Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community

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Summary. We examined the impact of pocket gopher disturbances on the dynamics of a shortgrass prairie community. Through their burrowing activity, pocket gophers (*Thomomys bottae*) cast up mounds of soil which both kill existing vegetation and create sites for colonization by competitively-inferior plant species. Three major patterns emerge from these disturbances: First, we show that 10 of the most common herbaceous perennial dicots benefit from pocket gopher disturbance; that is, a greater proportion of seedlings are found in the open space created by pocket gopher disturbance than would be expected based on the availability of disturbed habitat. Additionally, these seedlings exhibited higher growth rates than adjacent seedlings of the same species growing in undisturbed habitat. Second, we tested two predictions of the Intermediate Disturbance Hypothesis and found that species diversity was greatest for plots characterized by disturbances of intermediate age. However, we did not detect significant differences in diversity between plots characterized by intermediate and high levels of disturbance, indicating that many species are adapted to or at least tolerant of high levels of disturbance. Third, we noted that the abundance of grasses decreased with increasing disturbance, while the abundance of dicots increased with increasing disturbance.

Key words: Disturbance – Species diversity – Pocket gophers – Intermediate disturbance hypothesis

The importance of disturbance as a source of spatial and temporal variation in natural communities is becoming increasingly recognized in ecological theory. Recent hypotheses on the maintenance of species diversity have emphasized the role of natural disturbance, which both prevents competitive displacement and provides sites for colonization by competitively-inferior species (Grubb

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1977; Connell 1978; Huston 1979). In particular, the Intermediate Disturbance Hypothesis predicts highest diversity at some intermediate frequency or intensity of disturbance (Connell 1978; Sousa 1979). These ideas contrast with the long-held view of communities as equilibrium systems, with high species diversity resulting from resource subdivision reducing severe competitive interactions (MacArthur 1972; Schoener 1974).

In addition to being an important source of environmental heterogeneity, disturbance may act as a strong selective force influencing the life history characteristics of organisms (Loucks 1970; Harper 1977; Denslow 1980; Pickett 1980). Such selection should be particularly important when organisms are subjected to chronic disturbance throughout their lifetimes. Our studies suggest that these species may be adapted to tolerate or take advantage of a wide range of intermediate to high disturbance levels. In such communities, the Intermediate Disturbance Hypothesis may not be applicable because high species diversity may exist over a wide range of disturbance regimes.

The disturbance created by pocket gophers (Family Geomyidae) is unique for several reasons: 1) it is caused by a biotic agent, whereas most forms of disturbance that have been studied are abiotic (e.g. wind, fire, wave action), 2) it occurs in small patches (gopher mounds), in contrast to large-scale disturbance such as tree blowdowns, and 3) it occurs with a predictable frequency (gophers are active year-round and territorial, ensuring a rather constant level of disturbance within the territory) compared to more unpredictable disturbance events like fires and storms. Thus, we examined the impact of pocket gopher disturbance on two distinct groups of prairie plants, grasses and dicots, and the overall effect of gopher disturbance on plant species diversity.

Previous studies of pocket gophers have focused primarily on their effect on production of vegetation and range condition (Ellison and Aldous 1952; Laycock and Richardson 1975; Grant et al. 1980; Foster and Stubbendieck 1980). Other authors have examined the vegetation growing on pocket gopher mounds but not off

of gopher mounds (Laycock 1958; McDonough 1974), although Reichman and Smith (1985) studied the vegetation overlying pocket gopher tunnels. More recently Hobbs and Mooney (1985), Spencer et al. (1985), Williams and Cameron (1986), and Reichman (1988) have reported on the impact of pocket gophers on vegetational composition and plant yield. Hobbs et al. (1988) and Tilman (1983) studied the effect of fertilizer addition and subsequent gopher activity on plant species composition. However, only Tilman (1983), Williams et al. (1986), and Inouye et al. (1987) have addressed the role of gopher disturbance in maintaining plant species diversity, and none of these papers attempted to quantify the amount of disturbance.

Here, we report on the impact of the valley pocket gopher, *Thomomys bottae*, on a shortgrass prairie community. We hypothesize that the earth mounds cast up by pocket gophers create patches of habitat which are colonized by herbaceous dicots (forbs), thereby disrupting the competitive dominance of perennial grasses. First, we address the question: are a greater proportion of forb seedlings found in the open space created by gopher disturbance than would be predicted based on the availability of disturbed habitat? Second, because plants growing in pocket gopher disturbances have fewer competitors and presumably greater access to resources, we compare growth rates of plants growing in pocket gopher disturbances and plants growing in undisturbed habitat. Third, we tested two predictions of the Intermediate Disturbance Hypothesis: 1) that species diversity is highest at an intermediate magnitude of disturbance as measured by amount of pocket gopher mounds and 2) that species diversity is highest at intermediate ages of disturbance. Lastly, to explain the observed patterns of diversity, we compare the responses of the two major groups of prairie plants, perennial grasses and perennial dicots, to pocket gopher disturbance. We suggest that those plants which benefit from pocket gopher disturbance, the herbaceous perennial dicots, are so well-adapted that they thrive even at very high levels of disturbance.

Materials and methods

The study was conducted at the Fern Mountain Ranch (elevation 2700 m), Hart Prairie, on the western slope of the San Francisco peaks, 20 km NW of Flagstaff, Arizona. The area is made up of shortgrass prairie surrounded by aspen clones and mixed-coniferous forest. The prairie communities are dominated by grasses, of which *Bromus inermis, Sitanion hitrix,* and *Poa pratensis* are the most numerous. The entire study area has been uncultivated since 1920 and has been enclosed to exclude domestic livestock since 1950.

To examine the impact of pocket gopher disturbance on the abundance of herbaceous perennial dicots, we set up a series of 4×4 m plots in areas where there were at least 10 seedlings of the species of interest. A seedling was defined as a plant no larger than 4 rosettes which was isolated from conspecifics by at least 20 cm. This allowed us to control for the possibility that such small plants were produced asexually. We collected data on seedling establishment for the following species: *Potentilla hippiana, Helenium hoopesii, Geum triflorum, Antennaria parvifolia, Ipomopsis aggregata, Penstemon barbatus, Lupinus argenteus, Erigeron formo-*

sissimus, Viguiera multiflora, and *Cirsium wheeleri.* In terms of abundance, these 10 species make up 22% of the community (the abundance of perennial grasses is 67%). Each species was tested in four separate plots, for a total of 40 4×4 m plots.

This community is a closed grassland (Grubb 1977); in the absence of pocket gopher disturbance there is continuous cover. Individual seedlings were marked and classified as either growing in open (disturbed) or closed (undisturbed) habitat (see Tilman 1982). Thus, for each plot we obtained a proportion of plants growing in open habitat (i.e. the number of plants growing in pocket gopher disturbances divided by the total number of plants). To quantify the availability of open habitat, we sampled four transects through each 4×4 m plot: two diagonal transects and two which bisected the bases of the plot. At 20 cm intervals, the habitat was classified as either open (pocket gopher-disturbed) or closed. A total of 93 points were sampled (the middle point was sampled four times and three of these discarded), generating a proportion of available open habitat. These two proportions, the proportion of plants growing in open habitat and the proportion of available open habitat, were then compared statistically using a one-sided test of binomial proportions (Zar 1984).

To compare the growth rates of plants growing in open versus closed habitat, we selected pairs of seedlings, one growing in a pocket gopher mound and the other growing in undisturbed habitat. These plants were comparably-sized and within 1 m of each other. Early in the growing season, we measured total leaf number and length of the longest leaf on all pairs. At the end of the summer, the same measurements were taken. Increase in leaf number and increase in leaf length for plants growing in open and closed habitat were statistically compared using Wilcoxen's signed-rank test. These comparisons were made for *Potentilla hippiana, Helenium hoopesii,* and *Geum triflorum.*

For two species, *Ipomopsis aggregata* and *Penstemon barbatus,* we were able to obtain a more direct measure of the effect of habitat on fitness. These species produce a flowering stalk from a single basal rosette. For each species, we set up a 10×10 m plot and marked all individuals. After flowering was completed, plots were censused and plants classified with respect to habitat (open vs. closed) and flower stalk production (elongate vs. non-elongate). Thus, we obtained two proportions: a proportion of plants in open habitat which elongated and a proportion of plants in closed habitat which elongated. These two proportions were then compared using a one-sided test of binomial proportions.

To investigate the relationship between magnitude of disturbance and species diversity, we established three categories of disturbance level or magnitude: 1) low disturbance, <10% open habitat, 2) intermediate disturbance, 40–55% open habitat, and 3) high disturbance, >75% open habitat. We then identified parts of the prairie where discrete areas characterized by these three disturbance regimes occurred together (within 2 m of each other) and set up three 2×2 m plots (one triplet). Disturbance level was quantified for each plot by sampling four transects as described above except that sampling was done at 10 cm intervals. We established a total of seven triplets (21 plots).

We measured two components of species diversity: total number of species or species richness, and relative abundance. To measure relative abundance, we uniformly sampled vegetation at 100 points within each of the 2×2 m plots. At each point, we recorded the species present or bare ground. We calculated species diversity using the Shannon-Wiener Index (H'). To examine the relationship between disturbance magnitude and diversity, we generated a quadratic regression of species diversity (H') on disturbance magnitude (i.e., % disturbance).

Pocket gopher mounds can be separated into three age categories: new or <1 year old, intermediate or 1–2 years old, and old or >2 years old (Foster and Stubbendieck 1980). To compare the effect of age of disturbance on species diversity, we sampled groups of three 2×2 m plots, with each group containing one plot of each disturbance age class. Again, we established a total of seven such groups. These data were analyzed using a one-way analysis of variance. We performed arcsine square root transformations

to stabilize variances (Zar 1984). Linear contrasts were used to compare the three treatment means.

Finally, using the same data sets, we examined the impact of pocket gopher disturbance on the abundance of both perennial grasses and perennial dicots. We performed linear regressions of abundance on disturbance magnitude, and the disturbance age/abundance data were analyzed using a one-way ANOVA (Again, arcsine square root transformations were used to stabilize variances).

Results

Herbaceous perennial dicots successfully germinate and survive on pocket gopher disturbances more often than would be expected based on the availability of this disturbed habitat. This result was consistent for all 10 species studied. In every case, the proportion of plants establishing in disturbed habitat was greater than the proportion of available disturbed habitat, and this relationship was statistically significant for 37 out of 40 plots (Table 1). This result suggests that pocket disturbances provide important opportunities for these plants to colonize and be maintained in the community.

For the three species studied (*Potentilla hippiana, Helenium hoopesii*, and *Geum triflorum*), disturbed habitat provided the additional benefit of better growing conditions, which resulted in increased growth. Seedling plants growing in pocket gopher disturbances produced more leaves and larger leaves than seedlings growing in undisturbed habitat (Table 2). Plants in disturbed habitat had fewer competitors and more access to resources (light, nutrients, water) than those in undisturbed habitat. This increased resource availability probably accounts for the significantly higher growth rates.

Both *Ipomopsis aggregata* and *Penstemon barbatus* were more likely to flower when they were growing in disturbed habitat. *I. aggregata* in open habitat elongated and flowered 1.8 times more frequently than those growing in closed habitat, and *P. barbatus* elongated and flowered almost three times more often when growing in pocket gopher disturbance (Fig. 1). Again, these plants may be acquiring more resources than those growing in undisturbed habitat and devoting these additional resources to flower stalk production. This is a more direct measure than vegetative growth rate of the potential fitness benefit of growing in disturbed habitat.

Species diversity, as measured by both species richness and H', increased with magnitude of pocket gopher disturbance, but surprisingly did not then again decline at the highest levels of disturbance (Fig. 2). The binomial regression simulates Connell's original model. This model is a significantly better fit than the simple linear regression model ($t = 2.87$, $P < 0.01$). The fact that this model fits the data so well may be misleading. In particular, although there are clear differences in H' between low and increased levels of disturbance, the mean values for medium and high levels of disturbance are virtually identical (H' = 0.641 vs. H' = 0.653 respectively). The implications and potential causes of this pattern will be examined in the discussion.
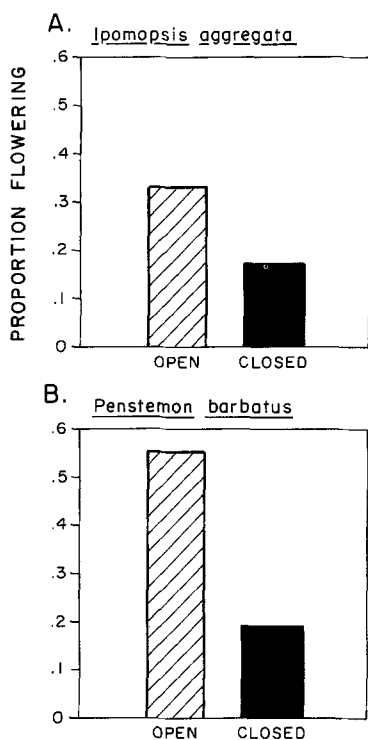
With respect to age of disturbance, those plots characterized by disturbance of intermediate age were signifi-

Table 1. A statistical comparison of the proportion of plants growing in pocket gopher disturbances (observed) and the proportion of available disturbed habitat (expected)

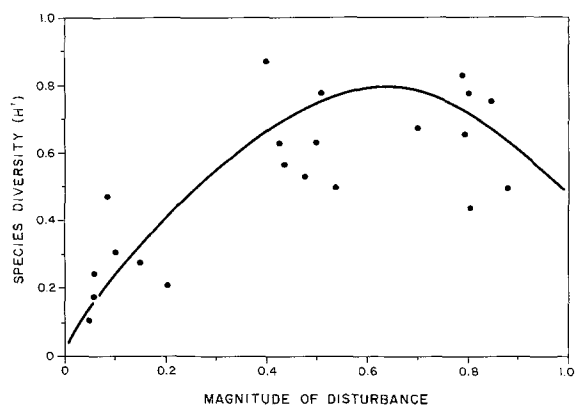| Species/Plot	Observed	Expected	Z	P
Geum triflorum				
Plot 1	0.750	0.462	2.34	0.0096
2	0.750	0.495	2.38	0.0087
3	0.833	0.398	3.39	0.0003
4	0.929	0.484	3.12	0.0009
Potentilla hippiana				
Plot 1	0.857	0.581	1.98	0.0239
2	0.875	0.667	1.67	0.0475
3	0.810	0.624	1.62	0.0526
4	1.000	0.560	3.25	0.0006
Lupinus argentus				
Plot 1	0.805	0.387	4.46	0.0001
2	0.833	0.527	3.73	0.0001
3	0.800	0.462	3.60	0.0002
4	0.781	0.419	3.53	0.0002
Ipomopsis aggregata				
Plot 1	0.771	0.602	1.79	0.0367
2	0.822	0.516	3.47	0.0003
3	0.842	0.581	2.14	0.0162
4	0.868	0.473	4.72	0.0001
Penstemon barbatus				
Plot 1	0.758	0.602	1.79	0.0537
2	0.744	0.548	2.18	0.0146
3	0.800	0.538	2.71	0.0034
4	0.800	0.570	2.26	0.0119
Antennaria parvifolia				
Plot 1	0.909	0.527	3.29	0.0005
2	0.929	0.516	2.91	0.0018
3	1.000	0.548	2.76	0.0029
4	1.000	0.538	2.94	0.0016
Cirsium wheeleri				
Plot 1	0.711	0.312	4.19	0.0001
2	0.773	0.344	3.66	0.0001
3	0.658	0.301	5.49	0.0001
4	0.853	0.398	4.50	0.0001
Erigeron formosissimus				
Plot 1	0.886	0.505	3.90	0.0001
2	0.789	0.516	2.19	0.0143
3	0.862	0.548	3.05	0.0011
4	0.865	0.527	3.59	0.0002
Helenium hoopesii				
Plot 1	0.800	0.548	1.53	0.0630
2	0.636	0.344	1.89	0.0294
3	0.727	0.344	2.47	0.0068
4	0.857	0.505	2.47	0.0068
Viguiera multiflora				
Plot 1	0.875	0.634	3.01	0.0013
2	0.851	0.581	3.21	0.0007
3	0.788	0.581	2.51	0.0060
4	0.955	0.570	4.56	0.0001

Table 2. A comparison of the growth rates of plants in open (disturbed) and closed (undisturbed) habitat

	Open $\bar{X}$ (S.E.)	Closed $\bar{X}$ (S.E.)	T	P
A) Increase in leaf number				
Potentilla hippiana	3.00 (0.33)	1.11 (0.35)	2.70	0.004
Geum triflorum	2.71 (0.60)	1.14 (0.55)	1.36	NS
Helenium hoopesii	3.30 (0.56)	1.30 (0.45)	2.45	0.007
B) Increase in leaf length				
Potentilla hippiana	16.78 (2.68)	8.00 (3.49)	1.78	0.040
Geum triflorum	4.71 (1.12)	1.85 (0.70)	2.39	0.009
Helenium hoopesii	58.20 (7.50)	51.80 (12.3)	0.66	NS

Fig. 2. The relationship between magnitude of pocket gopher disturbance and species diversity (H') for all 21 subplots ($y = 0.1 + 1.76x - 1.34x^2$; $r^2 = 0.67$; $P < 0.005$)

Fig. 3. The relationship between age of pocket gopher disturbance and species diversity (H') ($F = 17.87$; $P < 0.0001$). See text for definitions of new, intermediate, and old disturbance
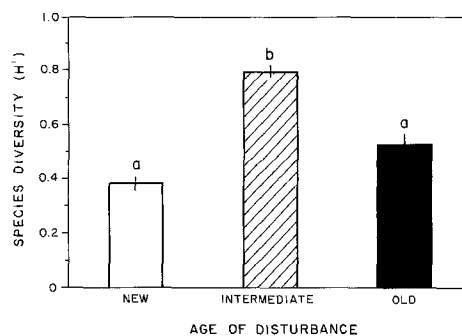

Fig. 1. A comparison of the proportion of plants flowering in open (disturbed) versus closed (undisturbed) habitat: **A** *Ipomopsis aggregata* ($Z = 3.15$, $P < 0.008$, **B** *Penstemon barbatus* ($Z = 2.66$, $P < 0.004$)

Fig. 4. The relationship between magnitude of pocket gopher disturbance and **A** abundance of perennial grasses ($y = 0.976 - 0.843x$; $r^2 = 0.70$; $P < 0.005$), **B** abundance of perennial dicots ($y = 0.0132 + 0.821x$; $r^2 = 0.71$; $P < 0.005$)
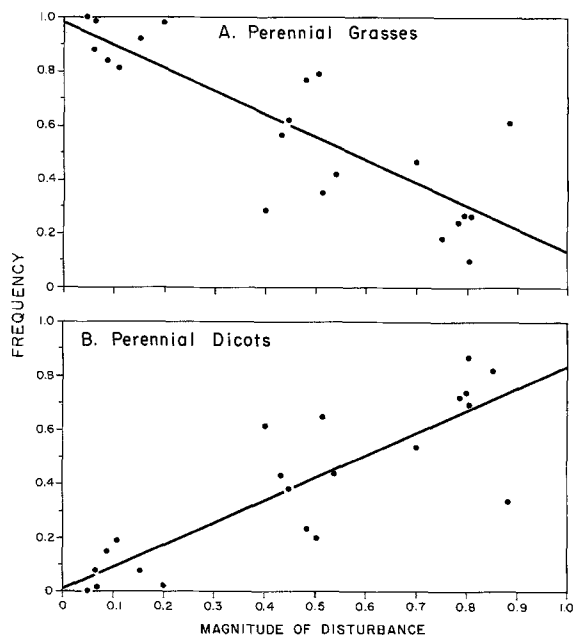
cantly more diverse than both plots characterized by old and new disturbance (Fig. 3). Plots that were newly-disturbed had not yet been colonized by herbaceous perennial dicots and were dominated by perennial grasses. Conversely, in plots that had been disturbed several years previously, competitive displacement had occurred such that grasses were once again dominant, and diversity was low. Diversity was highest in disturbances of intermediate age, where several species of perennial dicots had colonized and competitive displacement by perennial grasses had not yet occurred.

Fig. 5. The relationship between age of pocket gopher disturbance and **A** abundance of perennial grasses ($F=8.96$; $P<0.002$), **B** abundance of perennial dicots ($F=8.97$; $P<0.002$)

The two major groups of plants in this community, perennial grasses and perennial dicots, responded very differently to pocket gopher disturbance. In terms of disturbance magnitude, the abundance of grasses decreased with increasing disturbance, while the abundance of dicots increased with increasing disturbance (Fig. 4). With respect to age of disturbance, one would predict that the abundance of grasses would be lowest on disturbances of intermediate age, while the abundance of dicots would be highest on disturbances of intermediate age. The data for grasses fit this pattern, but the abundances of dicots on intermediate vs. old disturbance are not statistically different ($P=0.11$, Fig. 5).

Discussion

Consistencies with the intermediate disturbance hypothesis

The open space created by pocket gopher disturbance benefits herbaceous perennial dicots by 1) providing sites for colonization and 2) allowing them greater access to resources because of reduced levels of competition. Seedling plants are able to become established in the open disturbed areas and grow faster than plants which germinate in undisturbed control areas. Continued disturbance presumably breaks up the process of competitive displacement by perennial grasses, allowing these dicots to be maintained in the community. Areas that are undisturbed or lightly-disturbed are almost completely dominated by grasses (Fig. 4). Similarly, grasses are dominant both in areas that have not been recently disturbed and where disturbance is so recent that colonization by dicots has not yet occurred (Fig. 5). This result is in accordance with the findings of Hobbs and Mooney

(1985) and Hobbs et al. (1988), but differs from Tilman (1983), who argues that gophers maintain annuals by preferentially feeding on perennial species.

Consistent with the predictions of the Intermediate Disturbance Hypothesis, species diversity was highest in areas characterized by disturbance of intermediate age (Fig. 3). Coppock et al. (1983) reported a similar result for the disturbance created by prairie dog towns, although they did not frame it in terms of the Intermediate Disturbance Hypothesis. Plant species diversity was higher on a 3–8 year old prairie dog town than on both a town greater than 26 years old and an undisturbed site. These differences were attributed to reduced dominance of the grass *Andropogon scoparius* and colonization by several forb species on the young prairie dog town. The reduction of diversity on the old prairie dog town was due to a dominant shrub (*Artemesia frigida*). These results are remarkably similar to ours; disturbance allows colonization by forbs, increasing diversity, and eventually, in the absence of further disturbance, competitive displacement occurs, reducing diversity.

Inconsistencies with the intermediate disturbance hypothesis

Contrary to expectation, we did not detect significant differences in diversity between areas characterized by intermediate levels of disturbance and heavily-disturbed areas. Here, we discuss two hypotheses that attempt to explain this discrepancy. First, our results may reflect a problem with our definitions of medium and high disturbance. In particular, we may have neglected to sample both intermediate and high disturbance due to gaps in the data. For example, our categories of low, medium, and high do not include disturbances in the ranges of 20–40%, 55–70%, and >90% disturbance. If the peak or decline occurred in these ranges we would have missed it. If so, then we would have biased our analysis away from supporting the Intermediate Disturbance Hypothesis. This is also a general problem for other studies in which the magnitude of the disturbance has been categorized as low, medium, or high (Armesto and Pickett 1985).

An alternative interpretation of our results is the view that the forb species we studied are so well adapted to chronic disturbance that natural levels of disturbance are rarely high enough to negatively influence diversity. There may be a fundamental difference between the regular, predictable disturbance created by pocket gophers and the more unpredictable disturbances on which Connell's hypothesis is based (such as tree falls in tropical forests and storms over coral reefs). Disturbance in prairies ranges from small-scale patches produced by animals to large-scale disturbance such as prolonged drought and wind or water erosion (Loucks et al. 1984). Denslow (1980) argues that communities which are commonly subject to small-scale disturbance should contain species adapted to exploit this disturbance type (as opposed to species adapted to large-scale disturbance such as fire). In another review, Denslow (1984, p. 313) sug-

gests that "Ultimately, disturbance frequency may have as strong a selective effect on species as do the physical characteristics of the habitat." Extending this argument, we propose that the selective pressures in this community have caused species to either tolerate or take advantage of extreme variation in disturbance magnitude. As a result, high diversity is maintained across a wide range of disturbance levels.

Biotic vs. abiotic disturbance

Disturbance is caused by both biotic and abiotic agents (see reviews by White 1979; Sousa 1984). Examples of physical disturbance include fire (Hanes 1971; Wright 1974), windthrows in forests (Connell 1978; Hartshorn 1978; Hubbell 1979), storms over coral reefs (Connell 1978), and wave action in the intertidal (Dayton 1971; Paine and Levin 1981). The role of biotic disturbance agents is not as well documented. Paine (1966) demonstrated the importance of predators in preventing a single species from monopolizing space in the intertidal. Insect outbreaks may cause periodic vegetation changes (Blais 1954; Ghent et al. 1957). Platt (1975) described vegetation changes associated with disturbance of grassland prairies by badgers, and several studies have examined the effect of pocket gopher disturbance on plant communities (e.g. Inouye et al. 1987; Hobbs and Mooney 1985).

In addition to being important agents of disturbance, pocket gophers are also influential herbivores (Cantor and Whitham 1989; also see review by Anderson 1987). For example, gophers are known to eat various species of the perennial grass *Bromus*, and grasses are the single most important item of the winter diet of *Thomomys bottae* in California (Gettinger 1974). If this is the case in the mountain community we studied, the negative impacts of pocket gophers on perennial grasses may be twofold. The role of pocket gophers as herbivores that feed selectively on the competitve dominant may be similar to that of the marine snail *Littorina* in tide pools (Lubchenco 1978).

On the other hand, several studies of gopher food habits report that forbs are the major dietary component (Aldous 1951; Ward and Keith 1962; Vaughan 1967; Anderson and McMahon 1981). If this is the case in our community, pocket gophers indirectly benefit themselves by creating disturbances which maintain an important food source. Turner (1969) reported that exclusion of pocket gophers benefited their food plants (lupine, penstemon, dandelion), but resulted in decreased abundance of *Helenium*, which presumably depends on pocket gopher disturbance for establishment. We argue that the other forbs are also benefited by disturbance but are in turn eaten by gophers.

Random vs. predictable disturbance

Another unique feature of pocket gopher disturbance is that it occurs with a regular, predictable frequency.

As we suggested earlier, organisms that are subjected to frequent, predictable disturbance are likely to become adapted to the disturbance. Thus, it is not surprising that we found similar species diversity in areas of intermediate and high disturbance. In those systems that have supported the Intermediate Disturbance Hypothesis, the disturbance was 1) more unpredictable and 2) larger-scale, both factors that cause greater mortality at high levels of disturbance, resulting in lower species diversity.

Species that colonize highly-disturbed areas of grasslands or old fields are often introduced annuals (so-called weed or ruderal species). These Eurasian species may be adapted to disturbed soil conditions because of a long history of coevolution with humans (Denslow 1980). The scarcity of such species in this community is probably due to two factors: 1) a relatively harsh climate and short growing season and 2) isolation from human influence. Their role has been filled by native herbaceous perennial dicots, which have adapted to tolerate frequent and often heavy disturbance. Using Grime's (1977) terminology, these native plants are competitive ruderals, plants which commonly reproduce vegetatively and are adapted to frequent disturbance. In contrast, weedy annuals emphasize seed production and are mainly restricted to severely-disturbed habitats. Thus, this situation may represent an example of species evolving strategies to cope with the dynamics of their community (White 1979).

We suggest that the major inconsistency of our study with the Intermediate Disturbance Hypothesis (i.e. high plant species diversity at both intermediate and high levels of disturbance) is due to predictable biotic agents of disturbance in our system. Studies that have found a decline in diversity at high disturbance levels have dealt with random abiotic agents of disturbance. We argue that the plants in this community are so well adapted to chronic disturbance by pocket gophers that high diversity is maintained across a broad range of levels of disturbance.

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