et al.*, 2005) or a peak followed by a decline (Williams *et al.*, 1986; Collins, 1989; Reader and Buck, 1991).

Mounds can also affect the heterogeneity of meadow vegetation at larger spatial scales. Variation in species composition both within and among mounds may be high early in succession, reflecting chance colonization events or greater heterogeneity in resource availability than in undisturbed vegetation (Collins, 1989; Rogers *et al.*, 2001). As succession progresses, heterogeneity may decrease and mounds may become more similar to

³Current address: Department of Botany, Connecticut College, 270 Mohegan Avenue, New London, 06320

⁴Corresponding author

undisturbed vegetation (*i.e.*, exhibit convergence, Myster and Pickett, 1990). Alternatively, heterogeneity may increase (Inouye *et al.*, 1987b; Collins, 1990) leading to greater variation or patchiness in species composition.

Gopher mounds may also serve as safe sites (Grubb, 1977) for species that are poor competitors in the undisturbed community. For example, in grasslands, mounds commonly support a greater abundance of annuals (Laycock, 1958; McDonough, 1974; Laycock and Richardson, 1975; Platt, 1975; Foster and Stubbendieck, 1980; Gibson, 1989), perennial forbs (Williams *et al.*, 1986; Martinsen *et al.*, 1990; Hartway and Steinberg, 1997) or both (Tilman, 1983; Spencer *et al.*, 1985; Inouye *et al.*, 1987a; Collins, 1989). Mounds can ensure persistence of fugitive or subordinate forbs in systems that are dominated by competitively superior perennial grasses.

Much of our understanding of how gopher mounds contribute to the dynamics of grassland communities comes from studies of low elevation prairies or grasslands in central or eastern North America. These studies have demonstrated pronounced variation in the effects of gopher mounds, which may reflect inherent differences among systems and/or in the spatial scales of study. Similar research has not been conducted in mountain ecosystems of the Pacific Northwest, where the mounding activities of the western pocket gopher (*Thomomys mazama*) are conspicuous in natural meadows and other forest openings (Verts and Carraway, 2000). In contrast to most of the grasslands studied, high elevation meadows in the Pacific Northwest are characterized by a short growing season, summer drought and limited occurrence of annuals. These differences potentially influence rates and patterns of succession on gopher mounds, thus study of these meadows can contribute to our understanding of the mechanisms that underlie changes in diversity and composition.

In this study, we examine patterns of succession on gopher mounds and consider the broader implications of these patterns for plant community diversity and composition in montane meadows in the western Cascade Range of Oregon. We address the following questions: (1) How do plant abundance, community structure and species diversity change as mounds undergo succession?, (2) Are mounds more heterogeneous in composition than adjacent meadow and do these differences change over time?, (3) Do mounds provide safe sites for species that are absent from or uncommon in undisturbed meadow? and (4) How do mounds affect larger-scale patterns of meadow diversity and heterogeneity?

METHODS

STUDY SITE

The study site, Bunchgrass Ridge, forms a gently sloping plateau in the western Cascade Range of Oregon, east of Eugene (44°17'N, 121°57'W). The elevation is ~1350 m; slopes rarely exceed 5% and face primarily southward. The plateau supports a large (100 ha) mosaic of dry meadows and forests of varying age resulting from encroachment of *Pinus contorta* and *Abies grandis* into former meadow openings (Haugo and Halpern, 2007; Lang and Halpern, 2007). Three meadows were selected for sampling in Jul. 2004; they had little conifer encroachment, varied in size from 1 to 8 ha, and were separated by distances of 200–600 m. Meadow communities were dominated by a mix of graminoids (primarily *Festuca idahoensis* and *Carex pensylvanica*) and perennial forbs (*e.g.*, *Fragaria vesca*, *Achillea millefolium* and *Phlox diffusa*).

Meadow soils are Vitric Melanocryands (D. A. Lammers, unpublished data). They are deep (>170 cm), fine to very-fine-sandy loams derived from andesitic basalt and deposits of tephra, with a variable amount of glacially derived cobbles, stones and boulders. Annual precipitation at Santiam Pass (1488 m elevation), 17 km to the north, averages ca. 216 cm;

however, only 7.5% of this falls between Jun. and Aug., leading to frequent summer drought. Annual snowfall averages 1,152 cm; winter snow pack can exceed 2 m and persist into May. Minimum and maximum temperatures average -6.9 and 0.7 C in Jan. and 6.1 and 27.8 C in Jul. (Western Regional Climate Center; www.wrcc.dri.edu/summary/climsmor.html).

FIELD SAMPLING

Mound age classes.—We categorized mounds into three age classes, new, young and old based on the following criteria. New mounds were formed in the current growing season. Soil showed few signs of compaction, settling, or weathering and vegetation was absent. Young mounds were formed 1 (or perhaps 2) y prior to sampling and showed signs of compaction and weathering; however, mounds remained higher than the surrounding ground surface. Old mounds were formed at least two (and likely more) years before sampling; they showed pronounced compaction and weathering, with a surface only slightly if at all elevated.

Abundance and size distribution of mounds.—To determine the size and age structure of mounds, we extended a series of three to nine line transects within each meadow; transects were spaced at 15–20 m intervals across the short axis of each meadow. Each mound that intersected a line ($n = 142$) was assigned to an age class and measured along its two primary axes; mound area was estimated as an ellipse. We then computed the mean size and proportion of mounds in each age class.

Vegetation sampling.—For analysis of vegetation patterns, we selected a total of 37 young and 37 old mounds. Sample sizes differed among meadows, but equal numbers of young and old mounds were selected within a meadow. We did not consider new mounds because they lacked vegetation. Mounds were not restricted to those intersected by transect lines, but were selected randomly from those with radii of 0.3–0.6 m (rejecting larger mounds that may have formed from the merger of smaller mounds). From the center of each mound we established a line in a random direction. Beginning at the mound edge we placed along this line a series of three contiguous 10×10 cm quadrats on the mound and six contiguous quadrats off the mound (to sample adjacent meadow vegetation). We limited sampling to three quadrats on larger mounds to facilitate comparisons of richness among mounds of varying size. Quadrats off the mound were divided into two equal groups or “plots” — “near” and “far.” This allowed us to test whether presence of mounds exerted an effect on adjacent meadow vegetation (Grant *et al.*, 1980; Reichman and Seabloom, 2002) and whether it was necessary to utilize far plots to represent meadow conditions (*see* Analyses, below).

Within each quadrat, we recorded the presence of all species and estimated the total cover of forbs and of graminoids (grasses and sedges). We then calculated for each of the 10×30 cm plots (representing mound, near and far): total cover of forbs and of graminoids, relative cover of graminoids (graminoid cover/total plant cover), mean richness per quadrat, total richness per plot and frequency of each plant species (proportion of quadrats). Species’ frequencies were also used to calculate diversity (Shannon’s index, H') and evenness ($H'/\ln[\text{richness}]$) (McCune and Mefford, 1999).

ANALYSES

Prior to analyses of successional trends we conducted several tests to confirm that presence of mounds did not have a detectable effect on adjacent meadow vegetation and that succession was not influenced by mound size. We used a series of *t*-tests to determine whether near and far plots differed in diversity (richness, H' and evenness) or community

structure (total plant cover and cover of forbs and graminoids). We tested for differences in species composition between near and far plots using Multi-response Permutation Procedures (MRPP, Biondini *et al.*, 1988). MRPP tests whether species composition within groups is more similar than would be expected by chance (McCune and Grace, 2002). It produces a probability of significance and a measure of effect size, A (the chance-corrected, within-group agreement). Species frequency was used as the measure of abundance and Sørensen's distance as the measure of dissimilarity. MRPP yielded no difference in composition between near and far plots, thus near plots (hereafter "meadow") were used in subsequent analyses.

We used t -tests and MRPP to determine whether mound age (young vs. old) influenced diversity, community structure or composition in adjacent meadow. These tests also revealed no differences between meadow plots adjacent to young vs. old mounds. Finally, we used one-way analysis of variance (ANOVA) and MRPP to determine whether mound size (four classes based on radius) influenced diversity, community structure or composition. Here too, we detected no significant effects of mound size. Subsequent analyses of successional trends were thus based on three simple plot groups: young mounds, old mounds and meadow.

We used a chronosequence approach, comparing young, old and meadow plots to infer successional trends on gopher mounds. One-way ANOVA was used to test for effects of age (young, old and meadow) on measures of species diversity and community structure (as described above). Significant tests were followed by pairwise *post hoc* comparisons of means using the Bonferroni test. Heterogeneity in species composition within each age class was compared at two spatial scales: within plots (among quadrats) and among plots. Within-plot heterogeneity was calculated for each plot as the mean Sørensen's distance (McCune and Grace, 2002) between all pairs of quadrats (based on species presence/absence). Mean within-plot heterogeneity was compared among age classes using one-way ANOVA. Among plots, heterogeneity was calculated as the mean Sørensen's distance between all pairs of plots (using species frequency as the measure of abundance). However, we did not test for statistical differences among means at this spatial scale because distances among pairs of plots were not considered to be independent. Finally, we determined whether old mounds were more similar in composition to adjacent meadow than were young mounds. For each pair of mound and meadow plots we calculated Sørensen's distance ($n = 37$ per age class), then used a t -test to compare populations of young and old mounds.

We used two complementary methods to explore species compositional trends among age classes. MRPP was used to test whether species composition or species' distributions differed among age classes; an initial run included all age classes and subsequent runs compared pairs of classes. We then used Indicator Species Analysis (ISPAN, Dufrêne and Legendre, 1997) to identify species that showed an affinity for a particular age class. ISPAN uses relative abundance (in this case, frequency among quadrats) and relative frequency (proportion of plots) among groups (age classes) to calculate a maximum indicator value (IV_{max}) for each species. A Monte Carlo randomization is then used to test whether IV_{max} is greater than expected by chance (McCune and Grace, 2002). ANOVA and t -tests were run using SPSS ver. 12.0 (2003). MRPP and ISPAN were run with PC-ORD ver. 4.0 (McCune and Mefford, 1999).

RESULTS

Of the 142 mounds encountered along the transect lines, 33% were new, 40% were young and 27% were old. Most (62%) were smaller than 0.5 m^2 and several were larger than 2 m^2

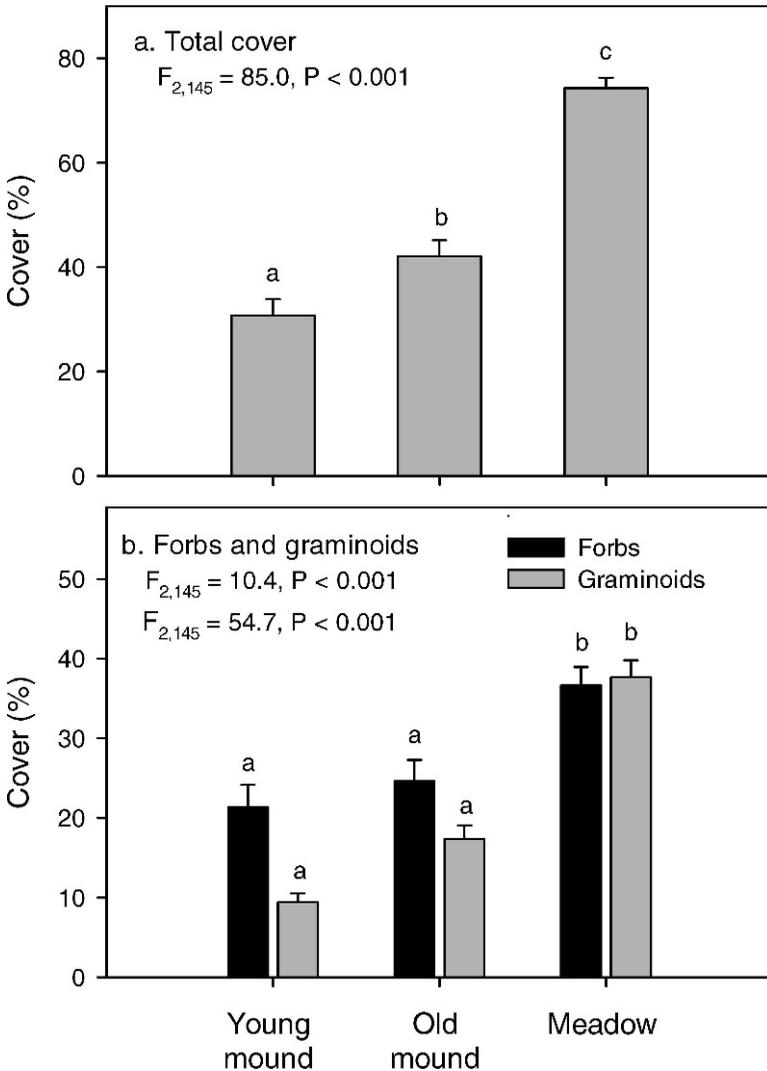
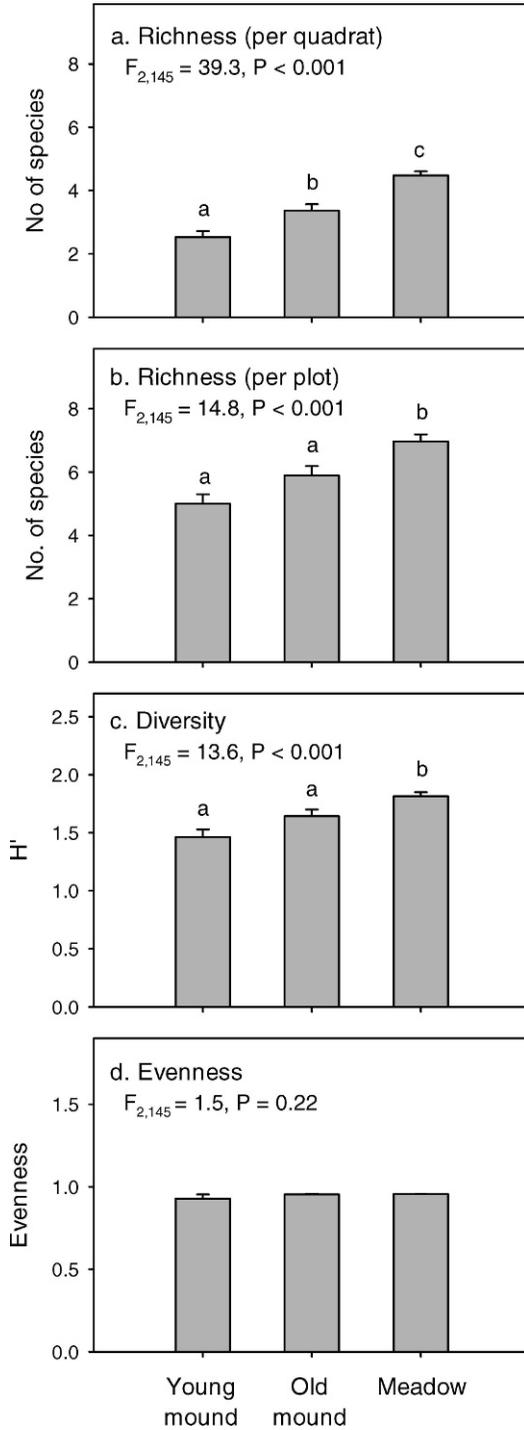


FIG. 1.—Changes among age classes in (a) total plant cover and (b) cover of forbs and graminoids. Values are means + 1 SE (n = 37 for young and old mounds, n = 74 for meadow). F and P values are from one-way ANOVA. Age classes with different letters differ in cover based on *post-hoc* Bonferroni comparisons of means

(probably formed from multiple mounds). Old mounds were slightly larger than younger mounds, but not significantly so (mean area of 0.87 m² for old mounds vs. 0.63–0.64 m² for new and young mounds).

Total plant cover increased with mound age, but old mounds supported significantly lower cover than did meadow plots (Fig. 1a). Forbs and graminoids showed similar temporal trends, but the increases in cover from young to old mounds were not significant (Fig. 1b). Relative cover of graminoids (graminoid cover/total plant cover) was lower on young



mounds (36%) than in meadows (51%) (one-way ANOVA: $F_{2, 145} = 5.4$, $P = 0.005$; *post-hoc* comparison: $P = 0.004$). Relative cover on old mounds was intermediate (44%).

A total of 34 taxa was observed in the plots. All were present in meadow plots and 28 on mounds. However, the six species unique to meadow were rare, present in only one or two of the 74 plots. Species richness at both the quadrat and plot scales increased significantly with age (Figs. 2a,b). H' showed a similar trend (Fig. 2c), but evenness remained similar among age classes (Fig. 2d).

Heterogeneity (compositional dissimilarity) within and among plots was greatest on young mounds and declined with age (Figs. 3a,b). Old mounds were more similar in composition to meadow plots than were young mounds (mean distances of 0.40 and 0.47, respectively; $t = 1.8$, $P = 0.03$). MRPP indicated significant differences in species composition among age classes, but the magnitude of the effect was small ($A = 0.03$, $P < 0.001$). In pairwise comparisons, both young and old mounds differed from meadow plots (young vs. meadow, $A = 0.03$, $P < 0.001$; old vs. meadow, $A = 0.02$, $P < 0.001$), but young and old mounds did not differ in composition ($A = 0.01$, $P = 0.07$).

Frequencies of most species increased with time, but all showed relatively small differences among age classes (Table 1). ISPAN yielded only three species (all graminoids) — *Festuca idahoensis*, *Carex pensylvanica* and *Danthonia intermedia* — with significant age-class associations, all with meadow. However, only *F. idahoensis* was a strong indicator of meadow. Several species were most frequent on mounds, but these associations were not significant (Table 1).

DISCUSSION

Gopher mounds are a common feature of these montane grasslands; individual mounds can persist for three or more growing seasons during which time they are gradually reduced in height by compaction and erosion. Succession appears rapid at first, as new unvegetated mounds quickly transition to young (>1-y-old) mounds that support ~30% plant cover on average. This rapid recovery of plant cover suggests that recolonization is dominated by regrowth of buried plants (*e.g.*, Laycock, 1958; Gibson, 1989), or vegetative expansion from adjacent meadow (*e.g.*, Laycock, 1958; Collins, 1989; Umbanhowar, 1995). In contrast to the initial colonization of new mounds, the transition from young mounds to meadow is subtle, characterized by a gradual increase in plant cover and diversity and limited turnover in species composition. However, one important consequence of mound formation for community structure is a shift to greater abundance of forbs at the expense of graminoids (*Festuca idahoensis* in particular). Forbs comprised half of the total plant cover in meadow plots, but 60–70% of total cover on mounds. Similar shifts in dominance have been observed in other grasslands (Foster and Stubbendieck, 1980; Tilman, 1983; Inouye *et al.*, 1987a; Collins, 1989; Martinsen *et al.*, 1990) and subalpine meadows (Sherrod *et al.*, 2005). Greater survival and more rapid emergence of dicots following burial has been attributed to their strong clonal potential (*e.g.*, Collins, 1989; Umbanhowar, 1995) and abundant storage of carbon in below-ground structures (Webber and May, 1977; Sherrod *et al.*, 2005, see also Lezberg *et al.*, 1999). In concert, these traits provide an advantage in relocating perennating

←

FIG. 2.—Changes among age classes in (a) species richness per quadrat, (b) species richness per plot, (c) H' and (d) evenness. Values are means + 1 SE ($n = 37$ for young and old mounds, $n = 74$ for meadow). F and P values are from one-way ANOVA. Age classes with different letters differ based on *post-hoc* Bonferroni comparisons of means

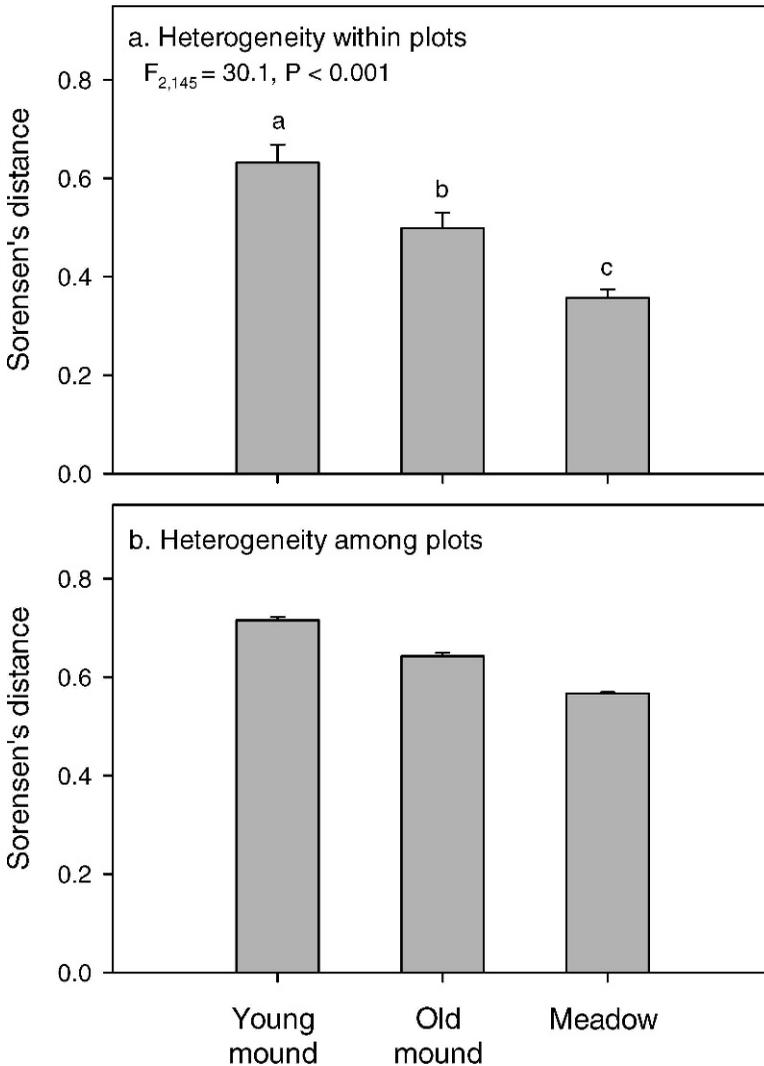


FIG. 3.—Changes in heterogeneity (a) within plots (among-quadrats) and (b) among plots. Values are means + 1 SE ($n = 37$ for young and old mounds, $n = 74$ for meadow). F and P values are from one-way ANOVA. Age classes with different letters differ in heterogeneity based on *post-hoc* Bonferroni comparisons of means. ANOVA was not performed on heterogeneity among plots because pairwise comparisons of plots were not considered to be independent

structures and moving shoots through new deposits of soil (Antos and Zobel, 1985, 1987). Experimental studies that excluded gophers from prairies provide additional evidence for these shifts in community structure: forbs typically become less common in the absence of mounding (Laycock and Richardson, 1975; Williams and Cameron, 1986). Anecdotal evidence from our system supports this observation: in a large area of one meadow where gopher mounding is rare, grasses dominate and forbs are virtually absent from the community. It is possible that other aspects of gopher behavior associated with mounding

TABLE 1.—Frequencies of occurrence (proportion of plots) and results of ISPAN for species present in $\geq 5\%$ of plots

| Species | Young | Old | Meadow | IV_{max} | P |
|-------------------------------|-------|------|--------|------------|--------------|
| Most abundant in meadows | | | | | |
| <i>Festuca idahoensis</i> | 0.57 | 0.65 | 0.88 | 51.1 | 0.001 |
| <i>Carex pensylvanica</i> | 0.78 | 0.92 | 0.95 | 37.6 | 0.006 |
| <i>Achillea millefolium</i> | 0.32 | 0.30 | 0.51 | 22.5 | 0.11 |
| <i>Danthonia intermedia</i> | 0.16 | 0.19 | 0.36 | 21.7 | 0.01 |
| <i>Fragaria</i> spp. | 0.38 | 0.46 | 0.53 | 20.1 | 0.48 |
| <i>Phlox diffusa</i> | 0.27 | 0.19 | 0.28 | 13.7 | 0.33 |
| <i>Lathyrus nevadensis</i> | 0.22 | 0.24 | 0.31 | 13.7 | 0.43 |
| <i>Lupinus latifolius</i> | 0.11 | 0.16 | 0.23 | 11.7 | 0.22 |
| <i>Elymus glaucus</i> | 0.22 | 0.30 | 0.30 | 11.5 | 0.77 |
| <i>Hieracium gracile</i> | 0.24 | 0.11 | 0.23 | 9.6 | 0.62 |
| <i>Vicia americana</i> | 0.19 | 0.22 | 0.26 | 8.8 | 0.91 |
| <i>Comandra umbellata</i> | 0.11 | 0.14 | 0.15 | 6.1 | 0.81 |
| <i>Poa pratensis</i> | 0.03 | 0.11 | 0.11 | 5.4 | 0.53 |
| <i>Penstemon procerus</i> | 0.05 | 0.08 | 0.09 | 3.6 | 0.91 |
| Most abundant on old mounds | | | | | |
| <i>Bromus carinatus</i> | 0.30 | 0.49 | 0.38 | 21.5 | 0.09 |
| <i>Aster radulinus</i> | 0.35 | 0.62 | 0.58 | 26.1 | 0.12 |
| <i>Cirsium callilepis</i> | 0.05 | 0.11 | 0.03 | 6.2 | 0.24 |
| <i>Stellaria</i> sp. | 0.08 | 0.22 | 0.19 | 8.3 | 0.62 |
| Most abundant on young mounds | | | | | |
| <i>Iris chrysophylla</i> | 0.22 | 0.14 | 0.12 | 10.2 | 0.23 |
| <i>Stipa occidentalis</i> | 0.11 | 0.08 | 0.07 | 4.2 | 0.83 |

Species are grouped by their IV_{max} values, in descending order. Significant results are in bold

(e.g., direct herbivory) are responsible for these changes in community structure. However, in most grassland systems, gophers preferentially consume forbs (Burton and Black, 1978; Huntly and Inouye, 1988), which would benefit graminoids.

Species composition on mounds differed from that in undisturbed meadow, but young and old mounds were largely indistinguishable. Most taxa were present at all stages, increasing in frequency with time. Six species were more abundant on mounds, but all of these were also present in meadows. Thus, mounds in this system clearly do not serve as microsites for germination of fugitive or subordinate species as they do in other systems (Laycock, 1958; McDonough, 1974; Platt, 1975; Foster and Stubbendieck, 1980; Inouye *et al.*, 1987a; Collins, 1989; Gibson, 1989; Hartway and Steinberg, 1997). In fact, the rarest taxa — those with one or two occurrences — were restricted to meadow plots. This is surprising because ruderals dominate the soil seed bank in both meadows (Lang and Halpern, 2007) and forests in this region (Kellman, 1970; Halpern *et al.*, 1999) and are abundant after large-scale disturbance (e.g., Schoonmaker and McKee, 1988; Halpern, 1989). It is possible that the seed bank contributes minimally to plant establishment because the soils that comprise mounds are from depths below which most viable seeds are found. Moreover, burial of seeds beneath mounds may actually reduce the potential for emergence from the seed bank (e.g., Benvenuti *et al.*, 2001).

Trends in diversity on mounds did not support predictions of the intermediate disturbance hypothesis (Hobbs and Hobbs, 1987; Huntly and Inouye, 1988), but rather, a

model of gradual species accumulation (Odum, 1969). Richness at both the quadrat and plot scales increased from young mounds to meadow, explaining in large part the parallel increase in H' . In contrast, evenness did not vary: although frequency increased for the most common species (*Festuca idahoensis* and *Carex pensylvanica*), it also increased for less common taxa, resulting in no change in dominance structure. Formation of mounds reduces local richness, consistent with patterns in some prairie and alpine ecosystems (Rogers *et al.*, 2001; Sherrod *et al.*, 2005). However, it contrasts with patterns of increased richness in several other systems (Andersen and MacMahon, 1985; Williams *et al.*, 1986; Collins, 1989; Reader and Buck, 1991; Hartway and Steinberg, 1997). Two factors may help to explain why diversity did not peak on mounds in our meadows: annuals that are typically promoted by disturbance were absent, and there was little evidence of competitive exclusion of subordinate species. A short growing season, summer drought and frequent gopher disturbance may prevent dominant graminoids from excluding less competitive forbs in these high-elevation systems. Wright and Jones (2004) propose a model that reconciles these differing patterns of response to small-scale disturbance. They suggest that changes in richness depend on site productivity and whether disturbed patches are more or less fertile than the undisturbed matrix. Assuming that montane meadows are less productive than lowland prairies and grasslands, our results suggest that mound soils, originating from deeper horizons, are less fertile than adjacent meadow soils, consistent with a pattern of lower root productivity and soil organic matter at depth (*e.g.*, Dodd *et al.*, 2000). Studies of gopher mounds in higher elevation grasslands are too few to be able to draw broad conclusions, but it is possible that elevation, via effects on soil productivity and growing-season length, mediates the relationship between species richness and mound formation. At lower elevations richness is increased, whereas at higher elevations it is reduced by disturbance. Explicit study of these relationships across an elevational gradient would provide a test of this hypothesis.

Despite reducing local diversity, mounds increase variability in species composition and thus, may have an important effect on the spatial structure of meadow vegetation. Greater heterogeneity within and among mounds suggests that disturbance resets local composition, allowing for a greater diversity of assemblages among these newly formed patches. Whether this occurs through variation in mortality (*e.g.*, Zobel and Antos, 1997) or establishment is unclear. Over time, however, competitive interactions lead to convergence in composition. The few studies that have examined heterogeneity on mounds have found similar patterns (Collins, 1989; Rogers *et al.*, 2001).

In sum, although gopher disturbance in these montane meadows does not enhance species richness at local (alpha) or larger (gamma) spatial scales (Whittaker, 1972), it does increase heterogeneity within meadows, providing for a greater diversity of structural and compositional states. In the absence of gophers, it is possible that communities comprised of a diverse array of forbs and graminoids would become increasingly dominated by grasses.

Acknowledgments.—We thank Joe Antos and members the Halpern lab group for critical comments on earlier drafts of the manuscript. Logistical support was provided by staff at the USFS McKenzie River Ranger District and the Willamette National Forest, Oregon. Funding was provided by an NSF Research Experiences for Undergraduates (REU) Fellowship to Jessica Niederer; additional funds were provided by the Joint Fire Science Program (Agreement 1422RAH03-0021).

LITERATURE CITED

- ANDERSEN, D. C. AND J. A. MACMAHON. 1985. Plant succession following the Mount St. Helens volcanic eruption - facilitation by a burrowing rodent, *Thomomys talpoides*. *Am. Midl. Nat.*, 114:62–69.

- ANTOS, J. A. AND D. B. ZOBEL. 1985. Plant form, developmental plasticity, and survival following burial by volcanic tephra. *Can. J. Bot.*, **63**:2083–2090.
- AND ———. 1987. How plants survive burial: a review and initial responses to tephra from Mount St. Helens, p. 246–261. *In*: D. E. Bilderback (ed.). Mount St. Helens 1980: botanical consequences of an explosive eruption. University of California Press, Berkeley, California, U.S.A.
- BENVENUTI, S., M. MACCHIA AND S. MIELE. 2001. Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. *Weed Sci.*, **49**:528–535.
- BIONDINI, M. E., P. W. MIELKE AND K. J. BERRY. 1988. Data-dependant permutation techniques for the analysis of ecological data. *Vegetatio*, **75**:161–168.
- BURTON, D. H. AND H. C. BLACK. 1978. Feeding habits of Mazama pocket gophers in south-central Oregon. *J. Wildlife Manage.*, **42**:383–390.
- COLLINS, S. L. 1989. Experimental analysis of patch dynamics and community heterogeneity in tallgrass prairie. *Vegetatio*, **85**:57–66.
- . 1990. Patterns of community structure during succession in tallgrass prairie. *B. Torrey Bot. Club*, **117**:397–408.
- CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. *Science*, **199**:1302–1310.
- DODD, M. B., W. K. LAUENROTH AND I. C. BURKE. 2000. Nitrogen availability through a coarse-textured soil profile in the shortgrass steppe. *Soil Sci. Soc. Am. J.*, **64**:391–398.
- DUFRENE, M. AND P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.*, **67**:345–366.
- FOSTER, M. A. AND J. STUBBENDIECK. 1980. Effects of the plains pocket gopher (*Geomys bursarius*) on rangeland. *J. Range Manage.*, **33**:74–78.
- GIBSON, D. J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. *Am. Midl. Nat.*, **121**:144–154.
- GRANT, W. E., N. R. FRENCH AND L. J. FOLSE. 1980. Effects of pocket gopher mounds on plant production in a shortgrass prairie ecosystem. *Southwest. Nat.*, **2**:215–224.
- GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, **52**:107–145.
- HALPERN, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology*, **70**:704–720.
- , S. A. EVANS AND S. NIELSON. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory reinitiation. *Can. J. Bot.*, **77**:922–935.
- HARTWAY, C. AND E. K. STEINBERG. 1997. The influence of pocket gopher disturbance on the distribution and diversity of plants in western Washington prairies, p. 131–139. *In*: P. Dunn and K. Ewing (eds.). Ecology and conservation of the south Puget Sound prairie landscape. The Nature Conservancy of Washington, Seattle, U.S.A.
- HAUGO, R. D. AND C. B. HALPERN. 2007. Vegetation responses to conifer encroachment in a dry, montane meadow: a chronosequence approach. *Can. J. Bot.*, **85**:285–298.
- HOBBS, R. J. AND V. J. HOBBS. 1987. Gophers and grassland - a model of vegetation response to patchy soil disturbance. *Vegetatio*, **69**:141–146.
- HUNTLY, N. AND R. INOUE. 1988. Pocket gophers in ecosystems - patterns and mechanisms. *Bioscience*, **38**:786–793.
- INOUE, R. S., N. J. HUNTLY, D. TILMAN AND J. R. TESTER. 1987a. Pocket gophers (*Geomys bursarius*), vegetation, and soil-nitrogen along a successional sere in east central Minnesota. *Oecologia*, **72**:178–184.
- , ———, ———, ———, M. STILLWELL AND K. C. ZINNEL. 1987b. Old-field succession on a Minnesota sand plain. *Ecology*, **68**:12–26.
- KELLMAN, M. 1970. The viable seed content of some forest soil in coastal British Columbia. *Can. J. Bot.*, **68**:1156–1162.
- LANG, N. L. AND C. B. HALPERN. 2007. The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. *Can. J. Bot.*, **85**:557–569.

- LAYCOCK, W. A. 1958. The initial pattern of revegetation of pocket gopher mounds. *Ecology*, **39**:346–351.
- AND B. Z. RICHARDSON. 1975. Long-term effects of pocket gopher control on vegetation and soils of a subalpine grassland. *J. Range Manage.*, **28**:458–462.
- LEZBERG, A. L., J. A. ANTOS AND C. B. HALPERN. 1999. Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. *Can. J. Bot.*, **77**:936–943.
- MARTINSEN, G. D., J. H. CUSHMAN AND T. G. WHITHAM. 1990. Impact of pocket gopher disturbance on plant-species diversity in a shortgrass prairie community. *Oecologia*, **83**:132–138.
- MCCUNE, B. AND J. B. GRACE. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, U.S.A. 300 p.
- AND M. J. MEFFORD. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4. MjM Software Design, Gleneden Beach, Oregon, U.S.A.
- MCDONOUGH, W. T. 1974. Revegetation of gopher mounds on aspen range in Utah. *Great Basin Nat.*, **34**:267–274.
- MYSTER, R. W. AND S. T. A. PICKETT. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. *Am. Midl. Nat.*, **124**:231–238.
- ODUM, E. P. 1969. The strategy of ecosystem development. *Science*, **164**:262–270.
- PEET, R. K. 1992. Community structure and ecosystem function, p. 103–151. *In*: D. C. Glenn-Lewin, R. K. Peet and T. T. Veblen (eds.). *Plant succession: theory and prediction*. Chapman & Hall, London, U.K.
- PLATT, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. *Ecol. Monogr.*, **45**:285–305.
- READER, R. J. AND J. BUCK. 1991. Community response to experimental soil disturbance in a midsuccessional, abandoned pasture. *Vegetatio*, **92**:151–159.
- REICHMAN, O. J. AND E. W. SEABLOOM. 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends Ecol. Evol.*, **17**:44–49.
- ROGERS, W. E., D. C. HARTNETT AND B. ELDER. 2001. Effects of plains pocket gopher (*Geomys bursarius*) disturbances on tallgrass-prairie plant community structure. *Am. Midl. Nat.*, **145**:344–357.
- SCHOONMAKER, P. AND A. MCKEE. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *Forest Sci.*, **34**:960–979.
- SHERROD, S. K., T. R. SEASTEDT AND M. D. WALKER. 2005. Northern pocket gopher (*Thomomys talpoides*) control of alpine plant community structure. *Arct. Antarct. Alp. Res.*, **37**:585–590.
- SPENCER, S. R., G. N. CAMERON, B. D. ESHELMAN, L. C. COOPER AND L. R. WILLIAMS. 1985. Influence of pocket gopher mounds on a Texas coastal prairie. *Oecologia*, **66**:111–115.
- SPSS. 2003. SPSS 12.0 for Windows. SPSS Inc., Chicago, Illinois, U.S.A.
- TILMAN, D. 1983. Plant succession and gopher disturbance along an experimental gradient. *Oecologia*, **60**:285–292.
- UMBANHOWAR, C. E. 1995. Revegetation of earthen mounds along a topographic-productivity gradient in a northern mixed prairie. *J. Veg. Sci.*, **6**:637–646.
- VERTS, B. J. AND L. N. CARRAWAY. 2000. *Thomomys mazama*. *Mammalian Species*, **641**:1–7.
- WEBBER, P. AND D. MAY. 1977. The magnitude and distribution of belowground plant structures in the alpine tundra of Niwot Ridge, Colorado. *Arct. Alp. Res.*, **9**:157–174.
- WHITTAKER, R. H. 1972. Evolution and measurement of species diversity. *Taxon*, **21**:213–251.
- WILLIAMS, L. R. AND G. N. CAMERON. 1986. Effects of removal of pocket gophers on a Texas coastal prairie. *Am. Midl. Nat.*, **115**:216–224.
- , ———, S. R. SPENCER, B. D. ESHELMAN AND M. J. GREGORY. 1986. Experimental analysis of the effects of pocket gopher mounds on Texas coastal prairie. *J. Mammal.*, **67**:672–679.
- WRIGHT, J. P. AND C. G. JONES. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology*, **85**:2071–2081.
- ZOBEL, D. B. AND J. A. ANTOS. 1997. A decade of recovery of understory vegetation buried by volcanic tephra from Mount St. Helens. *Ecol. Monogr.*, **67**:317–344.