Gopher Disturbance and Plant Community Dynamics In Montane Meadows

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Note

This thesis grew out of research conducted for my Spring Junior Paper. My focus and research plan changed significantly since then, but where appropriate I cite ideas that I first introduced in the JP.

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Abstract

Pocket gophers (Geomyidae) are a major agent of disturbance in grassland plant communities throughout North America. By depositing excavated soil on the ground surface, they bury existing plants and restart succession on a local scale, potentially influencing community structure and diversity by providing opportunities for less competitive species to persist. This study examined the impact of the Mazama pocket gopher (*Thomomys mazama*) on montane meadow plant communities in four plots established at Bunchgrass Ridge in the Oregon Cascade Range. Each plot contained 20 transects that were sampled for percent cover of gopher disturbance and plant species present. In higher-altitude systems such as Bunchgrass Ridge, gopher disturbance occurs as mounds, which are piles of excavated soil, as well as tunnel castings, which are created when gophers tunnel through a deep snow pack and fill these tunnels with soil that settles on the ground surface after snow melt. The relationship between castings and vegetation has not previously been studied. I found that both mounds and castings negatively affected plant cover, and that species richness and spatial heterogeneity were positively correlated with total cover of disturbance. Cover of graminoids declined and the ratio of forb/graminoid cover increased with mound cover, which is consistent with the literature, but the relationship between graminoid cover and cover of castings appeared variable across the four plots sampled. As one explanation for these findings, I present a simulation model that demonstrates how the presence of a highly competitive species might alter the relationship between graminoids and disturbance. This study illustrates the critical role disturbance can play in structuring natural communities.

Chapter 1

Introduction

Ecologists have long recognized the importance of disturbance in shaping biological communities. Although equilibrium theories once dominated ecological discourse, presuming that communities of organisms were stable through time and existed in a constant environment, it has become apparent that “the normal state of communities and ecosystems is to be recovering from the last disturbance” (Reice 1994). A disturbance is a punctuated disruptive event that restarts succession, the process of change in community structure and composition over time, by killing or damaging individuals and creating openings for new individuals to establish (Sousa 1984). Disturbances can vary widely in size and intensity, from a fire that consumes an entire forest, to the fall of a single tree that opens a gap in the canopy.

We typically think of disturbance in terms of abiotic processes – fire, wind, or water – that disrupt ecological communities (Sousa 1984). Yet in some systems, the organisms themselves can be powerful agents of natural disturbance. Gophers are one such example. Physical disturbances caused by gopher activity often comprise one of the most frequent and widespread forms of disturbance in grassland plant communities (Reichman 2007).

The pocket gopher is “a classic example of an ecosystem engineer” (Case 2011, Reichman & Seabloom 2002), an organism that modifies its physical environment in a substantial way on a scale that differs from direct biotic interactions such as herbivory (Hastings *et al.* 2007). Pocket gophers (Geomyidae) are a family of fossorial rodents that inhabit grassland environments throughout North America. They live almost entirely underground in complex networks of burrows. This subterranean lifestyle requires that gophers move a great deal of soil; one estimate puts the average rate of soil excavation by Geomyidae at 18 m^3 ha^{-1} $year^{-1}$ (Smallwood & Morrison 1999). Gopher activity can have profound effects on the abiotic environment of grasslands (Case 2011), creating heterogeneity in ground-surface topography (Inouye *et al*. 1987), soil texture (Sherrod & Seastedt 2001), soil moisture (Kyle *et al*. 2008), light availability (Inouye *et al*. 1987), and nutrient availability (Tilman 1983; Inouye *et al*. 1987; Sherrod & Seastedt 2001).

The impacts of gophers on the abiotic environment have serious consequences for vegetation. Gophers push excavated soil into abandoned tunnels or expel it onto the ground surface in piles known as gopher mounds, which bury existing plants and create fresh ground for new plants to colonize. Mounds can range from 20-50 cm in diameter and 5-25 cm in height (Reichman 2007) and remain visible for years, gradually becoming part of the surrounding matrix as a result of physical weathering and re-vegetation by plants (Fig. 1.1). In systems where grassland is covered by snowpack for part of the year, gophers also burrow through the snow and fill these tunnels with excess soil, resulting in tunnel castings that melt out of the snow and settle on the ground surface each spring (Reichman 2007, Knight 2009). Castings (Fig. 1.2) are typically shallower in depth than gopher mounds and more quickly assimilated into the surrounding matrix, but still amount to a substantial form of gopher disturbance. Mounds and castings are ubiquitous in gopher habitats, covering up to 25-30% of the ground surface each year (Huntly & Reichman 1994).

Figure 1.1. Gopher mounds ≥ 1 year old at Bunchgrass Ridge, Oregon.

Figure 1.2. Gopher castings (and holes leading to subterranean tunnels) soon after snow melt at Bunchgrass Ridge, Oregon. PVC rectangle included for scale measures 20 cm x 50 cm.

Through studying the ways in which gopher disturbance affects plant community structure and diversity, we can better understand the powerful role disturbance plays in shaping ecosystems. In this chapter I will first review the relevant ecological theories and hypotheses regarding how communities respond to disturbance, then consider how these phenomena play out in communities affected by gophers, and lastly present the questions and objectives driving my own study of gopher disturbance and plant communities in montane meadows of Oregon's Cascade Range.

Theories of response to disturbance

While the word "disturbance" connotes destruction and damage – and indeed, for an individual organism that dies in a disturbance event, such negative connotations hold true – the effects of disturbance at the population and community level can be more complex. For some species, disturbance represents opportunity. A disturbance event creates a patch of newly available resources such as space, light, or nutrients. Organisms that establish quickly after a disturbance – whether by surviving the disturbance and re-growing, or by colonizing from adjacent or distant patches – can capitalize on the open niche space and reduced competition (Reice 1994). There are typically trade-offs, however, between colonization ability and competitive ability. Species adapted to rapid establishment after disturbance are often less capable of persisting once more competitive species move in (MacArthur & Wilson 1967, Platt 1975, Connell & Slatyer 1977, Grime 1979).

Higher-level community patterns may emerge from this interplay between disturbance, competition, and species composition. A fascinating question for ecologists, and a question that has driven much of the research on gopher disturbance, has been whether disturbance actually facilitates species coexistence and thus maintains diversity. The Intermediate Disturbance Hypothesis (IDH), a classic non-equilibrium theory of biological community structure – first proposed by Grime (1973) and further described by Horn (1977) and Connell (1978) – predicts that maximum species diversity is maintained at intermediate frequencies and intensities of disturbance. The IDH postulates that while pioneer species dominate immediately after disturbance, and the more competitive late-successional species eventually take over, both types of organisms can coexist at intermediate levels or frequencies of disturbance.

Although the IDH predicts a unimodal, peaked relationship between diversity and disturbance, empirical studies of disturbance have found that peaked, increasing, decreasing, and nonsignificant diversity-disturbance relationships are all common patterns (Mackey & Currie 2001). This may be an outcome of the broad definitions of terms such as "disturbance" and "diversity," as well as the question of whether a sufficient range of disturbance frequency or intensity has been sampled to see a peak at "intermediate" levels (Sousa 1984). Diversity consists of both species richness (the number of species) and evenness (the equitability of abundance among species) (Magurran 2004), and disturbance can have dramatically different effects on these two parameters within the same system (Reice 1994). Still, the IDH provides a useful conceptual framework for understanding how disturbance can interact with competitive hierarchies and facilitate species coexistence, and why disturbance can be considered important for diversity.

Plant community responses to gopher disturbance

In systems where gophers comprise a major form of disturbance, some plant species are more successful than others at establishing on or surviving gopher disturbances. In tallgrass prairie, some short-lived, disturbance-adapted species such as the legume *Medicago lupulina* may even depend directly on mounds for survivorship (Wolfe-Bellin & Moloney 2000). Across grassland ecosystems, a few general trends emerge: mounds tend to favor the establishment of forbs relative to graminoids (Mielke 1977, Foster & Stubbendieck 1980, Martinsen *et al*. 1990, Sherrod *et al*. 2005) and annuals relative to perennials (Foster & Stubbendieck 1980, Schaal & Leverich 1982, Tilman 1983). In some systems, however, perennial graminoids seem to be helped by gopher disturbance (Rogers *et al*. 2001, Hobbs & Mooney 1985). Given that many of the most problematic non-native invasive plants are adapted to take advantage of soil disturbance with rapid colonization (D'Antonio 2002), the potential that gophers will encourage invasion can be a concern in vulnerable ecosystems. Kyle *et al*. (2008), for example, found that gopher mounds suppress growth rates of native plants relative to invasives in a shrub-steppe environment.

The mechanisms by which some plant species gain an advantage in re-vegetating gopher mounds can vary dramatically between systems (Case 2011). In the serpentine grasslands of Jasper Ridge in California, gopher mounds are predominantly colonized by seed. The plant species that are most successful at colonizing mounds are those with the tallest flowering stalks, which enhance their chances of dispersal onto mounds (Hobbs & Mooney 1985). In the alpine tundra of Niwot Ridge, by contrast, reproduction by seed is rare and emergence from burial is the main mechanism by which plants re-vegetate mounds. The traits that confer an advantage in responding to disturbance, therefore, are quite different there compared to Jasper Ridge; Sherrod *et al.* (2005) hypothesize that forbs gain an advantage over graminoids on mounds at Niwot Ridge thanks to greater belowground carbon stores, which aid in recovery from burial. Comparisons such as these highlight the importance of studying gopher impacts in a variety of systems.

Support for the Intermediate Disturbance Hypothesis among studies of gopher disturbance and diversity has been mixed. In a shortgrass prairie community, Martinsen *et al*. (1990) found both consistencies and inconsistencies with the IDH. As expected, species diversity was greatest for plots characterized by disturbances of intermediate age (supporting the “frequency” dimension of the IDH), but diversity did not differ in plots with intermediate versus high levels of disturbance. Alternatively, in an abandoned agricultural field at Cedar Creek in Minnesota, Tilman (1983) found an increase in richness with level of gopher disturbance in plots. By contrast, Jones et al. (2008) found that richness increased with age of mounds and peaked in undisturbed vegetation in a high-altitude meadow in the Pacific Northwest. This would suggest a model of gradual accumulation of species over time without the inevitable decline in richness predicted by the IDH. However, this pattern may still be compatible with the IDH if we consider that even apparently “undisturbed” meadow is still “recovering from the last disturbance” (Reice 1994) and not in equilibrium. Perhaps species richness would eventually decline in the absence of further gopher disturbance.

Spatially explicit simulation models, a valuable tool for looking at how fine-scale processes scale up to emergent patterns, have also been used to investigate the consequences of various aspects of gopher disturbance patterns for the composition and diversity of plant communities. Such models allow researchers to ask questions that would be difficult to pursue experimentally (such as how changing the amount of overall gopher disturbance, or the spatial autocorrelation patterns of gopher mounds, would affect a given system). Moloney and Levin (1996), modeling the effects of different aspects of gopher disturbance architecture on the population dynamics of three species found at Jasper Ridge in California, found that species diversity was greatest at intermediate levels of disturbance (supporting the claims of the IDH). In a similar, patch-based model, Wu & Levin (1994) also found that gopher disturbance facilitated the coexistence of two competing plant species.

An important insight of these models is how spatial and temporal autocorrelation of gopher disturbance (clumping of disturbance in space and time) is a crucial feature for the facilitation of diversity. Patterns of autocorrelation are a common feature of gopher disturbance (Thomson *et al.* 1996, Klaas *et al.* 2000, Wolfe-Bellin & Moloney 2000, Overton & Levin 2003). The patchy nature of gopher disturbance in space and time puts gopher-disturbed grasslands in a special category of systems described by Levin (1992) as "spatio-temporal mosaics, variable and unpredictable on the fine scale, but increasingly predictable on large scales." On a small scale, it may be difficult for different species to coexist, and local extinctions may be common. On the landscape scale, however, a heterogeneous, dynamic mosaic of patches at different stages of succession can provide ample opportunity for multiple species to persist. The scale at which we consider the effects of gopher disturbance, therefore, can greatly affect the patterns we see.

Gophers and plants in montane meadows

Despite the wealth of research to date, there is still much we do not know about how disturbance by pocket gophers affects vegetation. In particular, most studies of gopher research have focused on lowland prairies (e.g. Foster & Stubbendieck 1980, Tilman 1983, Hobbs & Mooney 1985, Martinsen *et al.* 1990, Rogers *et al.* 2001), whereas relatively little is known about gopher-plant interactions in higher-elevation mountain meadows. Montane and subalpine grasslands differ in important ways from lowland systems, both in terms of environmental challenges and vegetation characteristics, and such differences can matter greatly in determining how plant communities responds to a patterns of gopher disturbance (Sherrod *et al*. 2005, Case 2011).

Bunchgrass Ridge, the high-elevation plateau in the Oregon Cascade Range where I conducted my study, is characterized by short, dry summers and a deep winter snow pack. Unlike in lowland systems, the forbs and graminoids inhabiting Bunchgrass Ridge's meadows are predominantly perennials, and vegetative reproduction is common (Jones *et al.* 2008). Most meadow species do not maintain viable seeds in the soil (Lang & Halpern 2007). Each of these characteristics of the system is relevant to how the activities of the resident population of Mazama pocket gophers (*Thomomys mazama*) affect the vegetation. Colonization by seed likely plays a much less central role in the process of re-vegetating mounds than in other systems, while recovery from burial and lateral vegetative growth by clonal plants are noteworthy mechanisms of re-vegetation after disturbance (Case 2011). Moreover, whereas the plants in this high-elevation system face a short growing season, gophers are active year-round, as evidenced by the ubiquitous pattern of winter tunnel castings that melt out of the snow in spring. To my knowledge, no other study to date has examined the influence of gopher castings on plant community composition.

In a previous study of gopher-plant interactions at Bunchgrass Ridge, Jones *et al*. (2008) studied plant succession on gopher mounds using a chronosequence approach, comparing plant community composition in small quadrats on young and old mounds and in adjacent undisturbed meadow. They found that plant cover and species richness increased with mound age, with the greatest species richness found in undisturbed meadow quadrats. In keeping with findings in other systems, they found that abundance of forbs relative to graminoids was greater on mounds than in adjacent meadow. Mound quadrats also showed greater variation in species composition than did quadrats in undisturbed meadow, suggesting that gopher disturbances might increase spatial heterogeneity of plant communities on a landscape scale. My research was motivated by a desire to extend these findings by examining the consequences of gopher disturbance at spatial scales considerably larger than those studied by Jones *et al*. (2008). In addition, previous work in this system did not consider the role of castings, which are abundant at Bunchgrass Ridge and potentially a significant component of gopher disturbance.

With these considerations in mind, I designed a study in which I sampled vegetation and gopher disturbance across five-meter transects, a scale which could span multiple patches of disturbance and the meadow matrix in between. I asked the following questions and hypothesized as described:

1. How would the amount of disturbance in a transect relate to total plant cover, cover of forbs and graminoids, and various measures of diversity and heterogeneity? If

patterns observed at small spatial scales by Jones et al. (2008) held at larger scales, I expected to find that with increasing disturbance, plant cover would decline, the ratio of forb to graminoid cover would increase, species richness would decline, and evenness would not change. Extrapolating from their finding of greater compositional variation between mound quadrats than meadow quadrats, I also expected to find that spatial heterogeneity in species composition would increase with disturbance.

2. How would disturbance type (mounds vs. castings) contribute to these effects? I expected that mounds and castings would both have significant effects on the vegetation in all the ways described above.

3. At what scale are there patterns of spatial autocorrelation in disturbance and vegetation? I expected that some spatial autocorrelation would be present at small scales, in keeping with findings of clumped patterns of disturbance in other systems.

In Chapter 2 of this thesis, I present the methods used to collect and analyze field data. Chapter 3 contains the results of my field research. Chapter 4 describes the results of a simulation model – motivated by my field study – which examines how the life history traits of plants can interact with gopher disturbance to produce different patterns of vegetation response depending on which plant species are present. In Chapter 5 I discuss my overall conclusions and directions for further research, with an eye toward how this study can help us to understand the role of gophers in montane meadows, and more generally the role disturbance plays in structuring plant communities.

Chapter 2

Field Research Methods

Study site

The study area, Bunchgrass Ridge (henceforth Bunchgrass), is a broad, raised plateau at an elevation of ~1220-1375 m in the Oregon Cascade Range (44°17’N, 121°57’W). Slopes are gentle (<5%) and generally south- or southwest-facing. Bunchgrass supports a patchy mosaic of dry montane meadows, older forests (>100-200 years old), and young forests (<90 years old) resulting from recent conifer encroachment into meadows. In recent years Bunchgrass has served as a study site for experimental treatments exploring the possibility of restoring meadows through tree removal and burning (Halpern *et al*. 2012). For this study I established plots in three distinct meadows roughly 1-8 ha in size that were not part of that experiment and had been relatively unaffected by conifer invasion.

Meadow communities at Bunchgrass Ridge are dominated by graminoids (e.g. *Carex pensylvanica*, *Festuca idahoensis*) and perennial forbs (e.g. *Phlox diffusa*, *Lupinus latifolius*, *Cirsium callilepis*, *Achillea millefolium*). Grasslands of this nature are typical of high-elevation plateaus and south-facing slopes in this region of the Cascades (Halpern *et al.* 1984). Disturbances attributed to the Mazama pocket gopher (*Thomomys mazama*) are abundant throughout meadow areas (Jones *et al.* 2008).

Meadow soils are deep (>170 cm) fine to very-fine sandy loams derived from andesitic basalt and volcanic ash deposits (Lammers & Dyrness 2004). The climate is characterized by warm, dry summers and cool, wet winters, with significant winter snowfall that can leave a deep snowpack persisting into late spring. Average annual temperatures at Santiam Pass (17 km to the north, at an elevation of 1488 m) range from 0.72 °C (max), -6.94 °C (min) in January to 22.8 °C (max), 6.06 °C (min) in July. Average annual rainfall is 216.5 cm, only 7.5% of which falls during the summer months. Snowpack at Santiam Pass peaks in March at an average depth of 2.6 m (data from 1948-1985, Western Regional Climate Center).

Field methods

Sampling design

With the help of Charles Halpern, a collaborator on this project, I established four 20 m x 5 m rectangular plots. Each plot contained twenty 5-meter transects spaced at 1-meter intervals (Fig. 2.1). We chose plot locations to represent a diversity of meadow community types, to capture a moderate amount of gopher disturbance with variation at the transect level, and to avoid close proximity to meadow/forest edges. At the time of plot establishment early in the summer when few of the plants were mature, the most evident difference in vegetation between plots was the abundance of *Phlox diffusa*, so these qualitative differences are noted here. Plots 1 and 2 were established in “Lodgepole Pine Meadow” roughly 20 m apart, with Block 2 located in a patch of greater *Phlox diffusa* cover. Plot 3 was established in “Summit Meadow,” a larger, slightly higher-elevation meadow with a great abundance of *Phlox*. Plot 4 was established in “White Pine Meadow,” on a gentle, south-facing slope; *Phlox* was absent from this meadow (Fig. 2.2).

After choosing the general location and orientation of each plot, one plot corner was established at the landing point of a chaining pin tossed blindly into the air. We surveyed a rectangle from this starting corner, verifying the accuracy of the rectangle side lengths to within +/- 1% of the expected perimeter. We marked each plot corner with a ~0.7 m segment of PVC pipe hammered into the ground and placed pin flags at 1-m intervals along the long sides of each plot to mark the endpoints of the transects. When pin flags occasionally disappeared throughout the summer due to elk trampling or other natural disturbance, I relocated them by measuring between the two adjacent flags.

Each five-meter transect was sampled with 25 contiguous quadrats (20 cm x 20 cm, Fig. 2.1). I measured the extent of gopher disturbance and vegetation as visual estimates of percent cover (100% being the total area of a quadrat square, 400 cm^2). Percent cover is a commonly used metric for ground surface variables as well as vegetation measurements, particularly in systems such as this one in which the presence of bunchgrasses and clonal plants makes counts of individuals impractical (e.g. Sherrod *et al.* 2005, Jones *et al.* 2008, McCain *et al.* 2010). I made all cover estimates myself, with my field assistant, Sarah Koe, recording data. I calibrated my estimates at the beginning of the summer by measuring and calculating the area of various plants with a centimeter ruler, and re-calibrated throughout the summer to ensure consistent estimation. I estimated cover values <1% as either 0.5% or 0.1%, values between 1 and 10% to the nearest 1%, and values >10% to the nearest 5%.

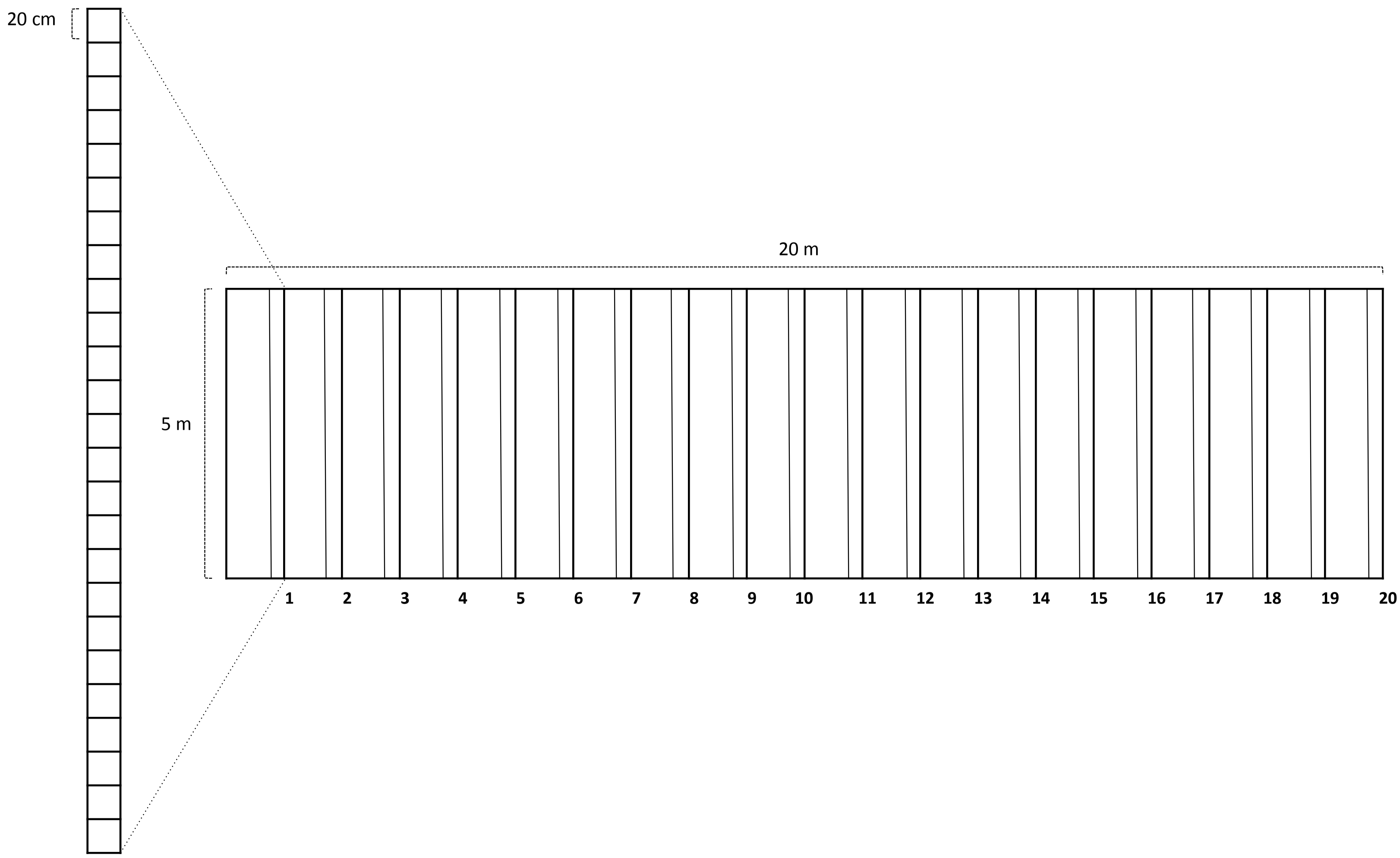


Figure 2.1. Plot layout. The long rectangle on the right shows the overall layout of a 20 m x 5 m sampling block, with 20 transects (narrow bands) crossing the plot at 1 m intervals. On the left is a close-up view of a transect, subdivided into twenty-five 20 cm x 20 cm quadrats.

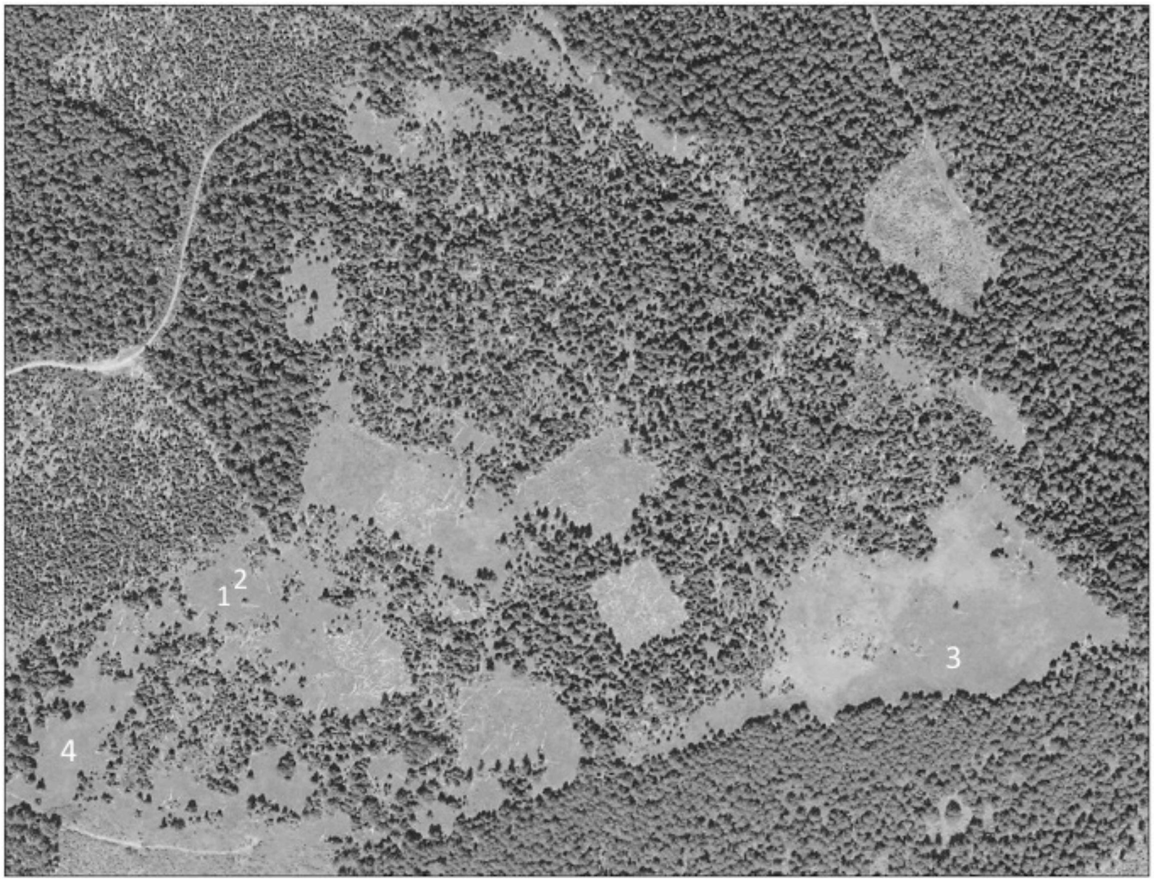


Figure 2.2. Aerial photo of Bunchgrass Ridge with sampling locations marked by plot number. The square or rectangular openings in the center of the photo are 1-ha experimental plots from which trees were removed in 2006.

Timing of sampling

I sampled all transects for gopher disturbance between June 20 and 30, 2011, and for vegetation between July 7 and August 12, 2011. This temporal separation between disturbance and vegetation sampling allowed us to measure disturbance soon after snow melt, when most plants had not yet emerged and gopher disturbance was most evident, and then to return for vegetation sampling when the plants were mature. The order in which we sampled the four plots for ground conditions and vegetation was determined by plant phenology.

Disturbance sampling

Gopher disturbance categories included fresh mound, old mound, casting, tunnel, and hole. Fresh mounds were defined as mounds created during the current growing season, consisting of loose, un-compacted soil with no vegetation cover (Fig. 2.3). All other mounds – which showed evidence of compaction or weathering, and typically had some vegetation cover – were defined as old mounds (Figs. 2.3-4).

Figure 2.3. Fresh mound (front) adjacent to old mound (back). Photo by Charles Halpern.

Figure 2.4. Old mound. Photo by Charles Halpern.

The classification of all mounds not created in the current growing season as "old" was a departure from the methods used by Jones *et al.* (2008), who differentiated "young mounds" (1-2 years old) from "old mounds" (at least 2 years old). Given that the criteria used by Jones *et al.* (2008) for differentiating young from old mound classes relied mostly on the degree of compaction and the height of the mound above the ground surface, I instead measured mound height directly to reduce subjectivity in classifying mound age. I measured the maximum height in centimeters of mound disturbance relative to the adjacent undisturbed ground surface within each quadrat. Mound height measurements were significantly correlated with mound cover, however, so they were not used in the analysis (Kendall's rank correlation, tau = 0.3359, z = 12.7445, $p < 2.2e\text{-}16$).

Figure 2.5. Gopher castings early in the summer. Arrow in lower right corner indicates exposed tunnel.

Castings were defined as the remnants of winter tunneling activity by gophers, where gophers had filled snow tunnels with excavated soil. These castings, melted out of the snow, appeared as tubes of bare soil snaking across the ground surface (Fig. 2.5). Where castings intermingled with mounds, the two could typically be distinguished by soil characteristics; castings contained fewer small stones and had a higher concentration of fine organic matter, such as small pieces of dead grass, than did mounds. Tunnels, which also likely resulted from winter tunneling activity between the ground surface and the snow, were defined as exposed hollow tunnels not backfilled with soil. Holes were defined as openings leading to subterranean tunnels. New disturbances (fresh mounds or holes) observed at the time of vegetation sampling were recorded, but were remarkably infrequent, and were not considered in the analyses of disturbance-vegetation relationships.

During ground surface and disturbance sampling I also measured percent cover of *Claytonia lanceolata*, an ephemeral herb that flowers soon after snow melt and senesces early in the summer, knowing that it would be largely absent by the time we began vegetation sampling.

Vegetation sampling

I identified all plant species in or above each quadrat and estimated foliar cover of each species as a vertical projection into the quadrat. Because of overlap among species, total cover of all species in a quadrat could sum to more than 100%. I identified all plants to species, with the exception of *Fragaria* spp. (which included *F. vesca* and *F. virginiana*) and a seedling of *Acer* sp. When I could not identify a plant in the field, I took detailed notes and photographs and/or collected a specimen from outside the plot, and identified it later with the help of herbarium specimens or other reference materials. Nomenclature follows Hitchcock & Cronquist (1973).

Statistical methods

Data aggregation and summary

I used the R statistical package (R Development Core Team 2011) for all analyses. I calculated total cover of forbs, graminoids, and all plants, as well as total gopher disturbance, for each transect (mean of 25 quadrats), and calculated the ratio of forb to graminoid cover at the transect level. I also calculated total percent cover of forbs with *Phlox diffusa* excluded. Although Jones et al. (2008) treated *Phlox* as a forb, it is more appropriately defined as a sub-shrub given its woody base and branches (Hitchcock & Cronquist 1973).

For each quadrat and transect I calculated species richness as the total number of species counted. I calculated an index of species evenness for each transect, using the modified Hill's ratio recommended by Alatalo (1981): $(N_2 - 1)/(N_1 - 1)$, where N_1 and N_2 are the Hill numbers of order 1 and 2, estimates of the effective number of species with different weights placed on rare species (Hill 1973). With p_i as the ratio of the total percent cover of the *i*th species to the total cover of all plants in the sample,

$$N_1 = \exp\left(-\sum p_i * \ln(p_i)\right)$$

$$N_2 = \frac{1}{\sum p_i^2}$$

(Hill numbers calculated with vegan package, Oksanen *et al.* 2011). I also calculated an index of mean community heterogeneity for each transect by taking the mean of the Bray-Curtis dissimilarity (Bray & Curtis 1957; ecodist package, Goslee & Urban 2007) of all pairs of quadrats within the transect.

Statistical models and tests

I investigated relationships between disturbance and vegetation using linear mixed-effects models (lme4 package, Bates *et al.* 2011), treating disturbance variables as fixed effects and plot as a random effect to account for potential correlation of errors within plots. Each model used the maximal random-effects structure justified by the data. For some models a random-intercept term was sufficient, but others required a random slope and random intercept because the addition of a random slope significantly improved the fit of the model. I obtained p-values for fixed effects (disturbance variables) using the pamer.fnc() function (LMERConvenienceFunctions package, Tremblay 2011), which computes upper- and lower-bound p-values for the analysis of variance for each fixed effect according to the range of possible degrees of freedom. The upper- and lower-bound p-values generally differed by less than 0.001, so for simplicity I report only the more conservative upper-bound p-value and the corresponding degrees of freedom (see Appendix A for further discussion of mixed-effects models and the computation of p-values).

For total disturbance, I fitted a mixed-effects model for each of several plant response variables at the transect scale: total plant cover, total forb cover, total graminoid cover, total forb cover with *Phlox* excluded, forb/graminoid ratio, species richness, evenness, and community heterogeneity. Because I might expect a peaked, unimodal relationship between richness and disturbance according to the Intermediate Disturbance Hypothesis, I also modeled richness as a quadratic function of disturbance and compared this to the linear model with a likelihood-ratio test. To assess the individual effects of old mound and casting (the two most common forms of gopher disturbance), I modeled each of the plant response variables as a function of old mound and casting as additive fixed effects, with plot as a random effect. I tested for correlation between cover of mounds and castings at quadrat and transect scales using a Kendall's rank correlation test because the data did not meet the requirements of normality.

The spatially explicit layout of the transects and quadrats within plots also allowed investigation of the spatial autocorrelation of cover of disturbance and plant variables. To understand the spatial correlation structure of the main variables of interest at the quadrat scale, I developed correlograms (0.2-10 m) for cover of total disturbance, old mounds, castings, total plants, total forbs, and total graminoids. Correlograms were produced using the spatial package (Venables & Ripley 2002).

Chapter 3
Field Results

Disturbance conditions

Old mounds and castings were the most common forms of gopher disturbance. Tunnels, holes, and fresh mounds were all infrequent. Mean total cover of gopher disturbance ranged from 24.6% (Plot 1) to 32.5 % (Plot 4). Roughly 60-70% of all quadrats in each plot contained at least some gopher disturbance (Table 3.1).

Table 3.1. Disturbance conditions across plots. Frequency represents proportion of quadrats occupied (for total disturbance this means quadrats occupied by any form of disturbance).

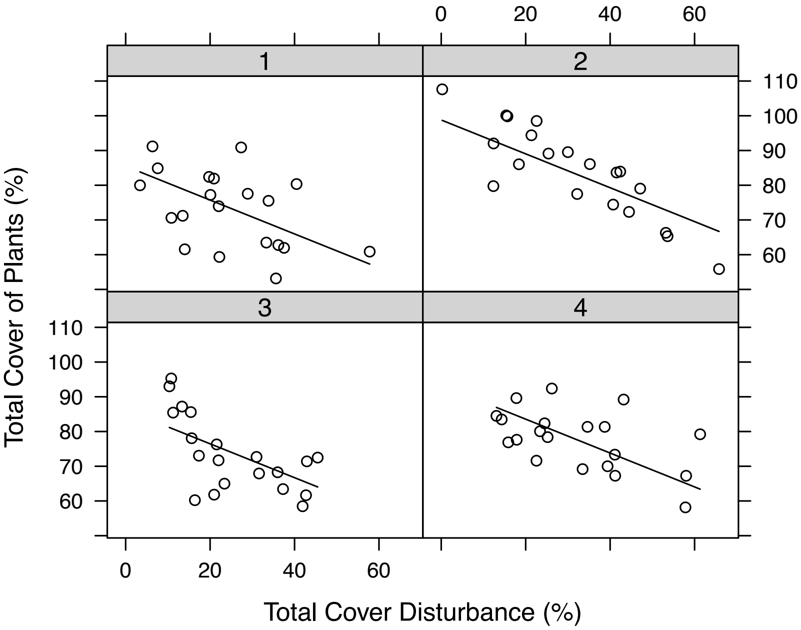
	Plot 1		**Plot 2**		**Plot 3**		**Plot 4**	
	Freq. (%)	**Cover (%)**	**Freq. (%)**	**Cover (%)**	**Freq. (%)**	**Cover (%)**	**Freq. (%)**	**Cover (%)**
Old mound	39.8	14.9	42.4	17.0	35.0	12.0	42.8	20.7
Casting	28.6	9.2	41.2	14.0	41.0	12.2	42.2	11.3
Tunnel	2.0	0.4	2.6	0.5	5.4	1.0	2.0	0.3
Hole	2.0	0.1	1.2	0.1	2.8	0.2	2.2	0.1
Fresh mound							0.2	<0.1
Total disturbance	60.4	24.6	68.4	31.5	70.8	25.4	70.6	32.5

Floristics

I observed a total of 34 taxa across the 4 plots. These included 23 forbs, 10 graminoids, and 1 shrub seedling (*Acer* sp.). Species richness by plot ranged from 21 species in Plot 3 to 27 species in Plot 2. Each plot contained 8 or 9 graminoid species, so differences in total richness among plots mostly reflect differences in forb richness (Table 3.2).

Table 3.2. Frequency and cover of plant species, summarized by growth form. Species are ordered within each growth form by mean cover among plots. Frequency represents proportion of quadrats occupied.

GROWTH FORM / *Species*	**Plot 1**		**Plot 2**		**Plot 3**		**Plot 4**	
	Freq. (%)	**Cover (%)**	**Freq. (%)**	**Cover (%)**	**Freq. (%)**	**Cover (%)**	**Freq. (%)**	**Cover (%)**
FORBS								
Phlox diffusa	35.8	6.2	97.0	27.6	81.0	35.8		
Lupinus latifolius	91.2	15.2	87.2	17.2	66.0	8.6	89.6	16.6
Hieracium gracile	2.0	0.1	2.6	0.4	16.8	1.5	79.4	10.4
Achillea millefolium	64.6	4.2	57.6	4.3	5.2	0.3	35.6	2.1
Arenaria macrophylla	84.4	3.8	92.0	4.6	16.8	0.5		
Orthocarpus imbricatus	11.4	0.3	88.4	7.2	25.8	0.7		
Cirsium callilepes	53.8	5.7	14.4	0.9			10.6	0.6
Fragaria spp.							63.8	7.0
Erigeron aliceae	19.8	3.3	20.2	2.8	2.2	0.2	2.0	0.2
Aster radulinus							34.4	4.8
Iris chrysophylla	2.4	0.2	0.4	<0.1	3.8	0.3	41.4	3.1
Claytonia lanceolata	27.4	0.5	28.6	0.5	75.6	1.8	1.8	<0.1
Penstemon procerus			6.0	0.8				
Comandra umbellata			16.2	0.6			6.2	0.2
Calochortus subalpinus	19.2	0.3	16.0	0.2	6.0	0.1	1.2	<0.1
Aster ledophyllus			4.2	0.5				
Viola nuttallii	3.6	0.1	8.8	0.2	4.4	0.1	4.8	0.1
Agoseris aurantiaca	4.6	0.2	3.4	0.1	5.0	0.2	0.4	<0.1
Lilium columbianum	2.6	0.1						
Lomatium triternatum	1.6	<0.1	1.2	<0.1	2.0	<0.1		
Rumex acetosella							1.8	<0.1
Fritillaria lanceolata			0.6	<0.1				
GRAMINOIDS								
Carex pensylvanica	99.6	20.0	93.2	7.3	99.2	10.2	99.6	12.8
Festuca idahoensis	86.8	5.8	85.6	6.8	70.8	8.7	97.0	15.4
Bromus carinatus	67.0	4.1	29.0	0.7	26.8	1.7	71.4	2.7
Danthonia intermedia	11.0	0.2	31.0	0.6	46.8	1.4	52.6	1.0
Elymus glaucus	42.2	2.0	23.0	0.4	4.6	0.1	11.6	0.4
Stipa occidentalis	7.0	0.6	4.6	0.3	18.8	1.0	1.6	0.1
Agropyron repens			1.6	<0.1	5.2	0.2	8.2	0.2
Poa pratensis	2.2	<0.1	6.4	0.1	1.6	0.1	1.8	<0.1
Festuca viridula	0.8	<0.1						
Luzula campestris			0.2	<0.1				
SHRUBS								
Acer sp.							0.1	<0.1
Number of forb species	15		18		13		14	
No. of graminoid species	8		9		8		8	
Total number of species	23		27		21		23	

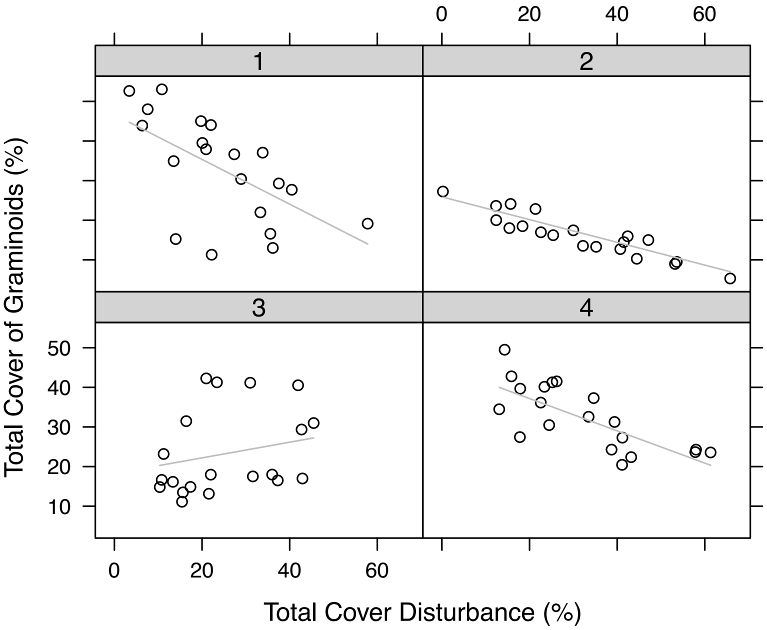


β	SE(β)	F	df	p
-0.48763	0.06656	53.68	74	<**0.001**

Figure 3.1. Relationship between total cover of disturbance and total cover of plants in each of the four plots. Points represent transect means. Regression lines for plots have different random-effects intercepts but a common slope (β).

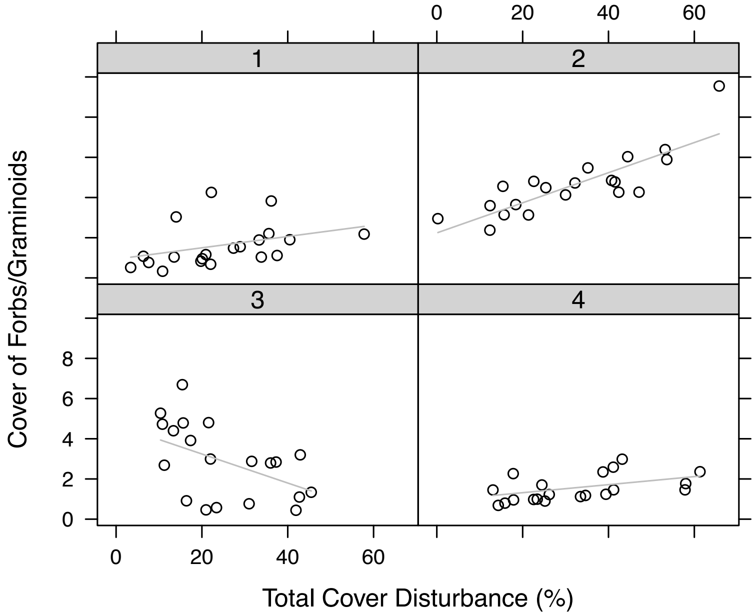
Disturbance and total cover of plants and growth forms

Total plant cover showed a highly significant negative relationship with total cover of gopher disturbance (random-intercept model; Fig. 3.1). However, for total graminoid cover (Fig. 3.2a), total forb cover (Fig. 3.3a), and the ratio of forb/graminoid cover (Fig. 3.2b), there was no significant overall effect of total disturbance due to variation among plots (random-slope models). Because I suspected that some of the between-plot variation in slope for forb cover might relate to the abundance of the most common (and semi-woody) species, *Phlox diffusa*, I also examined the forb-disturbance relationship with *Phlox* excluded. This relationship, fitted with a random-slope model, was also non-significant (Fig. 3.3b).



a.

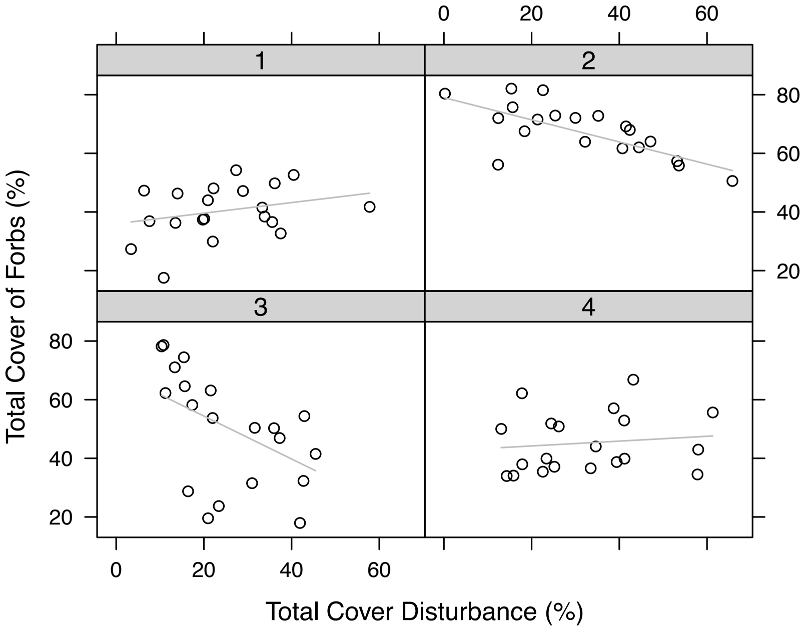
β	SE(β)	d^2	F	df	p
-0.2654	0.1869	0.1228	1.98	70	0.1637



b.

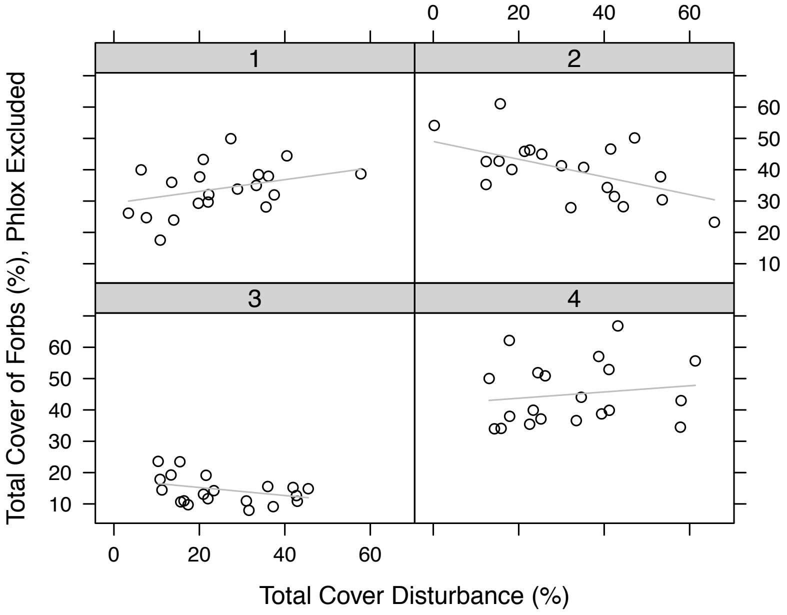
β	SE(β)	d^2	F	df	p
-0.01274	0.03316	0.00408	0.15	70	0.6954

Figure 3.2. Relationships between total cover of disturbance and **(a)** total cover of graminoids (points represent transect means) and **(b)** ratio of forb to graminoid transect mean cover in each of the four plots. Regression lines for plots have different random-effects intercepts and slopes (gray lines indicate a non-significant overall population slope). The random slope variance (d^2) determines the by-plot variation about the overall population slope (β). The p-value given assesses the null hypothesis that true β is zero.



a.

β	SE(β)	d^2	F	df	p
-0.2120	0.2447	0.2070	0.725	70	0.3976



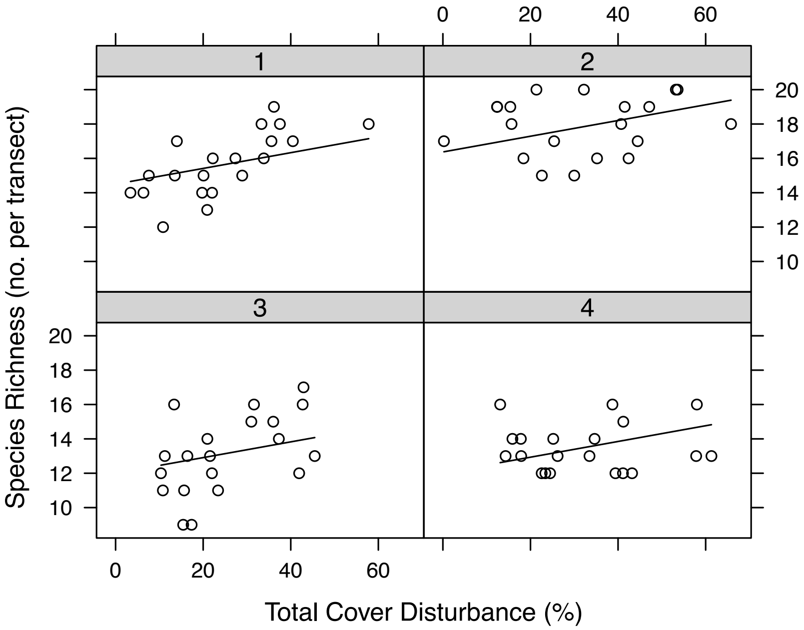
b.

β	SE(β)	d^2	F	df	p
-0.03109	0.13518	0.05785	0.049	70	0.8258

Figure 3.3. Relationships between total cover of disturbance and **(a)** total cover of forbs, and **(b)** total cover of forbs with *Phlox* excluded, in each of the four plots. Points represent transect means. Regression lines for plots have different random-effects intercepts and slopes (gray lines indicate a non-significant overall population slope). The random slope variance (d^2) determines the by-plot variation about the overall population slope (β). The p-value given assesses the null hypothesis that true β is zero.

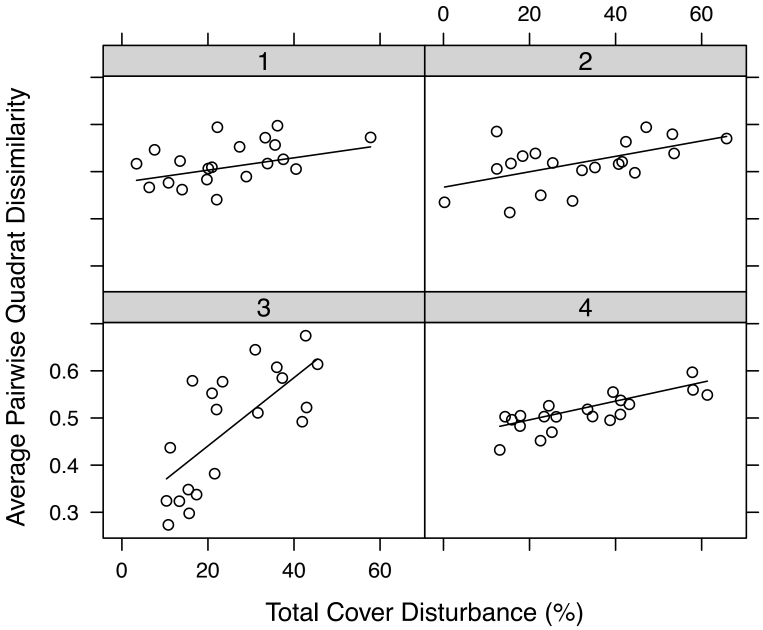
Disturbance and diversity

Species richness (number of species per transect) showed a highly significant positive relationship with total cover of disturbance (random-intercept model, Fig. 3.4). This amounted to an average increase of one species for each increase in percent cover of total disturbance by 20 percentage points. A model of species richness as a quadratic function of total disturbance was not a significantly better fit than the simple linear model (chi-squared = 0.23738, df=1, p=0.6261). Heterogeneity in species composition (average pairwise dissimilarity of quadrats) also showed a positive relationship to total disturbance, although slopes differed among plots (random-slope model; Fig. 3.5). Total disturbance had no significant effect on evenness (random-intercept model, Fig. 3.6).



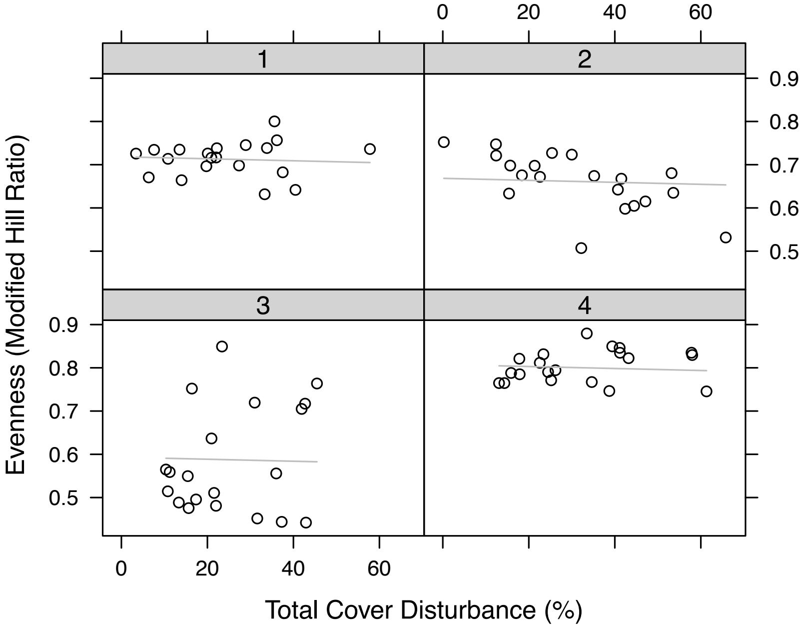
β	SE(β)	F	df	p
0.04577	0.01363	11.27	74	**0.0012**

Figure 3.4. Relationship between total cover of disturbance and transect-level species richness in each of the four plots. Points represent number of species observed per transect. Regression lines for plots have different random-effects intercepts but a common slope (β).



β	SE(β)	d^2	F	df	p
0.00304	0.00153	8.5794e-06	4.01	70	**0.0491**

Figure 3.5. Relationship between total cover of disturbance and heterogeneity index in each of the four plots. Heterogeneity is calculated as the average Bray-Curtis dissimilarity between all pairs of quadrats within each transect. Regression lines for plots have different random-effects intercepts and slopes. The random slope variance (d^2) determines the by-plot variation about the overall population slope (β). The p-value given assesses the null hypothesis that true β is zero.



β	SE(β)	F	df	p
-0.00023	0.00060	0.147	74	0.7025

Figure 3.6. Relationship between total cover of disturbance and evenness index in each of the four plots. Evenness is calculated as the modified Hill ratio $((N_2 - 1)/(N_1 - 1))$ for each transect. Regression lines for plots have different random-effects intercepts but a common slope (β).

Effects of different types of gopher disturbance

Cover of old mounds and castings were correlated within quadrats (Kendall's rank correlation, tau = -0.12256, z = -6.5776, p = 4.782e-11) but uncorrelated at the transect scale (Kendall's rank correlation, tau = 0.08076, z = 1.0556, p = 0.2912). Total plant cover showed significant negative relationships with both forms of disturbance. Total forb cover was not significantly affected by either mounds or casts. Total cover of graminoids, forb/graminoid ratio, and heterogeneity of species composition were all positively correlated with cover of mounds but not with castings. Species richness, however, was positively correlated with castings and approached a significant positive relationship (p = 0.0982) with mounds as well (Table 3.3, with estimated slopes for "intercept + slope" models summarized in Table 3.4).

Table 3.3. Results of mixed-effects models analyzing cover of old mound and cover of casting as additive fixed effects. "Intercept only" models have a common slope across plots for each fixed effect, whereas "intercept + slope" models have different intercepts and slopes for each plot (estimated slopes by plot are summarized in Table 3.4). For intercept + slope models, the random slope variance (d^2) determines the by-plot variation about the overall population slope (β). P-values for both model types assess the null hypothesis that β (the population slope parameter, which describes the overall relationship between explanatory and response variable) is zero.

Response variable/ *Random-effects structure*	**Disturbance type**	**β**	**SE(β)**	**d^2**	**F**	**df**	**p**
Total plant cover	Old mound	-0.4126	0.0913	n/a	23.33	73-77	**<0.001**
Intercept only	Casting	-0.5902	0.1046	n/a	31.86	73-77	**<0.001**
Total forb cover	Old mound	0.0004	0.1039	9.7e-07	0.000	65-77	0.9973
Intercept + slope	Casting	-0.0977	0.5277	1.0435	0.034	65-77	0.8535
Total graminoid cover	Old mound	-0.4403	0.0906	9.9e-03	37.87	65-77	**<0.001**
Intercept + slope	Casting	-0.3536	0.3672	5.0e-01	0.927	65-77	0.3391
Forb/graminoid ratio	Old mound	0.0517	0.0257	0.0022	9.60	65-77	**0.0029**
Intercept + slope	Casting	0.0225	0.0518	0.0101	0.189	65-77	0.6651
Species richness	Old mound	0.0280	0.0187	n/a	2.81	73-77	0.0982
Intercept only	Casting	0.0686	0.0214	n/a	10.33	73-77	**0.0019**
Heterogeneity index	Old mound	0.0014	0.0006	2.1e-09	6.74	65-77	**0.0116**
Intercept + slope	Casting	0.0037	0.0020	1.4e-05	2.03	65-77	0.1592

Table 3.4. Estimated slopes by plot for models with "intercept + slope" random-effects structure. (See Table 3.3 caption for further description of model parameters.) Slopes are approximate estimates, not subject to significance testing or quantitative comparison, and are provided to illustrate the extent of variation between plots in the relationships analyzed. Numbers are shown in bold if the overall population slope β for the given disturbance type and response variable (shown in Table 3.3) was found to be significant.

Response variable/ *Random-effects structure*	**Disturbance type**	**Plot 1**	**Plot 2**	**Plot 3**	**Plot 4**
Total forb cover	Old mound	0.00127	-0.00064	-0.00021	0.00117
Intercept + slope	Casting	0.67421	-0.56903	-1.26618	0.76991
Total graminoid cover	Old mound	**-0.36328**	**-0.49912**	**-0.54762**	**-0.35134**
Intercept + slope	Casting	-0.93851	-0.25934	0.57892	-0.79540
Forb/graminoid ratio	Old mound	**0.01530**	**0.07509**	**0.10537**	**0.01092**
Intercept + slope	Casting	0.07292	0.07415	-0.12382	0.06684
Heterogeneity index	Old mound	**0.00145**	**0.00142**	**0.00135**	**0.00143**
Intercept + slope	Casting	0.00113	0.00247	0.00889	0.00212

Correlograms

For all six variables analyzed (total disturbance, old mounds, castings, total plants, total forbs, and total graminoids), there was high spatial autocorrelation at small spatial scales that quickly dropped to no noticeable correlation within a distance of about 1 m. Correlogram plots can be found in Appendix B.

Chapter 4

Simulation Model of Three-Way Plant Interactions

Introduction

Hypothesis about Phlox dominance may explain variation in graminoid response

In this chapter I will present the methods and results of a simulation model inspired by questions that my field results raised. One of the most surprising findings was that, contrary to my expectations, cover of graminoids did not consistently decline with total disturbance, nor did the ratio of forb to graminoid cover always increase. Jones *et al.* (2008) had found a higher ratio of forb to graminoid cover on mounds than in undisturbed meadow in a previous study at Bunchgrass Ridge, and much of the literature similarly indicates that gopher disturbance places graminoids at a disadvantage relative to forbs (e.g. Mielke 1977, Foster & Stubbendieck 1980, Martinsen *et al*. 1990, Sherrod *et al*. 2005). I had predicted that my findings would confirm this trend.

The predicted random slope coefficients suggest that trends in Plot 3 were the least consistent with these expectations. While my study was not designed to compare plot or meadow characteristics (hence the treatment of plot as a random effect), I did observe qualitative differences between the plots in the process of sampling. In much of Plot 3 *Phlox diffusa* was clearly dominant and had made a thick mat that seemed to be broken up only by gopher disturbance. Under such conditions, perhaps a certain amount of disturbance could actually aid the establishment of graminoids, which would otherwise be crowded out by the *Phlox* – even if elsewhere disturbance would adversely affect the abundance of graminoids.

A modeling approach to exploring the Phlox hypothesis

The simulation model described in this chapter was designed to test my *Phlox* hypothesis. Was it feasible for the presence of a highly competitive plant such as *Phlox* to mediate the nature of the relationship between disturbance and the abundance of another plant species? Could I construct a model in which a graminoid-like species declined with increasing disturbance when *Phlox* was not present, but increased in response to increasing disturbance when *Phlox* was added to the system?

In more general terms, this model can be seen as an extension of the basic conceptual framework behind justifications of the Intermediate Disturbance Hypothesis, which classifies organisms as either good colonizers or good competitors (Connell 1978). Most studies of gopher disturbance categorize plants in a similarly binary fashion: forbs vs. graminoids, annuals vs. perennials (Martinsen *et al.* 1990, Rogers & Hartnett 2001, Jones *et al.* 2008). Here I complicate this basic concept of trade-offs by exploring the interactions of three types of plants located along a spectrum from colonization ability to competitive ability, with forbs considered the best colonizers, *Phlox* the best competitor, and graminoids somewhere in between.

Modeling methods

Description of the model

The basic structure of this model was inspired by other grid-based spatially explicit models of gopher-plant interactions (Moloney & Levin 1996, Seabloom & Reichman 2001). The model universe consists of a square grid of 100x100 cells, with periodic boundary conditions to avoid edge effects. The presence or absence of each plant species in each grid cell is tracked over time. Multiple plant species can occupy the same cell but will compete if they do, resulting in a certain amount of competition-driven mortality. This model contains three plant species: A, which represents non-*Phlox* forbs; B, which represents graminoids; and *Phlox*. Overall abundance of each species is represented as the proportion of grid squares occupied by that species.

The simulation model consists of a gopher disturbance module and a plant community dynamics module. The grid is initialized with each plant species present randomly distributed across the grid at a given initial frequency. Each time step in the simulation begins with the gopher disturbance module, in which gopher disturbance is distributed randomly across the grid at a given rate of proportion of ground surface disturbed per year (G). This occurs in two steps, to reflect some degree of small-scale spatial autocorrelation in the disturbance: 1) "seed" cells are selected randomly across the grid, at a proportion of $G/9$, and 2) the cells immediately adjacent to the seed cells are also designated as disturbed, resulting in 3x3 clusters of disturbance.

The plant community dynamics module begins with mortality due to gopher disturbance. Species B and *Phlox* die if gopher disturbance occurs in a cell occupied by either plant. Species A can either survive or die, depending on E, its probability of emerging from burial (this is based on the hypothesis that one mechanism of forb dominance on gopher mounds is the ability to recover from burial – see Sherrod *et al.* 2005, Case 2011).

The second stage in the plant community dynamics module is plant reproduction. Species A and B both reproduce by dispersing propagules randomly across the grid. To simplify the parameterization of the model, so that it was not necessary to find a suite of appropriate parameters for reproduction, germination, and survival probabilities, I assumed that a propagule automatically becomes a new plant if it lands in a grid square not already occupied by a conspecific. The number of propagules produced per A or B plant is determined by R_A and R_B, their respective reproductive rates. *Phlox* reproduces vegetatively, with each *Phlox*-occupied cell capable of expanding into an adjacent cell not occupied by *Phlox*, with a given probability of vegetative reproduction R_P.

The final stage in the plant community dynamics module is competition-driven mortality. *Phlox*, in this model, does not die from competition, only from gopher disturbance. Species A and B, however, are susceptible to mortality due to the presence of each other and/or the presence of *Phlox* in the same grid square, with a mortality probability assigned to each of these possible interspecific interactions.

I coded this model in R (R Development Core Team 2011). The code used can be found in Appendix C.

Parameterizing the model

Empirically based plant demographic parameters like those typically used in gopher-plant simulations (e.g. Moloney & Levin 1996, Wu & Levin 1994) were not available for this system. Moreover, the goal of this model was not to produce quantitatively sound predictions of meadow dynamics, as might be possible with empirically based parameters, but to determine whether it was possible to produce a certain qualitative pattern given particular assumptions about the system.

With this in mind, I first left *Phlox* out of the model and set out to define a set of parameters for Species A and B that met the initial qualitative assumptions of the model

(A as a better colonizer, B as a better competitor) and produced the expected pattern (in the absence of *Phlox*, B declines with increased disturbance). The superior colonization ability of A was represented by a higher reproductive rate ($R_A > R_B$) and a non-zero probability of recovering from gopher disturbance (E_A). The superior competitive ability of B was represented by an interspecific competition rate C_{BA} (the effect of B on A) higher than C_{AB} (the effect of A on B).

The criteria for acceptable parameters also demanded that A and B be capable of coexisting over the range of gopher disturbance rates (G) that would be tested. Coexistence was defined as both species being present after 100 time steps, which I found to be a sufficient amount of time for the system to stabilize. I set the lower bound of G at 0, and the upper bound at 0.3, a rate at which 30% of the ground surface would be disturbed by gophers per year. We can assume that this figure reasonably exceeds any yearly rate of gopher disturbance that occurs in the meadows I studied, since the maximum total cover of disturbance in any plot was roughly 30% and that represented the accumulation of multiple years of disturbance.

By trial and error I found a set of parameters for Species A and B (Table 4.1) that met all the criteria outlined above. Both plants were initialized at 50% frequency.

Table 4.1. Reproduction and competition parameters for Species A and B.

Parameter	**Value**	**Description**
E_A	0.5	Probability that plant of Species A recovers from disturbance
R_A	6	Number of propagules per plant of Species A
R_B	4	Number of propagules per plant of Species A
C_{BA}	0.2	Probability that Species A dies if it shares a cell with B
C_{AB}	0.1	Probability that Species B dies if it shares a cell with A

Adding Phlox

Once the parameters for Species A and B were set, I held those conditions constant while searching for reasonable parameters for *Phlox*. I postulated that *Phlox* would reproduce by a low rate of vegetative spread (low enough to make it less capable of persisting than Species A and B under high rates of disturbance) and that it would be highly competitive with the other species, with C_{PA} (the effect of *Phlox* on A) greater than C_{BA} (the effect of B on A), and C_{PB} (the effect of *Phlox* on B) greater than C_{AB} (the effect of A on B). The competitive effects of Species A and B on *Phlox* were set to zero.

By trial and error I found a set of parameters for *Phlox* that met the above criteria, and for which all three species coexisted at the rate of gopher disturbance $G = 0.1$. Testing for coexistence ensured that the parameters chosen were at least within the ballpark of reasonable parameters that could describe species that do coexist in nature. I then tested the patterns that emerged given these parameters, running the simulation for 100 time steps for a range of G from 0-0.3 in increments of 0.01. I did this for ten trials and averaged the results (Fig. 4.2). I did the same (averaging over ten trials, each of which consisted of running the simulation for 100 time steps for a range of G from 0-0.3) for a system containing only Species A and B (Fig. 4.1).

Table 4.2. Reproduction and competition parameters for *Phlox*.

Parameter	**Value**	**Description**
F_P	0.25	Initial frequency of *Phlox*
R_P	0.05	Probability that *Phlox* in one cell spreads vegetatively to an adjacent cell
C_{PA}	0.5	Probability that Species A dies if it shares a cell with *Phlox*
C_{PB}	0.3	Probability that Species B dies if it shares a cell with *Phlox*

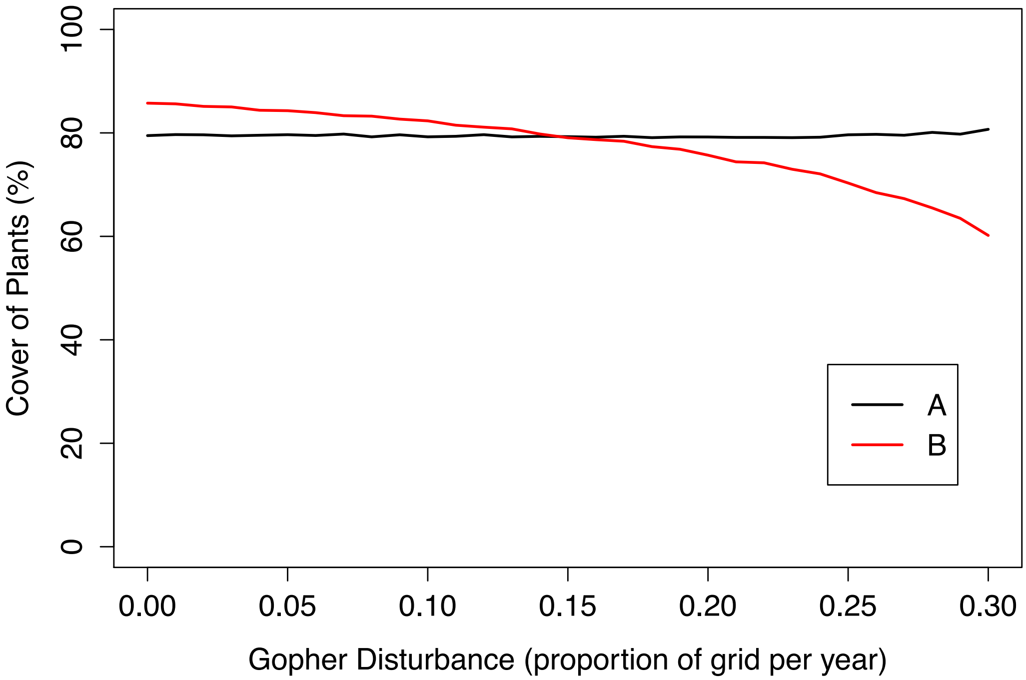


Figure 4.1. Cover of Species A and B, averaged over 10 simulation trials, for a range of gopher disturbance in a system where *Phlox* is absent. Cover data are recorded after 100 time steps of the simulation.

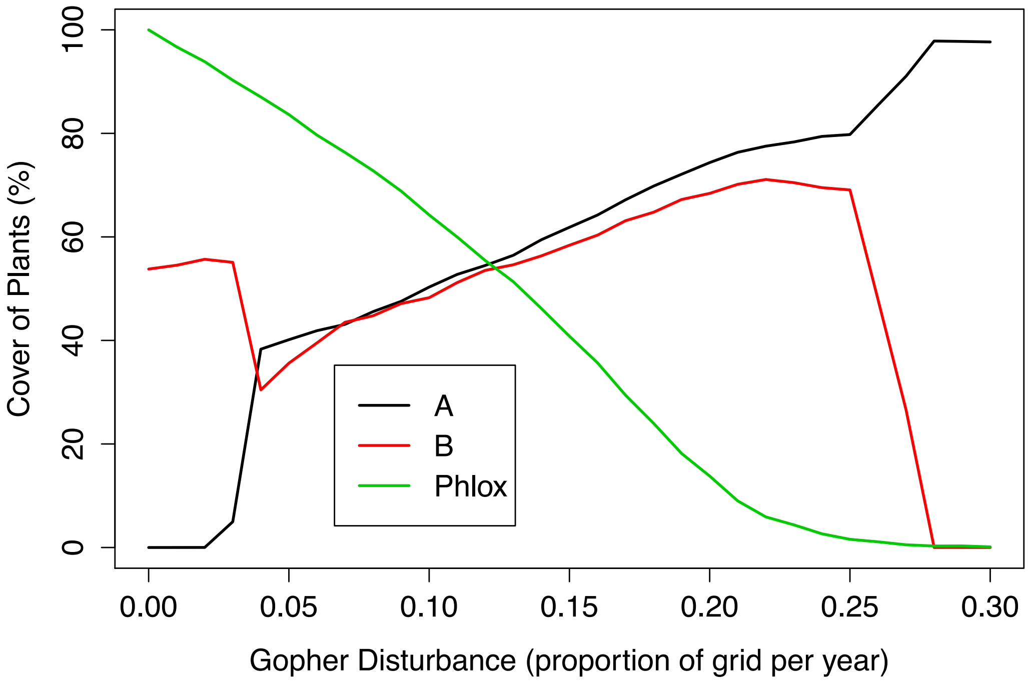


Figure 4.2. Cover of Species A, B and *Phlox,* averaged over 10 simulation trials, for a range of gopher disturbance in a system where all three species are present. Cover data are recorded after 100 time steps of the simulation.

Model findings

Using parameters constructed from a basic set of assumptions, I was able to show that it could be possible for the presence of a dominant species such as *Phlox* to reverse the nature of the relationship between disturbance and graminoids. With reproductive and competitive parameters for Species A and B held constant, I found that when *Phlox* was not present Species B declined with increasing disturbance, but once *Phlox* was added to the system Species B increased over a certain range of disturbance (roughly 0.04 to 0.22).

Phlox shows a monotonic negative relationship with disturbance. Species A was constant in abundance across the range of disturbance tested when only Species A and B were present, and once *Phlox* was added Species A showed a more pronounced positive relationship with disturbance. At the outer limits of the range of disturbance tested in the three-species case, the hypothetical system is less stable and only one or two species can persist (presenting, consequently, an illustration of the Intermediate Disturbance Hypothesis). Species A is absent for very low rates of disturbance (up to about $G = 0.04$, at which point the abundance of Species B drops because Species A is also present and competing for space). For roughly $G > 0.27$, both Species B and *Phlox* disappear or nearly disappear and Species A dominates.

Chapter 5

Discussion

This study sought to investigate the effects of gopher disturbance on plant community structure in montane meadows at Bunchgrass Ridge, Oregon. Two primary goals were (1) to explore relationships at larger spatial scales than previously studied in this system (Jones *et al*. 2008), and (2) to assess the contributions of the two main forms of disturbance—mounds and castings—to these relationships. The effects of castings were of particular interest because relationships between castings and vegetation have not been studied before. As a way of explaining unexpected variation in the relationships between disturbance and vegetation among individual plots, I also created a simulation model that showed how the presence of a particularly competitive species could alter these relationships. In this chapter I will interpret my findings, discuss their broader implications, and suggest additional studies that could inform our understanding of the role of gopher disturbance in the community structure of montane meadows.

Castings are a considerable form of disturbance

One objective of this study was to explore the contributions of mounds and castings to the broader effects of disturbance on plant communities. Gopher castings are a striking feature of higher-altitude meadows, where extensive winter tunneling can occur in a deep, long-lasting snow pack. The effects of castings on plant communities have so far been ignored in the literature, perhaps because they are not present in the lowland communities where most studies of gopher-plant interactions have been conducted, or because they are a more ephemeral form of disturbance and are less conspicuous than mounds once meadow vegetation matures. The only mentions of castings I have found do not explore their potential effects on vegetation (Reichman 2007, Knight 2009). Upon observing the ubiquity of castings at Bunchgrass, however, I hypothesized that the castings would have an impact on plants.

I found that plant cover was negatively correlated with cover of mounds and cover of castings. This finding indicates that castings are a significant form of gopher disturbance that impacts plants and should not be ignored. Castings are abundant at Bunchgrass, covering about 10% of the ground surface on average and making up roughly one-third to one-half of all gopher disturbance present in each meadow sampled. The remainder of gopher disturbance sampled consisted mainly of old mounds, which had been created at least one year previously. The two types of disturbance are different in several notable ways, which I will explore further as these differences relate the interpretation of my findings. Mounds are deeper and longer-lasting, and the soil composition of mounds and castings appears to differ. The mounds and castings sampled also differed in age; old mounds had been created in the previous growing season or earlier (in effect, integrating over multiple years of past disturbance), whereas castings were created more recently over the course of the winter.

Fresh mounds that had formed in the current growing season were extremely infrequent in the plots, even during vegetation sampling in July and early August. I observed a greater abundance of fresh mounds beginning to appear in the meadows in mid-August, just before I concluded vegetation sampling. Given these observations, it seemed likely that most mound-forming activity occurs in late summer to fall. This agrees with reports from lowland prairies in Western Washington, which share the same pattern of summer drought common in higher-elevation grasslands in the Pacific Northwest, that *Thomomys mazama* is most active when fall rains begin (G. Olson, pers. comm.). In July 2004, however, Jones *et al*. (2008) found that 33% of mounds intersected by line transects across three meadows at Bunchgrass were fresh mounds. Snow melt occurred unusually late in the summer when I conducted my study, with snow pack persisting into mid-June in some meadows. Perhaps these conditions affected the level of gopher activity in early summer because the period of time between snow melt and summer drought was shortened. The plant cover I observed could easily have differed had there been more fresh mounds present, but my findings are still useful for assessing the effects of castings and older mounds.

Spatial correlation patterns show clumping at small scales

Cover of mounds and castings were correlated with each other within quadrats (20 cm x 20 cm), but uncorrelated on the scale of transects (5 m x 20 cm). This correlation at small spatial scales may be due to gophers tunneling around or through mounds as a means of structural support under the snow. Elsewhere in the meadows I observed castings built up next to fallen logs and the bases of trees, possibly for the same reason.

For each form of disturbance – as well as for total plant, forb, and graminoid cover – I also found high spatial autocorrelation at distances < 1 m. Given that mounds are typically much less than 1 m in diameter (Jones *et al.* 2008), this finding suggests that mounds are clustered spatially. The finding of similar autocorrelation patterns among cover of disturbance and plant variables could mean that the spatial structure of gopher disturbance determines the spatial patterns of plant abundance, or vice versa. This could also be a coincidence, however, as there are plausible reasons intrinsic to disturbance and plants for why each would show autocorrelation at that scale: mounds could be correlated within 1 m because multiple mounds are created around the same gopher hole; plant cover could be correlated within 1 m because plants spread clonally or have limited seed dispersal distances. Regardless, my findings of spatial autocorrelation for both forms of disturbance add to the existing literature on similarly clustered patterns found in other grassland systems (Thomson *et al.* 1996, Klaas *et al.* 2000, Wolfe-Bellin & Moloney 2000, Overton & Levin 2003).

Disturbance effects on forbs and graminoids

As expected, plant cover declined with increasing total disturbance. The relationships between total disturbance and forb and graminoid cover, however, appeared inconsistent across plots, with no significant overall relationship found for either forbs or graminoids or the ratio between the two. These non-significant overall relationships may be related to a high degree of variability among plots in the slopes that describe the relationships. Random slope coefficients suggested that graminoids did not decline with disturbance in Plot 3, in contrast to apparent declines in the other three plots, and that forbs (whether or not *Phlox* was included as a forb), declined with disturbance in some plots but increased in others. The ratio of forb to graminoid cover, consequently, was also not consistent across plots.

Many other studies (including the previous study at this site) have found that gopher disturbance benefits forbs relative to graminoids (Mielke 1977, Foster &

Stubbendieck 1980, Martinsen *et al*. 1990, Sherrod *et al*. 2005, Jones *et al.* 2008), so I had expected to find similar relationships in my plots, particularly for the forb/graminoid ratio. All previous studies of gopher disturbance, however, have focused only on mounds (ignoring castings), so it is thus possible that lack of consistency with the literature in my analyses simply reflects differences in the definitions of "disturbance." Breaking down total disturbance into the different types of disturbance present, we see that the relationship between mounds and relative abundances of growth forms is consistent with previous studies. Graminoid cover was negatively correlated with mound cover and consequently the forb/graminoid ratio increased with mound cover. Castings, meanwhile, had no significant effect on either graminoids or the forb/graminoid ratio. These results suggest that the neutral or variable effect of the castings on graminoids masks the strong negative relationship between mounds and graminoids when both forms of disturbance are summed.

There is still the question of what might explain non-significant relationships between castings and the relative abundance of different growth forms. Castings did have a strong negative relationship with total plant cover, so the answer is not that castings were not affecting plants at all, but that relationships with individual growth forms were not consistent. The differing slopes predicted for graminoids vs. castings across the four plots mirrored the variability in slopes found for graminoids vs. total disturbance (negative in Plots 1, 2, and 4, and positive in Plot 3), and likewise for the suggested relationships between the forb/graminoid ratio and castings (positive in Plots 1, 2, and 4, and negative in Plot 3). It is also worth noting that neither mounds nor castings affected forb cover significantly, which is also likely due to variability among plots, given that the predicted slopes are positive for some plots and negative for others. We can examine these findings in two ways: first, why might castings and mounds have different effects on vegetation, and second, why might growth form relationships with disturbance vary among plots?

A likely answer to the first question is that mounds and castings differ in size and longevity, which could explain some of the differences in how the two forms of disturbance affect vegetation. Mounds tend to be larger than castings in diameter and height; mounds are typically round or oblong and range from 20-50 cm in diameter and 5-25 cm in height (Reichman 2007) while castings are long and skinny, typically 5-10 cm across and no more than a few cm in height. While castings are assimilated into the meadow matrix relatively quickly, most likely within a single growing season (Halpern, pers. comm.), mounds can last for years before the gradual process of weathering and re-vegetation obscures them (Reichman 2007). In combination, the greater size and longevity of mounds might present more substantial barriers to re-emergence from burial for graminoids, if vegetative recovery is an important factor in differentiating between forb and graminoid responses. Sherrod *et al.* (2005) hypothesized that the relative success of forbs in colonizing mounds in alpine tundra at Niwot Ridge could be attributed to their greater belowground carbohydrate stores, which facilitated emergence from burial.

My own observations of excavated root systems of plants growing on mounds suggest that many of the forb species in these meadows appear capable of recovering from burial. I have found examples of *Iris chrysophylla, Lupinus latifolius, Cirsium callilepis, Hieracium gracile*, *Erigeron aliceae*, and *Comandra umbellata* where old root systems could be found 5-10 cm below the surface of the mound (at the former ground surface) and plants had sent up emergent shoots and developed new clusters of roots near the new soil surface. The only graminoid that I found exhibiting this trait, by contrast, was the highly rhizomatous sedge *Carex pensylvanica*, a dominant species in these meadows. Other graminoid species – *Bromus carinatus, Danthonia intermedia*, and *Festuca idahoensis* – that I excavated from mounds had shallow fibrous root systems and appeared to have colonized the mounds by seed. On mounds, the ability of forbs to emerge from burial and persist in a location where they are already established could give them an advantage. Castings, however, may be shallow enough that even graminoids buried by castings can survive, and as a result the ratio of forbs to graminoids may not be affected by castings even if plant cover is reduced.

Another key distinction is that the mounds and castings analyzed in this study represent disturbances of different ages. Because fresh mounds were virtually absent, I was comparing old mounds, which had been present since at least the previous growing season and possibly multiple years previous, and recent castings, which had appeared at the beginning of the current growing season. Considering the age differences of the two types of disturbance, it is not surprising that their effects differ. Old mounds and castings represent different moments in the process of succession. As fresh sites of disturbance, the main effect of recent castings may be simply to reduce plant cover indiscriminately. Old mounds are at a slightly later point in the process of re-vegetation, where plants have had a chance to respond but differences between growth forms in their early success on mounds are still apparent. Combining this observation with the differences in size and longevity of disturbance types noted above, we can hypothesize that castings may transition quickly from a state with no plant cover to a state at which all plant species have had a chance to re-vegetate castings, with the result that castings do not modify species composition as appreciably as mounds do.

The second question raised by my findings is why the relationships between different growth forms and disturbance might vary across plots or meadows. One plausible explanation is that growth form categories do not capture all of the relevant variation in plant traits that determine responses to disturbance. The species abundance data in Table 3.2 illustrate that while plots shared many species in common, no two plots contained exactly the same collection of species in the same abundances. Within each growth form, there is still substantial variation in many plant traits that may affect susceptibility to or resistance to effects of burial: large forbs that stand taller than their neighbors (*Lupinus latifolius, Hieracium gracile*) and small forbs that grow underneath other plants (*Arenaria macrophylla, Viola nuttallii*); non-rhizomatous bunchgrasses (*Festuca idahoensis, Stipa occidentalis*) and highly rhizomatous sedges (*Carex pensylvanica*). Species within a growth form could vary tremendously in growth rates, modes of reproduction, and strength of competition with other species, so we cannot assume that all species within a growth form will show the same relationship to disturbance. The overall relationships between disturbance and total cover of growth forms, therefore, might vary depending on the particular combination and relative abundance of species present in each meadow.

Modeling results

The simulation model presented in Chapter 4 offers another possible explanation for variability in patterns of graminoid response to disturbance. Motivated by my observations that *Phlox* appeared particularly dominant in Plot 3, where the data also suggested a neutral or positive relationship between disturbance and graminoids, the model shows that the prevalence of a highly competitive species such as *Phlox* can potentially alter the nature of the relationship between disturbance and other plant species. The graminoid-like species in the model, Species B, declined with higher yearly rates of disturbance when *Phlox* was absent, but benefited from higher rates of disturbance when *Phlox* was present. This shift occurs about because *Phlox* is a poor colonizer after disturbance, and a better competitor than Species B if not disturbed. With only Species A and B present, Species B was the best long-term competitor in the system, so it benefited from lower rates of disturbance. When *Phlox* was present, however, the *Phlox* dominated the meadow unless gopher disturbance created openings; under these conditions, the abundance of Species B was largely determined by how many gaps were opened in the *Phlox* matrix, so Species B showed a general trend of increasing with disturbance.

The model simplifies many aspects of this meadow ecosystem, and without information on actual growth and reproduction rates of the species involved it is not possible to demonstrate that it represents the true interactions that structure these communities. It does illustrate, however, that disturbance effects may depend on the species composition of each meadow and where each species falls on the hypothetical spectrum from “good colonizer” to “good competitor”. A highly competitive dominant species has the potential to alter the relationships between other species and disturbance.

Effects of disturbance on diversity

In addition to effects on growth-form abundance, I was also interested in the relationship between disturbance and species diversity and whether the Intermediate Disturbance Hypothesis could apply to these meadows. I found a positive relationship between species richness at the scale of transects and total cover of disturbance. Spatial heterogeneity (variation in species composition), which can be considered another aspect of diversity, also showed a positive relationship with total disturbance. Evenness (calculated as a modified Hill ratio) was uncorrelated with total disturbance, which agreed with the previous finding in this system of no difference in evenness between mounds and undisturbed meadow (Jones *et al.* 2008). Examination of the scatterplots of evenness index vs. disturbance by plot, as well as the finding that a random slope term did not improve the fit of the model, suggested that there was no relationship in any plot (rather than differing relationships among plots as with some of the other response variables).

It is unclear whether my richness results are consistent with the Intermediate Disturbance Hypothesis. In this study, cover of disturbance reflects both frequency and intensity of disturbance; because mounds can last multiple years, a high cover of disturbance could result from gopher activity that is either more frequent, or more intense in spatial extent within a single year. The relationship I found between richness and disturbance was best modeled with a positive linear relationship, whereas the IDH predicts a humped relationship that peaks at intermediate levels of disturbance (Connell 1978). However, since none of the transects exceeded 60% total disturbance, it could be argued that I did not sample a broad enough range of disturbance to be able to observe a peak or decline in richness associated with greater cover of disturbance. Indeed, along a spectrum from 0-100% disturbance, 60% could be considered approximately intermediate. If a transect were 100% disturbed, one can imagine that plant cover would be so minimal that a high species richness would be unlikely, so it is plausible that richness would indeed decline for cover of disturbance greater than the maximum sampled in this study.

Comparing my findings on diversity-disturbance relationships to those of Jones *et al.* (2008) requires a consideration of scaling effects. Jones *et al.* (2008) found greater species richness in small quadrats in undisturbed vegetation than on mounds (young or old), from which they inferred a pattern of gradual accumulation of species as mounds age. If we simplify this result to one of disturbed vs. undisturbed patches on a small scale, disturbed patches contain fewer species than undisturbed patches, which suggests a negative relationship between disturbance and species richness.

In my study, however, I found a positive relationship between disturbance and species richness at the transect scale. Does this finding contradict Jones *et al.* (2008)? Not necessarily, if we consider the role of spatial heterogeneity, which Auerbach & Shmida (1987) argue becomes a more important factor in determining richness as the spatial scale of inquiry begins to exceed the size of any individual organism. Jones *et al.* (2008) found that species composition differed more between quadrats on mounds than between quadrats in undisturbed vegetation, and based on this result hypothesized that on a larger scale gopher disturbance would increase spatial heterogeneity in meadows. My finding that the transect-scale compositional heterogeneity increased with disturbance supports this hypothesis.

We can think of a transect as consisting of an aggregation of many small disturbed and undisturbed patches. An individual patch of disturbed meadow might contain fewer species than its undisturbed neighbor. Any two disturbed patches, however, are more likely to contain unique species (Jones *et al.* 2008). This implies that a greater amount of disturbance increases the potential for rarer species to establish, leading to greater heterogeneity of composition as well as a richer assemblage of species at the transect scale. In this way, it is possible to reconcile the small-scale findings of Jones *et al.* (2008) with my larger-scale findings. My findings reinforce the notion that diversity-disturbance relationships seen in nature are highly dependent on the spatial scale of inquiry (Chaneton & Facelli 1991).

Heterogeneity in species composition was positively correlated with mounds, while the effect of castings was insignificant. This result may have emerged from the greater impact mounds seem to have on the relative abundance of major growth forms, which would help make quadrats containing mounds more compositionally different from other quadrats in a transect. Species richness, however, was positively correlated with cover of castings, while only marginally significant in its relationship with mounds. This finding is more difficult to explain. One possible justification is that the soil composing mounds and castings may have been excavated from different depths. As noted in the description of the methods, castings contained fewer small stones and more bits of organic matter such as small pieces of grass. This seems to indicate that much of the soil that makes up castings comes from tunnels excavated at the interface between the snow and the ground surface. Thus castings might be more likely to contain viable plant parts or seeds that have been transported by the gophers from elsewhere in the meadow, resulting in an enrichment of the number of species present in a transect. Given that the soil seed bank is relatively poor in these meadows, however (Lang & Halpern 2007), the possibility of castings containing numerous relocated propagules is fairly unlikely. The near-significance of the effect of mounds on richness suggests that in this case, the physical differences between mounds and casts are probably not particularly important, and with a greater sample size we might find that both forms of disturbance contribute significantly to an increase in richness.

Future directions

Long-term and experimental studies

Montane meadows are dynamic systems. There is only so much we can learn, consequently, from the static snapshot of meadow conditions gained in this observational study, or even from the chronosequence approach used by Jones *et al*. (2008), which used a comparison of mounds of different ages as a proxy for observation through time. Long-term studies of gopher impacts in other systems have proven very informative, particularly in illustrating how gopher disturbance and plant community dynamics can vary from year to year and interact with fluctuations in climate (Hobbs & Mooney 1991, Wolfe-Bellin & Moloney 2000, Forbis *et al.* 2004). Further study at Bunchgrass Ridge or similar study sites should allow for the possibility of observing changes through time, ideally over multiple years (my transects are still marked, so there is in fact an existing opportunity for re-sampling gopher disturbance and vegetation at Bunchgrass). In particular, observation of succession on mounds and castings over time would allow for clearer comparisons between the two types of disturbance, avoiding the confounding effects inherent in this study's comparisons of recently created castings to mounds at least a year old.

Another limitation of the observational approach used in this study is that it makes causal inference difficult, especially given the potential for feedback mechanisms between gophers and plants. I treated gopher disturbance as the explanatory variable and plant community characteristics as the response variables, but it is conceivable that the distributions of plants could also determine where, and to what extent, the gophers create disturbance. Indeed, multiple studies have considered how the distribution of gopher disturbance can be seen as a non-random response to the distribution of plants, whether because gophers preferentially dig their burrows in areas populated by the plants they prefer to eat (Seabloom & Reichman 2001), or because gophers avoid digging through the ground underneath plants with more obstructive root systems (Watts 2010). By simply observing the patterns of gopher disturbance and associated plant cover, it is difficult to say for sure how much the gophers are influencing the plants or vice versa.

Fortunately, there is potential for experimental manipulations, which can help unravel cause-and-effect relationships. Studies in other systems have investigated factors driving gopher preferences in digging location by monitoring gopher response to fertilization treatments (Tilman 1983) and by establishing monocultures of common plants to compare which species seem to invite greater gopher activity (Eviner & Chapin 2003). Conversely, to isolate gopher disturbance as the cause and plant response as the effect, Sherrod *et al*. (2005) created artificial gopher mounds using soil from fresh mounds, which allowed them to measure pre-treatment vegetation and directly observe which species were most successful at recovering from burial over the course of a year. Such an approach could potentially be applied at Bunchgrass Ridge as well. This was, in fact, my original research plan (Case 2011), but time constraints and a lack of fresh mounds early in the summer made it infeasible. An experiment that involved creating gopher mounds and measuring the vegetation on them a year later, or even over the course of multiple years, could give us a more precise understanding of the path of succession on mounds.

Studies of plant regenerative traits

As a potential explanation for the variation in growth-form response among plots, I suggested that individual species within each growth form could vary greatly in the traits that determine their disturbance responses. Consequently, a more detailed understanding of key differences in regenerative and other functional traits could provide insight into what drives patterns of plant community response to gopher disturbance. One important avenue of exploration would be a more systematic study of the belowground characteristics of plants via excavations of plants experiencing different amounts of natural disturbance (as suggested in Case 2011). Such excavation studies have been conducted in forest environments of the Pacific Northwest, illustrating the ways in which belowground characteristics of understory species are important to patterns of successional change (Antos & Halpern 1997, Lezberg *et al.* 1999). An artificial mound experiment, as outlined above, could also allow for focused monitoring and excavation of particular species to determine patterns and relative rates of lateral growth and emergence from burial.

More realistic modeling approaches

The simulation model I designed as part of this study was an initial, relatively simple attempt to better understand this system better through modeling. My model was conceived of as a qualitative test of a hypothesis using parameters invented to match the starting assumptions, which works to show that a proposed relationship between *Phlox*, graminoids, and disturbance is theoretically possible. This model could be modified to better reflect the processes that determine survival and reproduction following disturbance. The characterization of reproduction by Species A and B as a random dispersal of propagules over the grid that are guaranteed to germinate and survive is a simplification that was used to streamline the process of finding reasonable parameters for A and B. Given the prevalence of vegetative reproduction in this system, a major step in improving this model would be to modify the mechanism of reproduction of all species involved, not just *Phlox*, to better reflect vegetative processes. In addition, most models of gopher-plant interactions have made use of parameters drawn directly or indirectly from empirical studies, allowing more confident conclusions about how their results apply to the real world (Hobbs & Hobbs 1987, Moloney & Levin 1996, Wu & Levin 1994). My model should be seen as a starting template, into which actual parameters for growth, competition and reproduction could be inserted to produce results that are more quantitatively applicable.

Conclusions

My results show that mounds and castings both impact plants. Future studies of how gopher disturbance affects plants should take care to consider the role of castings, which has been ignored until now. Comparisons between mound and casting relationships with plant response variables, and my finding of inconsistency in some of these relationships among plots, illustrate that interactions between disturbance and community composition are variable and complex. The physical and temporal distinctions between mounds and castings as well as differences in species composition among meadows can all play a role in determining the patterns that emerge. As my simulation model demonstrates, it is conceivable for the presence or absence of a highly competitive species to drastically change the nature of disturbance-vegetation relationships.

My study also illustrates important considerations of spatial structure in gopher disturbance. I found a high degree of clumping in gopher disturbance and plant cover at small spatial scales, which leads to a spatially heterogeneous landscape overall. Hence the spatial scale at which we observe patterns of diversity and heterogeneity matters greatly, as illustrated by the contrast between my findings and those of Jones *et al*. (2008) regarding the relationship between disturbance and species richness.

The montane meadows at Bunchgrass Ridge, like many natural systems, are driven by non-equilibrium dynamics. This study helps show how persistent disturbance can play a critical role in shaping the structure of plant communities.

Appendix A

Brief Overview of Mixed Effects Models

A mixed effects model is a statistical model that combines both fixed and random effects. Mixed effects models are useful for avoiding pseudoreplication in analyzing clustered data, which is what I had in this study with multiple transects sampled per plot. The fixed component accounts for the overall relationship between the explanatory variable(s) of interest and the response variable, while the random component accounts for variation among individuals or plots. A typical formulation of a linear mixed effects model is thus:

$$\mathbf{Y}_i = \mathbf{X}_i \times \beta + \mathbf{Z}_i \times \mathbf{b}_i + \varepsilon_i$$

Here, $\mathbf{Y}_i$ is the response variable, $\mathbf{X}_i \times \beta$ is the fixed component (the parameter β has no index because it applies across all individuals), $\mathbf{Z}_i \times \mathbf{b}_i$ is the random component, and ε_i is the random error term. Like ε_i, the term $\mathbf{b}_i$ is assumed to be an i.i.d. normally distributed random variable; we are assuming, essentially, that individual variation about the central tendency of the population is normally distributed with a certain variance (Zuur *et al.* 2009).

Linear mixed effects models can be constructed with different random effects structures: random intercept only, or random intercept and slope. In a random intercept model, the intercept is allowed to vary by individual, but there is no variation in slope about the overall population slope β. In a random intercept and slope model, both intercepts and slopes are allowed to vary according to random effects (Zuur *et al.* 2009). In this study I used random intercept and slope models unless a likelihood-ratio test showed that the random intercept only model presented an equally good or better fit to the data.

The question of how best to calculate a p-value for the significance of a fixed effects term in a mixed effects model is debated. Douglas Bates, creator of the lme4 package in R, declines to include an output of p-values in the lmer() function (the function I used for my analysis) because he argues that the calculation of denominator degrees of freedom used by mixed effects model functions in other statistical programs is suspect (Bates 2006). Bates recommends using Markov Chain Monte Carlo sampling to estimate a p-value for fixed effects; the function designed to do this, however, has not yet been developed to work with random intercept and slope models with correlated random effects, so it was not applicable to many of my analyses. As an alternative I used the pamer.fnc() function from the LMERConvenienceFunctions package (Tremblay 2011), which deals with the issue of uncertain degrees of freedom by calculating a plausible upper and lower bound on degrees of freedom and finding p-values accordingly.

Appendix B

Correlogram Plots

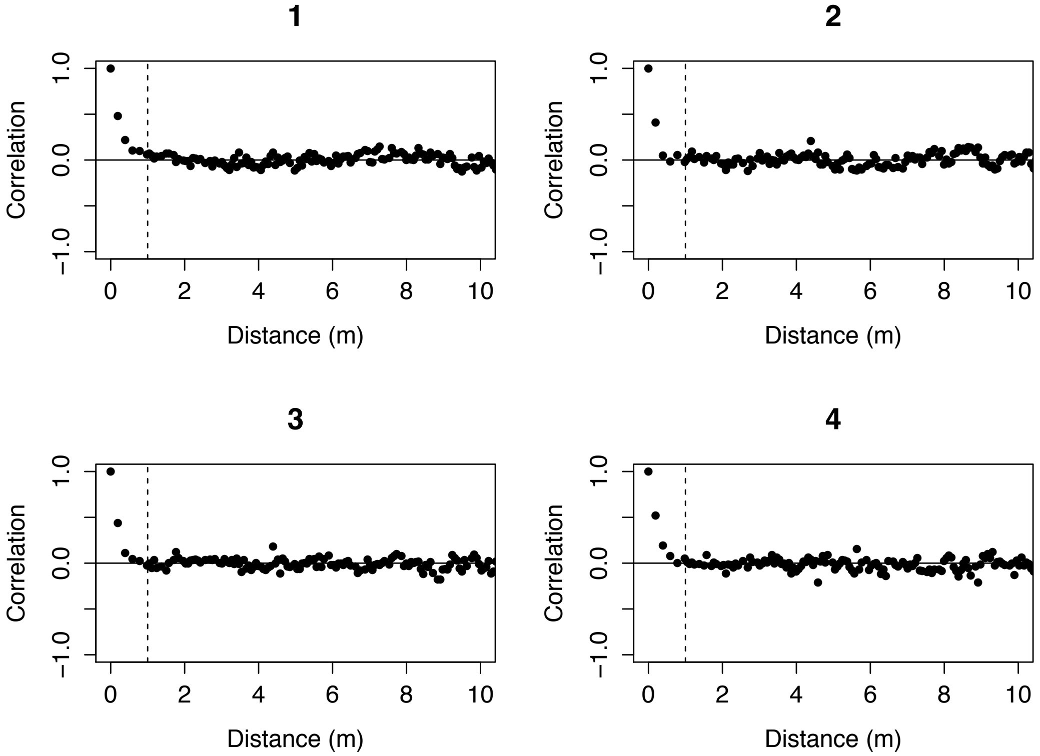


Figure B.1. Spatial correlograms of total cover of disturbance, by plot. Dotted vertical line delineates 1-meter distance.

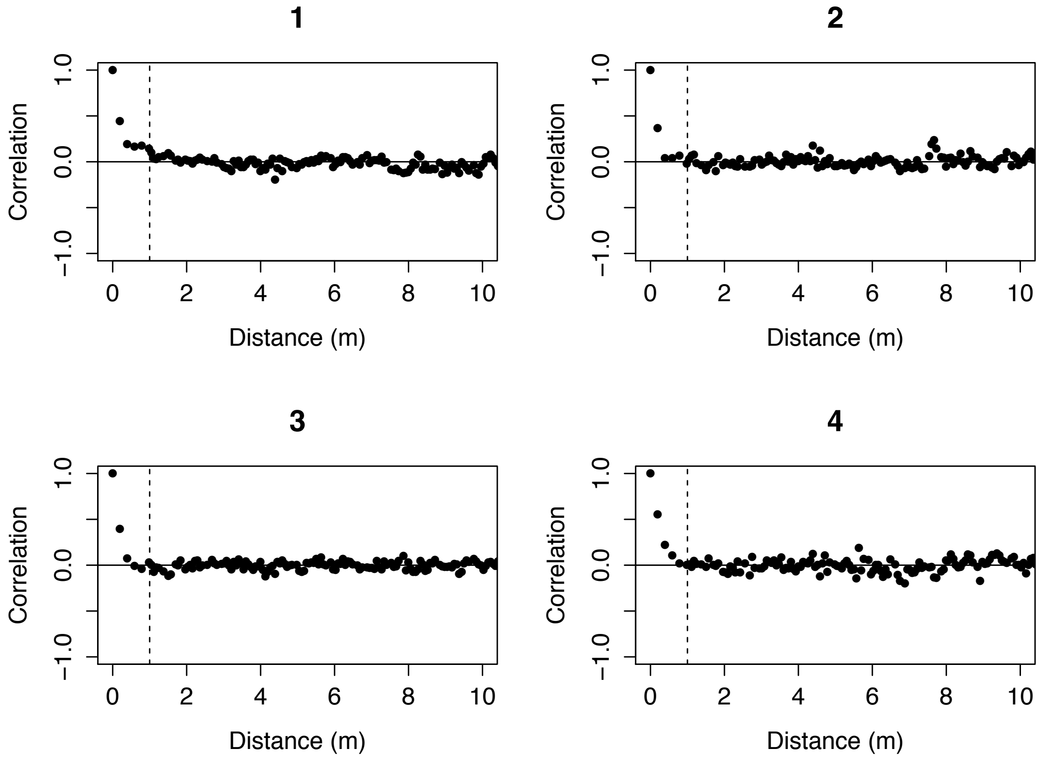


Figure B.2. Spatial correlograms of cover of old mounds, by plot. Dotted vertical line delineates 1-meter distance.

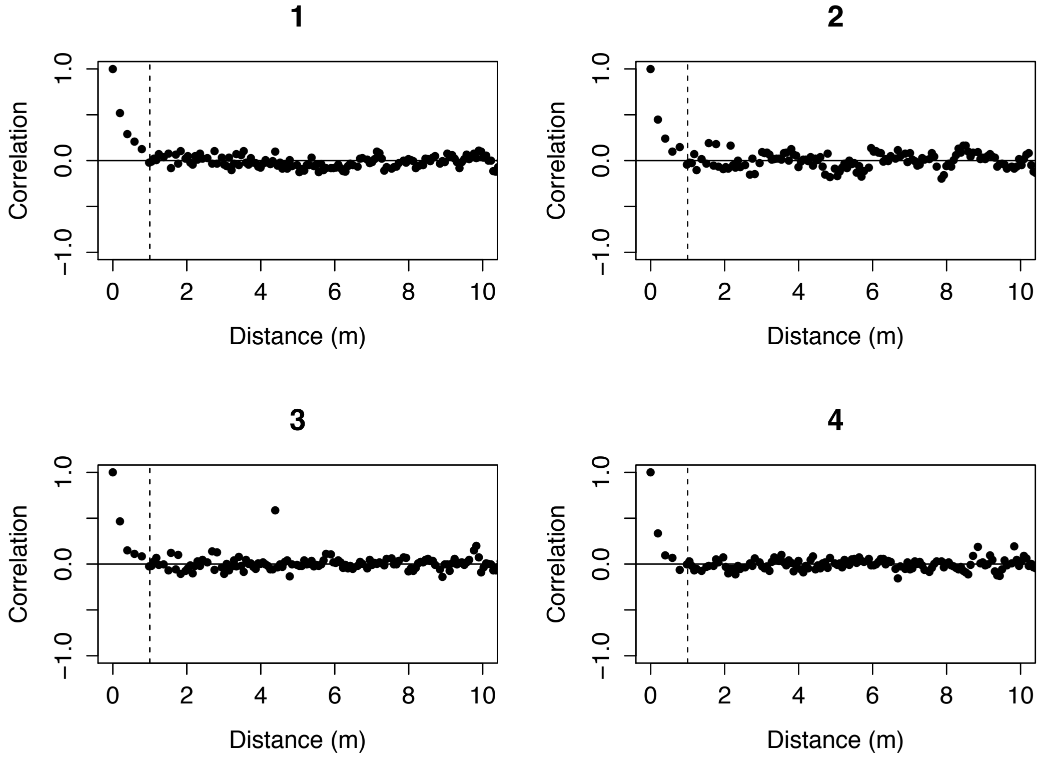


Figure B.3. Spatial correlograms of cover of castings, by plot. Dotted vertical line delineates 1-meter distance.

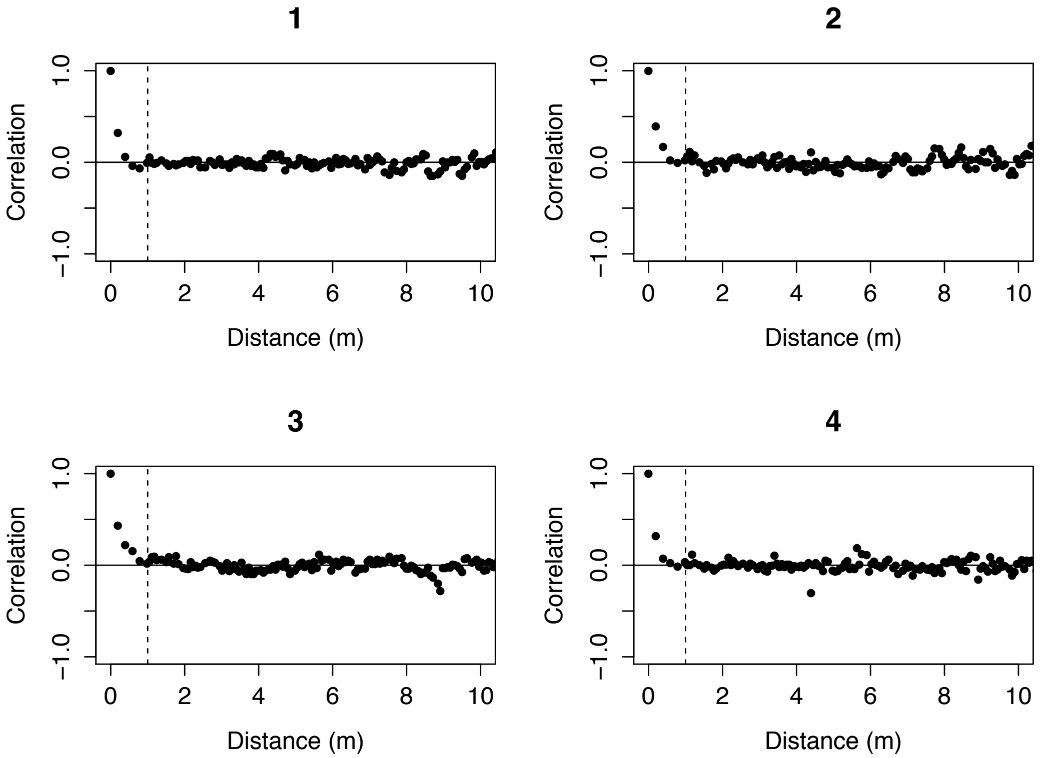


Figure B.4. Spatial correlograms of total cover of plants, by plot. Dotted vertical line delineates 1-meter distance.

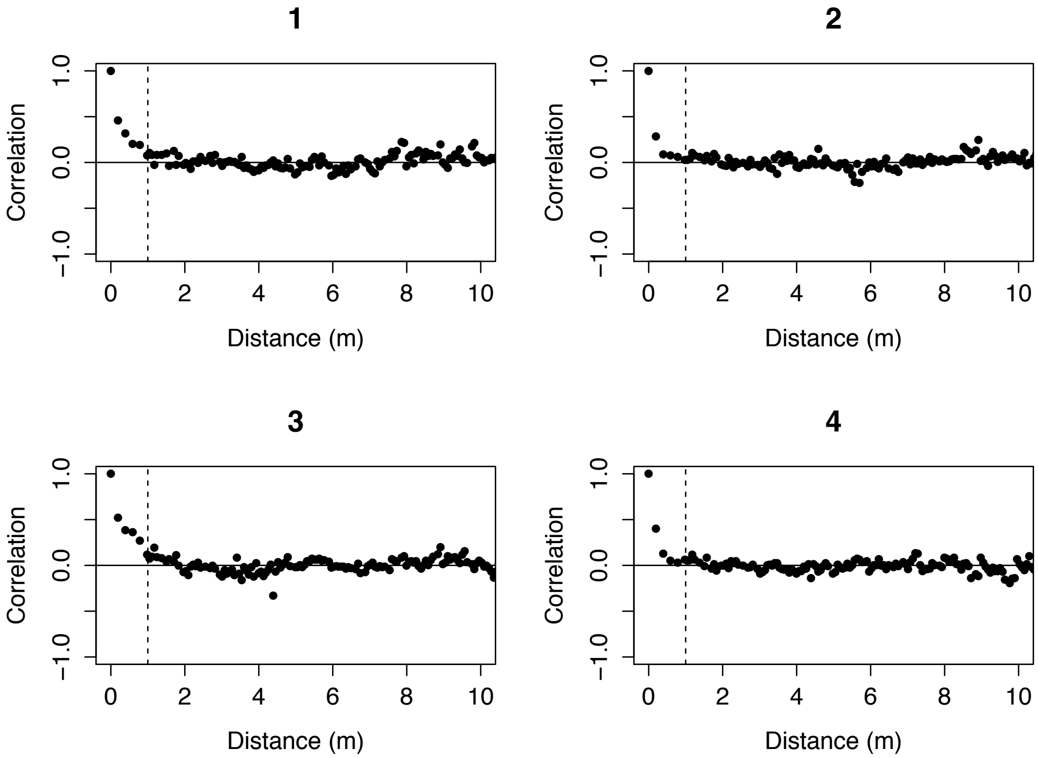


Figure B.5. Spatial correlograms of total cover of graminoids, by plot. Dotted vertical line delineates 1-meter distance.

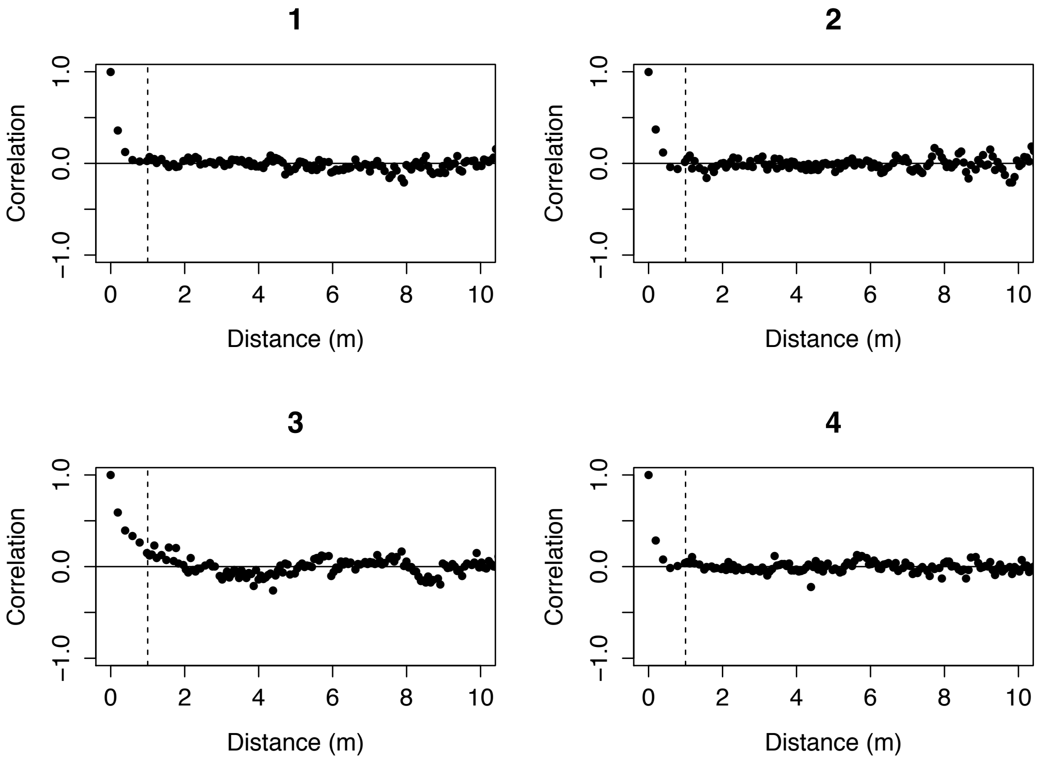


Figure B.6. Spatial correlograms of total cover of forbs, by plot. Dotted vertical line delineates 1-meter distance.

Appendix C

Simulation Model Code

```
###### Model set-up ######
# Periodic boundary conditions for a 100x100 universe - 3-cell buffer
margins <- function(N) {
  edges <- matrix(rep(0,11236),nrow=106)
  edges[4:103,4:103] <- N
  edges[1:3,4:103] <- N[98:100,]
  edges[104:106,4:103]<-N[1:3,]
  edges[4:103,1:3]<-N[,98:100]
  edges[4:103,104:106]<-N[,1:3]
  edges[1:3,1:3]<-N[98:100,98:100]
  edges[104:106,104:106]<-N[1:3,1:3]
  edges[1:3,104:106]<-N[98:100,1:3]
  edges[104:106,1:3]<-N[1:3,98:100]
  edges}

# Creates array of 3 100x100 matrices for storing plant data
P = array(0, dim=c(100,100,3))


###### Parameters ######
# Phlox presence or absence (0 or 1)
Phlox_presence = 0
# Reproductive rates (A, B)
R = c(6,4)
# Phlox vegetative growth rate
Phlox_growth = 0.05
# Emergence survival rates (chance of recovering from burial)
Emergence_A <- 0.5
# Competition
Competition_BA = 0.2 # effect of species B on species A
Competition_AB = 0.1 # effect of species A on species B
Competition_PA = 0.5 # effect of Phlox on species A
Competition_PB = 0.3 # effect of Phlox in species B
# Starting frequencies of plants (A, B, Phlox)
Plant_Frequency = c(0.5,0.5,0.25)


###### Running the simulation ######
# Number of trials
trials <- c(1:10)
# Range of gopher disturbance rates over which to run each trial
Goph <- seq(0,0.3,0.01)
# Number of time steps
time <- 100

# Initialize matrix and array to store plant abundance data
traces <- matrix(rep(0,3*length(Goph)),nrow=3)
traces.array <-
array(rep(traces,length(trials)),dim=c(3,length(Goph),length(trials)))
```

```
# Initialize disturbance matrix
M <- matrix(rep(0,10000),nrow=100)

# Run simulation
for (tri in trials) {
  print(tri)
    for (G in Goph) {
      print(G)

      # Initializes distribution of plants
        for (i in 1:3) {
          N = rep(0,10000)
          N[sample(1:10000, size=10000*Plant_Frequency[i])] = 1
          P[,,i] = matrix(N,nrow=100)
          }

        for (t in 1:time) {

          # Gophers make disturbance in 3x3 clusters
          M <- 1*(matrix(runif(10000),nrow=100)<(G/9))
          if(sum(M)>0) {
            mt <- margins(M)
            m_ind <- which(M!=0,arr.ind=TRUE) + 3
            for (i in 1:nrow(m_ind)) {
              mt[(m_ind[i,1]-1):(m_ind[i,1]+1),
                 (m_ind[i,2]-1):(m_ind[i,2]+1)] <- 1
            }
            M <- mt[4:103,4:103]
          }
          M0 <- array(rep(M,3),dim = c(100,100,3))

          # Determine where species A will recover from burial
          Emergence_matrix <-
             1*(M*matrix(runif(10000),nrow=100)<Emergence_A)*M*(N==1)

          # Erase plants where gopher disturbance happened, except
            where species A recovers from burial
          P <- P*(1-M0)
          P[,,1] <- P[,,1] + Emergence_matrix

          # Species A and B reproduce
          for (i in 1:2) {
            seeds <- sum(P[,,i])*R[i]
            P[,,i] <- 1*((P[,,i] +
               matrix(rpois(10000,lambda=seeds/10000),nrow=100)) > 1)
          }

          # Phlox reproduces
          if (Phlox_presence>0) {
            # Compute neighborhood density of Phlox for every cell
            nt <- margins(P[,,3])
            tots <- matrix(rep(0,10000),nrow=100)
              for (ai in 4:103) {
                for (bi in 4:103) {
                  tots[ai-3,bi-3] <- nhood(nt,ai,bi)
                }
              }
```

```
            # Fill some unoccupied cells with Phlox via vegetative
              growth
            Veg <- 1*(P[,,3]==0)*
               (matrix(runif(10000),nrow=100)<(Phlox_growth*tots))
            P[,,3] <- P[,,3] + Veg
          }

          # Plants compete and die
          D1 = 1*((1*(matrix(runif(10000),nrow=100)<Competition_BA)*
            (P[,,2]==1) +
            1*(matrix(runif(10000),nrow=100)<Competition_PA)*
            (P[,,3]==1))>0)
          D2 = 1*((1*(matrix(runif(10000),nrow=100)<Competition_AB)*
            (P[,,1]==1) +
            1*(matrix(runif(10000),nrow=100)<Competition_PB)*
            (P[,,3]==1))>0)
          P[,,1] = P[,,1]*(1-D1)
          P[,,2] = P[,,2]*(1-D2)

          # Record plant abundance data
          traces[,which(Goph==G)] <- apply(P,3,sum)

  }
  }

  # Save traces from trial
  traces.array[,,tri] <- traces
}

# Average traces across trials
traces.average <- apply(traces.array,1:2,mean)

# Plot plant abundances vs. gopher disturbance
plot(Goph,traces.average[1,]/100,type="l",ylim=c(0,100),col=1,lwd=2,xla
b="Gopher Disturbance (proportion of grid per year)",ylab="Cover of
Plants (%)")
lines(Goph,traces.average[2,]/100,col=2,lwd=2)
if (Phlox_presence>0) {lines(Goph,traces.average[3,]/100,col=3,lwd=2)}
```

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