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Effects of Grizzly Bear Digging on Alpine Plant Community Structure

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Abstract

In Alaskan alpine tundra, grizzly bears excavate deep holes in search of ground squirrels, but few studies have tested the importance of grizzlies, or other large mammals, in maintaining plant community structure. We examined 43 bear digs, asking how they affect plant species richness and diversity, recolonization patterns, and plants with different clonal growth strategies. Bears remove most vegetation from digs, and recovering digs had lower species richness than adjacent mature tundra. Mature tundra alone, however, had significantly fewer species than mature tundra and bear digs combined, suggesting that bear digs contribute to the overall richness of tundra communities. Digs develop the highest plant richness and diversity at intermediate ages, but even in new digs the overall species composition is similar to adjacent tundra. Plants of different clonal growth forms reacted differently to bear digs. The two species significantly more common in digs than elsewhere have a nonspreading (phalanx) clonal habit, whereas five of six plant species significantly more common in mature tundra are capable of rapid, diffuse (guerrilla) clonal growth. Overall, bear digs cause less pronounced effects on community composition than mammalian diggings in some other systems, possibly because subarctic alpine tundra is already characterized by high levels of abiotic disturbance.

Introduction

“Keystone species” and the true extent of their role in controlling community structure remain important and controversial topics in ecology (Mills et al., 1993; Power et al., 1996). These issues have particular urgency in conservation biology, especially for understanding the community-wide importance of vertebrate species often targeted by conservation efforts. Although the keystone species concept was originally applied to predators (Paine, 1969), more recent studies have documented the importance of animal-induced disturbance for maintenance of plant community structure (Platt, 1975; McKendrick et al., 1980; Hobbs and Mooney, 1985; Williams et al., 1986; Whicker and Detling, 1988; Gutterman et al., 1990; Shachak et al., 1991). In addition, more speculative studies have suggested that mammalian disturbance may have had large-scale effects on plant communities in the past (Mack and Thompson, 1982; Owen-Smith, 1987; Zimov et al., 1995).

Together, these studies are important in revealing the mechanisms that may maintain plant species diversity and also in emphasizing the importance of animal conservation in maintaining the overall structure of natural ecological communities. It has become increasingly clear that the influence of disturbance on community structure, including disturbances caused by animals, can often be best understood in light of differential impacts on plant species with varying life histories (Bengtsson et al., 1994; Boeken and Shachak, 1994; Huston, 1994; Tilman, 1994; Tilman et al., 1994). Like keystone predators, disturber species may effect local reductions in the abundance of competitive dominants, thus allowing competitively inferior species to establish and reproduce. In any single community, this often means favoring species with certain life histories over ones with alternative strategies. However, few studies have linked disturbance effects with differences in clonal growth form, even though both empirical (Bulow-Olsen et al., 1984; Schmid and Harper, 1985; Schmid, 1986; de Kroon et al., 1992; Price and Hutchings, 1996) and theoretical (Lovell and Lovell, 1985; Crawley and May, 1987; Sutherland and Stillman, 1988) studies have illustrated the important role of clonal growth in mediating plant

competition. Ultimately, generalizations about the effects of biotic disturbances, particularly those caused by large mammals, still rest on very few case studies.

Here we document the effects of grizzly bears (*Ursus arctos*) on the plant community structure of Alaskan alpine tundra. The varied foraging behaviors of grizzly bears include frequent excavation of holes in search of ground squirrel (*Spermophilus parryi*) prey. These excavations, which are typically much deeper than those created in search of plant food (Butler, 1992), are conspicuous and relatively long lasting in the alpine landscape. Their impact on plant community structure, however, has not been previously described. Therefore, we investigated the effects of grizzly bear digs on mature alpine plant communities, with special reference to the differential effects of disturbance on plants with differing growth forms. In particular, we asked the following questions: (1) How does the species richness and diversity of bear digs compare with those of neighboring mature tundra? (2) How does that relationship evolve over the life of the dig? (3) Do bear digs influence community structure, at least in part, by differentially favoring plant species with particular clonal forms?

Methods

STUDY AREA

We made observations in the Wrangell and Chugach Mountains, two heavily glaciated mountain ranges within the Wrangell–St. Elias National Park and Preserve of south-central Alaska. The regional climate is transitional between maritime and continental, with long, cold winters and short, moderately warm growing seasons. Regional mean annual temperature is -4°C , and mean annual precipitation is 60 cm—distributed fairly evenly throughout the year (Hulten, 1968). Alpine tundra communities are found at elevations between 1100 and 2500 m and are subject to a variety of abiotic (avalanches, frost heaving, solifluction, and landslides) and biotic (digging by various mammals and localized trampling by Dall sheep, mountain goats, and human visitors) disturbances.

All alpine plant communities in this region are dominated by perennial species (there were no annuals in our study plots) with at least some clonal growth. To group plants by clonal type, we used a modified form of the binary classification of “guerrilla” versus “phalanx” clonal strategies (Lovett Doust, 1981). Formally, we distinguished between the two strategies by asking whether daughter ramets are typically placed outside the parent ramet’s canopy on long rhizomes or stolons (guerrilla species) or remain tightly clustered under the parent (phalanx species). This system allows comparison of large numbers of species with contrasting sizes and morphologies. We further distinguished between plants that maintain their overwintering shoot meristems above ground (Raunkiaer’s phanerophytes/chamaephytes) or below (hemicyptophytes/geophytes). We therefore used four categories of clonal form: above- or belowground guerrilla species, and above- or belowground phalanx species. To classify plant species in this manner, over the course of several years we excavated multiple individuals of each species found in the sampling quadrats. If a species was highly variable, we excavated a large number of individuals before making a classification.

Scott (1974a) and Viereck et al. (1992) have developed detailed alpine plant community classifications for this region, but most communities grade into one another across the small spatial scales we studied, making an elaborate classification scheme difficult to use. Instead, we broadly stratified our study sites into two plant community types: “snowbeds,” characterized by cold summer temperatures, long snowpack duration, and wet soils; and “mesic meadows,” characterized by relatively warmer summer temperatures, a longer growing season, and drier soils. Despite considerable variation of species composition within these two broad categories, the presence or absence of late-lying snowbeds is considered a primary determinant of gross community composition in alpine plant communities (Detwyler, 1974; Scott, 1974b) and provided a simple system with which to stratify our samples. In our study area, snowbeds are typically dominated by *Saxifraga punctata*, *Salix polaris*, and *Luetkea pectinata*. Mesic meadows are characterized by *Vaccinium vitis-idaea*, *Pyrola secunda*, and *Artemisia arctica*.

BEAR DIGS

We focused on the disturbances caused by grizzly bears in their pursuit of arctic ground squirrel prey. Although grizzly bears also dig for plant roots (primarily *Hedysarum* spp.), those digs—where only the top layer of sod is removed—are significantly and recognizably different from what we describe here: deep excavations of sod and mineral soil in pursuit of squirrels. These digs range in size from less than 1 to nearly 20 m², exposing bare ground with little or no vegetative matter remaining. As a consequence, recolonization of digs proceeds both by clonal growth from the edges and from seedling establishment (pers. obs.). As in other digging systems (Platt, 1975; Gutterman et al., 1990) grizzly bear digging creates both depressions and mounds of displaced sod. We focused on the depressions, or digs, because these appear to be less transitory (pers. obs.). Sod mounds are frequently grown through by underlying vegetation within the same year as the dig and are much harder to delineate after even 2 yr (pers. obs.). Arctic ground squirrels are ubiquitous in alpine areas of this region, and bears will apparently dig wherever they are present. Our observations suggest that dig sites are determined more by a bear’s presence for other reasons (e.g., convenient travel routes) than by factors intrinsic to a particular microsite.

DATA COLLECTION

During the 1989, 1992, and 1993 growing seasons, we collected data from bear digs and neighboring mature tundra in both plant

community types. A total of 103 0.5 × 0.5–m quadrats were sampled. Most quadrats were sampled in pairs consisting of a quadrat centered within a bear dig and another in a randomly chosen area of mature tundra (apparently undisturbed by bears) within 3 m of the dig. Forty-two of these paired quadrats were sampled, along with an additional 19 unpaired quadrats (mature tundra = 18, bear dig = 1). Sampling sites were chosen opportunistically; most digs encountered were sampled. In an exception to this rule, no more than 2 digs were sampled from sites where we found numerous digs of the same estimated age and in close proximity. Although these sites indicate that bears frequently spend one or more days in a restricted area making a large number of digs, we never found two or more bear digs overlapping each other. We also measured the dimensions of an additional 24 digs to estimate the volume of material excavated by grizzlies. The minimum horizontal dimension of these digs ranged from 0.3 to 3.0 m, indicating that for most digs there would be little difference in the magnitude of edge effects when sampled by our 0.5 by 0.5–m quadrats.

The occurrence and percent cover of all vascular plant species found in each quadrat were recorded, as were the percent cover of bare ground, rocks >2 cm, mosses, and lichens. For cover estimates, quadrats were subdivided into 25 1-dm² squares, and total percent cover was estimated by the proportions of these 1-dm squares covered by a species within the quadrat. Species present at very low abundances were assigned a cover value of 0.4%. Frequency (the number of 1-dm squares in each quadrat within which a species occurred) was also recorded. Plants that were not clearly identifiable to species were designated by either a number (e.g., “unknown #1”) or a genus (e.g., “*Carex* spp.”). All quadrats were sampled after 29 June in each year to ensure that the plants exhibited close to maximum aboveground biomass at the time of sampling.

ANALYSIS

In all analyses, species richness is reported as the number of distinct vascular plant species, and diversity is reported as the Shannon-Weaver diversity index $-\sum p_i \ln(p_i)$, where p_i is the proportion of total plant cover accounted for by species i (Shannon and Weaver, 1963). Mosses and lichens were not included in these analyses. For the simple grouped comparisons of plot means (Table 1), we include distinct but unknown vascular plant species and use all plots (both paired and unpaired). To evaluate the marginal increase in community richness contributed by bear digs (Fig. 1), for each pair of plots we compared species richness in the mature tundra quadrat alone with species richness of the mature tundra and bear dig quadrats together. Because the latter measure of richness is based upon twice the sampling area and in all cases a larger number of individual plant observations, we used rarefaction to normalize richness values. Rarefaction is a probabilistic sampling technique (originally formulated by Sanders [1968]; see Gotelli and Graves [1996]) that allows standardization of species richness estimates for samples with differing numbers of individuals. Using a rarefaction routine from the software package EcoSim (Gotelli and Entsminger, 2001), we used measured frequencies of all vascular plants to calculate rarefied richness for tundra/dig plots: the number of plant species we would expect to encounter if we had examined the same number of individual plants that we actually observed in tundra plots alone. Mean richness values were then compared using a paired 2-sample t-test. Unpaired plots were excluded from this analysis.

Having no direct estimate of the age of each dig, we use total vascular plant cover in a dig as a relative index of age since disturbance (square-root transformed for normality). Effects of bear digs on richness and diversity over time are presented as pairwise richness ratios [RR = $\ln(R_{bd}/R_{mt})$] and diversity ratios [DR = $\ln(D_{bd}/D_{mt})$], where R_{bd} and R_{mt} refer to the richness in a bear dig plot and its paired mature tundra

TABLE 1

Summary statistics for 103 plots (25-dm² each) examined between 1989 and 1993 in the Wrangell and Chugach Mountains, Alaska. Vascular plant species richness and Shannon-Weaver diversity are summarized for all plots combined, and for plots stratified either by disturbance type (mature tundra or bear digs) or by plant community (snowbed or mesic meadow)

	N Plots	Richness total	Richness		Diversity	
			Plot mean	SD	Plot mean	SD
Mature tundra	60	88	13.80	4.21	1.23	0.54
Bear digs	43	62	10.49	3.92	1.28	0.59
Snowbed	47	62	12.54	3.71	1.18	0.49
Mesic meadow	56	81	12.42	4.92	1.32	0.61
All plots	103	91	12.96	4.39	1.25	0.56

plot, respectively, and likewise for diversity. This approach allows us to compare the richness and diversity of each bear dig to nearby undisturbed tundra, hence reflecting the marginal contribution of a dig to its immediate surroundings and controlling for site-specific differences in species richness and diversity. Ratios are log-transformed for normality, so values greater than 0 indicate higher richness (or diversity) in bear digs. We use multiple regression to look for the effects of plant cover and plant community type (snowbed or mesic meadow) on richness and diversity ratios. Regressions use data from all paired plots, testing models with linear or quadratic functions of square-root plant cover (in the bear digs, as a surrogate for age) with and without community type. Unpaired plots and unknown species were excluded from this analysis.

Effects of digs on plant community composition were examined using the Sorensen Coefficient of Community [$C_s = 2C/(A + B)$], where A and B are the number of species in bear digs and mature tundra, respectively and C_s is the total number of species in common between the two (Mueller-Dombois and Ellenberg, 1974). After examining the Sorensen Coefficient (i.e., similarity of species composition, C_s) between each bear dig quadrat and its paired mature tundra quadrat, we compared those values to the typical within-community similarity of mature tundra. To do this, we calculated C_s for every possible combination of mature tundra plots within each plant community type and used the mean as an expected within-community similarity.

To detect plant species strongly associated with either mature tundra or bear digs, we tested for significant differences between bear digs and mature tundra in the ranked percent cover of individual plant species using Kruskal-Wallis one-way analysis of variance. Finally, we examined changes in proportional cover of different clonal types between mature tundra and adjacent bear digs, testing for significant changes with paired 2-sample t-tests.

Results

A total of 91 vascular plant species were identified in 103 study plots (Table 1). Of these, all but 4 were identified at least by genus (most by species). In total, 88 species were found in mature tundra, compared with only 62 in bear digs. In new digs, grizzly bears had excavated an average of 0.41 m³ of soil, removing virtually all vascular plant cover. Digs varied widely in surface area and ranged from 0.25 to 0.77 m in depth. Over time, plants recolonize bear digs, but the total vascular plant cover in digs (averaged among all digs we sampled) was still much less (22.2%, standard deviation [SD] 18.1) than in nearby mature tundra (47.6%, SD 17.4). Mature tundra plots have higher average plant species

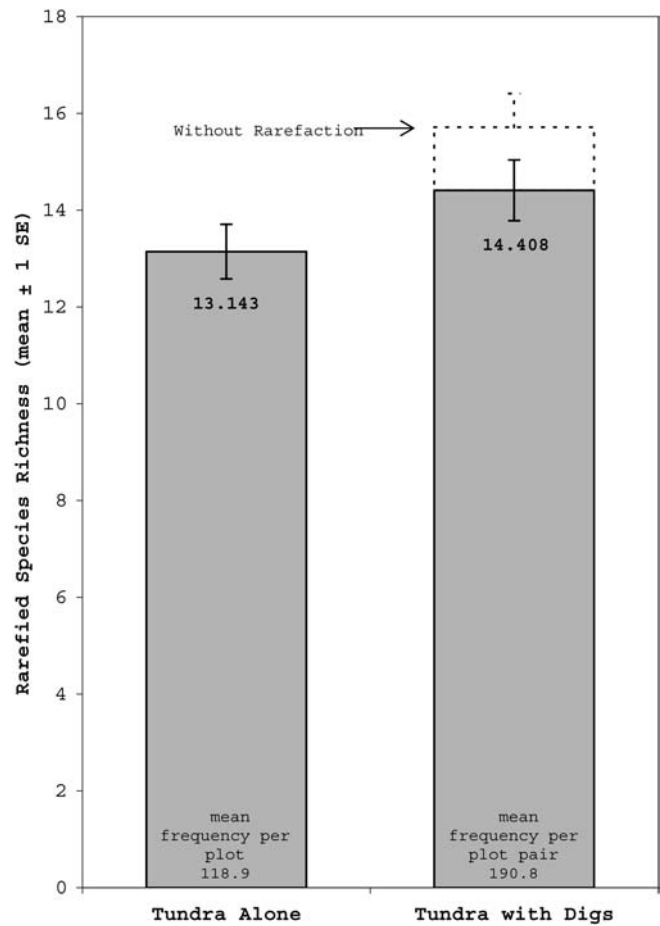


FIGURE 1. Plant species richness of undisturbed mature tundra compared to paired richness of mature tundra with bear digs. Values shown are means and standard errors from 42 plots (tundra alone) or 42 plot pairs (tundra with bear digs). Richness values for each tundra/dig pair were rarefied to compensate for their greater observation frequencies (mean combined frequency for paired plots = 190.8; for tundra alone = 118.9; see text for details). The unrarefied mean is shown with a dashed line for comparison. Means are significantly different (paired samples t-test, $df = 41$, $P < 0.001$).

richness (13.8, SD 4.2) than bear dig plots (10.5, SD 3.9), and very slightly lower mean species diversity (1.3, SD 0.6) than bear digs (1.2, SD 0.5). Comparing the two plant community types, without regard for bear dig disturbance, species richness and diversity were marginally higher in mesic meadows (Table 1).

Focusing on paired plots only, we next asked whether bear digs provide a marginal increase in plant species richness at any given site. The combined richness of mature tundra with bear digs was in fact greater than the richness of mature tundra alone (Fig. 1), even after rarefaction to account for greater frequencies of individual plant observations in paired plots (mean frequency for paired plots = 190.8; for tundra alone = 118.9). Although the absolute difference was relatively small (14.4 compared with 13.1 species), the relationship was significant (paired 2-sample t-test, $df = 41$, $P < .001$) and did not change if computed separately for each of the two plant community types.

We found significant effects of plant community type and vascular plant cover on the richness and diversity of bear digs (Fig. 2), which in all cases are plotted as log-ratios that compare individual digs to their mature tundra neighbors. Increasing plant cover (a proxy for increasing time since disturbance) had significant positive effects on the species richness of bear digs—as a linear function in mesic meadow

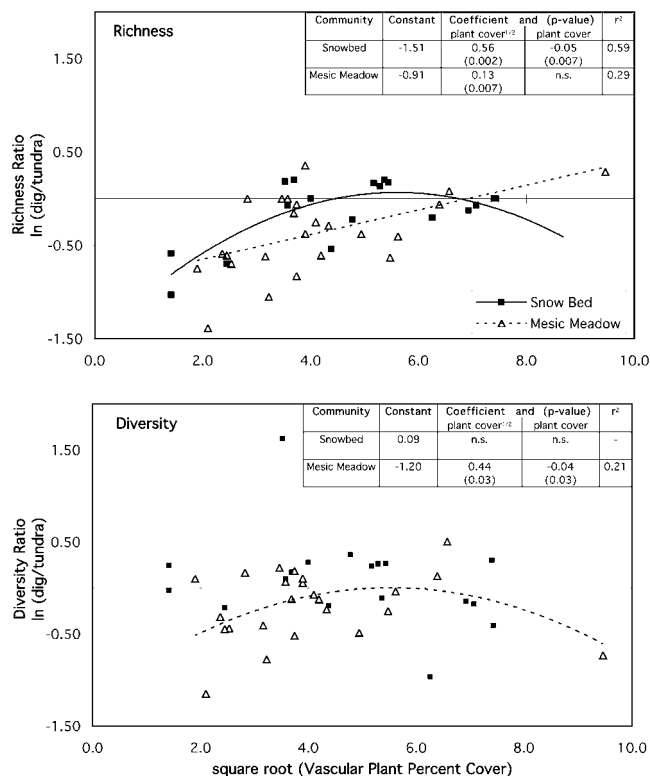


FIGURE 2. Two measures of plant community diversity on bear digs relative to adjacent mature tundra, plotted against each bear dig's vascular plant cover (a proxy for time since disturbance). Upper panel shows results for total plant species richness; lower panel shows Shannon-Weaver diversity index. Graphed values are log-transformed ratios of paired measurements (bear digs:mature tundra); ratios <0 indicate bear digs were less rich and/or diverse than adjacent mature tundra. Data are plotted separately for snowbed (squares and solid lines) versus mesic meadow communities (triangles and dashed lines). Regression curves indicate significant effects; there is no significant effect of percent cover on diversity for snowbed communities (mean diversity ratio = 0.09). Insets show regression statistics in upper right of each panel. Plant cover is square root transformed for normality.

community ($r^2 = 0.29$, $P < .05$) and as a unimodal function in the snowbed community ($r^2 = 0.59$, $P < .05$). Similarly, species diversity within bear digs was a unimodal function of vascular plant cover in mesic meadows ($r^2 = 0.21$, $P < .05$), showing the highest diversity at intermediate dig ages. We found no significant relationship between diversity and plant cover in the snowbed community.

From the time of first colonization, species composition of bear digs is very similar to immediately adjacent mature tundra. Interestingly, the species composition of bear digs shows no tendency to become either more or less similar to neighboring tundra over time: comparing bear digs to adjacent mature tundra, the Sorensen Coefficient shows no significant trend with increasing vascular plant cover (Fig. 3). The mean value is high, however (0.68), especially when compared with the typical Sorensen Coefficient obtained in comparisons between mature tundra plots of either plant community type: snowbed (0.42) or mesic meadow (0.37). In other words, the species composition in a given plot of mature tundra will commonly exhibit more resemblance to a neighboring bear dig than to other, more distant patches of similarly undisturbed tundra.

We were able to classify 69 plant species by clonal type, which included the vast majority of all individual plants sampled. Of the remaining (unclassified) plants, only two had a mean frequency of

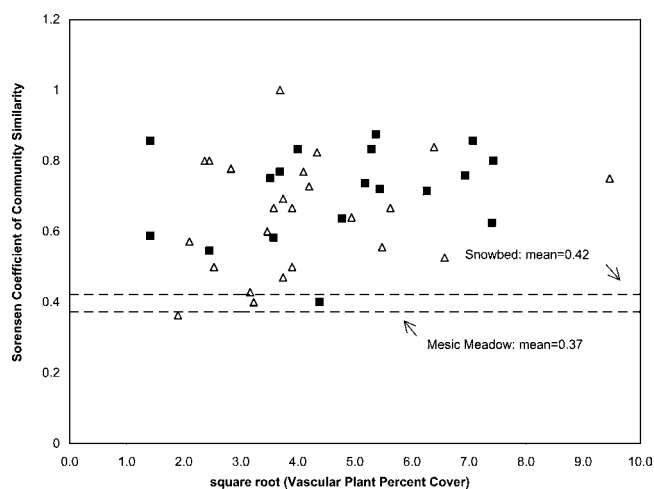


FIGURE 3. Similarity in plant community composition between bear digs and adjacent mature tundra, plotted against each bear dig's vascular plant cover (a proxy for time since disturbance). Values from mesic meadow plant community are shown as filled squares; snowbed values are hollow triangles. Mean Sorensen Coefficients are also shown, as horizontal lines, for the within-community comparisons of mature tundra plots in snowbed and mesic meadow communities. These are means of comparisons between all possible pairings of mature tundra study plots. Plant cover is square root transformed for normality.

per-plot occurrence greater than 0.5: unknown grasses (10.6/plot) and *Luzula spp.* (2.6/plot). Of those we classified, there were notably fewer plant species in the aboveground, guerrilla clonal type, but these conspicuous spreading plants were the first- or second-most common species on a disproportionately large number of plots in both mature tundra and bear digs (Table 2). Overall, belowground, phalanx species were most frequently the first- or second-most common, and aboveground, phalanx species were least frequently dominant. At this coarse level, no single clonal type clearly dominated either bear digs or mature tundra. However, in most study plots the clonal form of the second-most common species was different from that of the most dominant species (analyses not shown), implying that spatially varying abiotic conditions did not intrinsically favor one clonal form over others.

We also used the paired tundra/dig plots to compare the changes in relative cover of different clonal types as a result of bear digging (Fig. 4). In the snowbed plant community type, all but one clonal type increased their relative cover on bear digs. Aboveground guerrilla plants, which accounted for more than 50% of the plant cover on mature tundra, decreased significantly on bear digs ($P < .05$). Plants in the mesic meadow plant community type showed a different pattern, with the two most common clonal types on mature tundra actually increasing slightly on bear digs. These increases in coverage by the two belowground clonal types were not statistically significant, however.

Two plant types were significantly more common on bear digs than in mature tundra (Table 3). These two—*Minuartia spp.* and *Epilobium anagallidifolium*—are both of the nonspreading, phalanx clonal type. Three additional species, also of the phalanx type, were completely absent on mature tundra, but they were too rare (in bear digs) for this pattern to be considered significantly different. In contrast, six plant species were significantly more common in mature tundra. Five of these belong to the spreading, guerrilla clonal type: *Viola spp.*, *Anemone parviflora*, *Campanula lasiocarpa*, *Salix polaris*, and *Equisetum scirpoides*. Only one phalanx species—*Antennaria spp.*—was significantly more common on mature tundra. Twenty-nine species were found only in mature tundra plots, but so rarely that we cannot consider their absence from bear digs significant.

TABLE 2

Vascular plants identified and classified into one of four clonal types in mature tundra and grizzly bear digs. Unclassified species are not shown. Species are grouped by clonal type, and the number of quadrats in which a given species was first or second most common (by % cover, including ties) is indicated

	Tundra		Bear Dig		
	1st	2nd	1st	2nd	
Aboveground, phalanx					
<i>Cassiope Stelleriana</i>		1			heather
<i>Cassiope tetragona</i>	1	1			heather
<i>Cerastium</i> spp.					mouse-ear chickweed
<i>Dryas octopetala</i>	2	1	1		dryas
<i>Empetrum nigrum</i>	1	1		1	crowberry
<i>Lycopodium selago</i>					clubmoss
<i>Minuartia</i> spp.				1	sandwort
<i>Salix reticulata</i>	1				netleaf willow
<i>Salix phlebophylla</i>					skeleton-leaf willow
<i>Saxifraga bronchialis</i>					spotted saxifrage
<i>Saxifraga oppositifolia</i>					purple mountain saxifrage
<i>Selaginella sibirica</i>	2	1		1	spikemoss
<i>Sileneiac aulis</i>					moss campion
<i>Stellaria</i> spp.					chickweed
<i>Vaccinium uliginosum</i>					blueberry
<i>Vaccinium vitis-idaea</i>					cranberry
Aboveground, guerrilla					
<i>Luetkea pectinata</i>	15	2	9	2	luetkea
<i>Lycopodium alpinum</i>	3	3		1	alpine clubmoss
<i>Salix polaris</i>	9	10	2	1	willow
Belowground, phalanx					
<i>Aconitum delphinifolium</i>					monkshood
<i>Anemone narcissiflora</i>					narcissus anemone
<i>Antennaria</i> spp.					pusstoe
<i>Aquilegia formosa</i>					columbine
<i>Artemisia arctica</i>	11	15	7	8	wormwood
<i>Castilleja hyperborea</i>					paintbrush
<i>Castilleja unaslaschcensis</i>					paintbrush
<i>Dodecatheon frigidum</i>					shooting star
<i>Epilobium anagallidifolium</i>		2	15	9	willow herb
<i>Erigeron humilis</i>					fleabane
<i>Festuca altaica</i>					fescue
<i>Gentiana glauca</i>					glaucus gentian
<i>Gentiana propinqua</i>					gentian
<i>Geranium erianthum</i>		5			geranium
<i>Heracleum lanatum</i>					cow parsnip
<i>Hieracium triste</i>					hawkweed
<i>Lupinus arcticus</i>					arctic lupine
<i>Mertensiana paniculata</i>	2			2	bluebell
<i>Polygonum viviparum</i>					bistort
<i>Ranunculus Eschscholtzii</i>		3		3	buttercup
<i>Ranunculus occidentalis</i>				1	buttercup
<i>Senecio sheldonensis</i>					groundsel
<i>Sibbaldia procumbens</i>	4	1	1	3	sibbaldia
<i>Solidago multiradiata</i>					goldenrod
<i>Solidago</i> spp.					goldenrod
Belowground, guerrilla					
<i>Achillea borealis</i>					yarrow
<i>Anemone parviflora</i>	5	3		3	windflower
<i>Anemone Richardsonii</i>	1	4	1		yellow anemone
<i>Arnica latifolia</i>					arnica
<i>Campanula lasiocarpa</i>		4			harebell
<i>Claytonia sarmentosa</i>					spring beauty
<i>Epilobium angustifolium</i>	1		4	2	fireweed
<i>Epilobium latifolium</i>			1	2	river beauty
<i>Equisetum arvense</i>				1	horsetail

TABLE 2

(Cont.)

	Tundra		Bear Dig		
	1st	2nd	1st	2nd	
<i>Equisetum scirpoides</i>		4		2	horsetail
<i>Galium boreale</i>					bedstraw
<i>Lloydia serotina</i>					alp lily
<i>Myosotis alpestris</i>				1	forget-me-not
<i>Oxyria digyna</i>					sorrel
<i>Petasites frigidus</i>			1	1	coltsfoot
<i>Pyrola asarifolia</i>				1	wintergreen
<i>Pyrola secunda</i>					wintergreen
<i>Rubus arcticus</i>				5	nagoonberry
<i>Saxifraga punctata</i>					cordate-leaved saxifrage
<i>Trientalis europaea</i>					starflower
<i>Valeriana sitchensis</i>					valerian
<i>Veratrum viride</i>				1	false hellebore
<i>Veronica Wormskjoldii</i>					alpine veronica
<i>Viola Langsdoffii</i>					violet
<i>Viola</i> spp.					violet

Discussion

RICHNESS AND DIVERSITY

Compared with mature tundra, the disturbed ground associated with bear digs generally has lower vascular plant species richness. In contrast, Shannon-Weaver diversity levels are indistinguishable between mature tundra and digs, suggesting that the lower overall plant cover in bear digs allows a more even distribution of the abundances of plant species that are present. The results of this direct comparison are intuitive, but grizzlies' cumulative effect on community richness and structure is more appropriately thought of as marginal addition to the mature tundra community than as a contrast to it. At any given time, recognizable bear digs make up only a small fraction of the ground cover in mature tundra areas. In the northern portion of our study area, Christian (1993) found between 7 and 23 bear digs within sight of each kilometer-long transect through ground squirrel habitat, and grizzlies digging for glacier lily bulbs excavate no more than 6% of suitable meadow habitat in a given year in Glacier National Park (Tardiff and Stanford, 1998).

The results of our pairwise comparison show that overall, mature tundra alone has fewer plant species than mature tundra with bear digs. The difference in our plots was small (after rarefaction, just over one species less per plot pair) but statistically significant. So, although mature tundra harbors more plant species at the landscape level than bear digs, a potentially important effect emerges at the smaller scales relevant to most plants and many animals. Square meter by square meter, repeated samples from a landscape of mature tundra dotted with bear digs will exhibit greater species richness than samples from a landscape of pure bear digs (obviously) but also greater richness than samples from purely undisturbed tundra. Although our data cannot define the optimum level of disturbance, they suggest strongly that moderate levels of bear digging will modestly enhance local species richness.

In alpine tundra, grizzly bear digs undergo transient increases in plant species richness and diversity that develop over time as recolonization of the dig occurs. This result is consistent with other studies of mammalian disturbance. In desert (Guterman et al., 1990), coastal prairie (Williams et al., 1986), and serpentine annual grasslands (Hobbs and Mooney, 1985), digging mammals have significant impacts on species richness and diversity, with species numbers usually rising after a disturbance event. In some cases, richness and diversity appear to decline as digs undergo succession back to mature tundra. This pattern

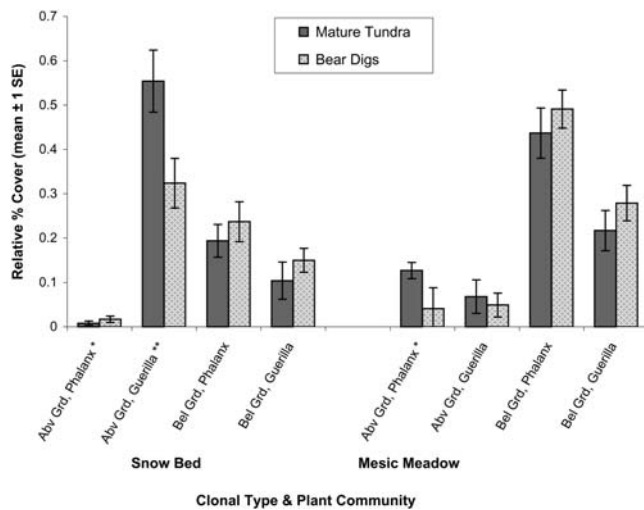


FIGURE 4. Community dominance, as measured by the relative percent cover of clonal plant types in two plant communities. Data show means and standard errors of each clonal type's proportion of total vascular plant cover in 42 bear dig plots paired with adjacent plots in mature tundra. Clonal types with double stars indicate significant differences ($P < .05$, paired 2 sample t -test) between digs and tundra; single stars indicate $P < .10$. Relative cover is arcsin-square root transformed.

fits that predicted by the intermediate disturbance hypothesis (Connell, 1978; Sousa, 1979), with highest diversity or richness at an intermediate stage in succession following the bear digging. We note this result with caution, however, because our data indicate relative (rather than absolute) richness and diversity of bear digs and because our proxy for dig age (plant cover) is inherently imprecise. As recolonization occurs, in any case, we have shown that species composition of bear digs remains very similar to that of the immediately surrounding tundra, implying that throughout the successional recovery of bear digs most colonization comes from nearby plants.

COMMUNITY STRUCTURE

In addition to changing community diversity, bear digs have differential impacts on plants with different life histories. In particular, these disturbances appear to favor plants with certain clonal growth strategies. The biological significance of these effects differs between the two plant communities we studied. In snowbed areas, all clonal types except the most dominant one were favored by digging, suggesting that the statistically significant reduction in aboveground guerrilla species may release species of other clonal types from competition, leading to the observed increases in species richness and diversity. In mesic meadows, by contrast, species of the dominant belowground phalanx clonal type were actually favored by digging, while two of the less common clonal types, aboveground guerrilla and phalanx species, were suppressed. In this case, it is possible that bear digs (and perhaps other disturbances) are frequent enough to prevent the dominance of aboveground species, even in what appears to be mature tundra. Our observations suggest that grizzly bear digs are very concentrated in some areas, but we cannot speculate on the recurrence interval for bear digs in any given location.

Ultimately, several of the changes in group dominance by plant species of different clonal types were statistically insignificant. Given the broad range of plant morphologies and strategies grouped within each of our coarsely classified clonal types, we expected to find more significant differences at the scale of individual species. In a study

TABLE 3

Vascular plants with significantly greater percent cover in either bear digs or mature tundra ($P < .05$; Mann-Whitney U based upon 43 sample plots in bear digs and 60 plots in mature tundra; values uncorrected for multiple tests)

Species	Clonal type	Mann-Whitney U	$P (< .05)$
More common in bear digs			
<i>Minuartia</i> spp.	aboveground phalanx	1012.0	0.002
<i>Epilobium anagallidifolium</i>	belowground phalanx	1013.5	0.045
More common in mature tundra			
<i>Antennaria</i> spp.	belowground phalanx	1597.5	0.005
<i>Viola</i> spp.	belowground guerrilla	1505.0	0.005
<i>Anemone parviflora</i>	belowground guerrilla	1647.0	0.009
<i>Campanula lasiocarpa</i>	belowground guerrilla	1634.0	0.013
<i>Salix polaris</i>	aboveground guerrilla	1601.0	0.018
<i>Equisetum scirpoides</i>	belowground guerrilla	1573.0	0.024

of short-grass prairie communities, for example, Platt (1975) showed that a small suite of "fugitive" plant species depended entirely upon badger disturbances for recruitment and reproduction. Unlike Platt, but in common with other studies of digging mammals (Hobbs and Mooney, 1985; Gutterman et al., 1990), we did not find individual species that appeared to absolutely require bear digs for establishment or reproduction. In retrospect, this result is not surprising, given the large number of abiotic disturbances that affect alpine communities; avalanches, frost heaving, solifluction, and freeze-thaw ground tears are all significant forces in shaping tundra communities (Sigafos, 1952; Washburn, 1979; Jonasson and Skold, 1983; Sonesson and Callaghan, 1991). Indeed, although the species most dependent on bear digs in this study, *Epilobium anagallidifolium*, also occurred in mature tundra plots, it did so almost exclusively in the cracks caused by frost heaving and ground tears. The degree to which bear digs' effects on biotic communities resemble the effects of these other, abiotic disturbances is not well understood, but it seems clear that the ground disturbance associated with bear foraging is not wholly unique in this environment.

Still, we found several plant species that showed a statistically significant difference in abundance between bear digs and mature tundra. Furthermore, both species dominant on bear digs were of the phalanx clonal type, while five of the six more common in mature tundra were guerrilla species. These results raise questions about the role of clonal growth form in mediating competitive interactions. Theoretical work has emphasized that differences in clonal form can mediate competitive interactions (Crawley and May, 1987), and Boeken and Shachak's (1994) work in the Negev desert documented various plant traits favored by disturbances, including seed size and dispersal characteristics. Given the low seedling recruitment rates and long life spans thought to be typical of most tundra species, we suggest that grizzly bear digs (and other disturbances) may provide critical microsites for reproduction and survival of phalanx-type plants that are at a competitive disadvantage relative to aggressively spreading guerrilla species in densely vegetated mature tundra. Clearly, though, these interactions occur within a diverse plant community where species with widely varying clonal forms interact on small spatial scales. This diversity is probably maintained by the interaction between a diversity of clonal growth forms in the context of numerous micro- and mesoscale disturbance events. Our observation that the second-most common species in a study plot frequently differs in clonal form from the dominant species supports the possibility that the varying clonal forms common in this system may help to allow coexistence of species.

CONCLUSIONS

We have documented modest but significant effects of bear digs on plant community structure, and our results indicate that the presence of bears is important for alpine plant communities in south-central Alaska. More work is needed to understand the impact of bear digs on plant richness, diversity, and competitive interactions among species of varying clonal form, but our work suggests that these effects *alone*, while important, are not sufficiently unique or pervasive to merit consideration of the grizzly bear as a keystone species. Still, the impacts of grizzly bears on more abundant (if less celebrated) members of their ecological communities suggest that the loss of bears from an area could have significant long-term ecosystem consequences. Although we did not follow digs through time, the time needed for a dig to return to mature tundra may be on the order of decades; each dig therefore represents a long-lasting change in the tundra community, and even a low rate of digging can result in a rich mosaic of patch ages and hence local community structures. Since grizzlies are equally prolific excavators in many other regions, it is likely that similar disturbance effects will be found elsewhere.

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