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SOIL BIOTA IN AN UNGRAZED GRASSLAND: RESPONSE TO ANNUAL GRASS (*BROMUS TECTORUM*) INVASION

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Abstract. *Bromus tectorum* is an exotic annual grass that currently dominates many western U.S. semi-arid ecosystems, and the effects of this grass on ecosystems in general, and soil biota specifically, are unknown. *Bromus* recently invaded two ungrazed and unburned perennial bunchgrass communities in southeastern Utah. This study compared the soil food-web structure of the two native grassland associations (*Stipa* [S] and *Hilaria* [H]), with and without the presence of *Bromus*. Perennial grass and total vascular-plant cover were higher in S than in H plots, while quantities of ground litter were similar. Distribution of live and dead plant material was highly clumped in S and fairly homogenous in H. Soil food-web structure was different between H and S, with lower trophic levels more abundant in H and higher trophic levels more abundant in S. In *Bromus*-invaded plots, the quantity of ground litter was 2.2 times higher in *Hilaria–Bromus* (HB) than in H plots, and 2.8 times higher in *Stipa–Bromus* (SB) than in S plots. Soil biota in HB generally responded to the *Bromus* invasion in an opposite manner than in SB, e.g., if a given component of the food web increased in one community, it generally decreased in the other. Active bacteria decreased in H vs. HB, while increasing in S vs. SB. Soil and live plant-infecting fungi were the exception, as they increased in both types of invaded plots relative to uninvaded plots. Dead-plant-infecting fungi decreased in H vs. HB and increased in S vs. SB. Most higher-trophic-level organisms increased in HB relative to H, while decreasing in SB relative to S. Given the mixed response to invasion, the structure of these soil food webs appears to be controlled by both plant inputs and internal dynamics between trophic levels. When compared to non-invaded sites, soil and soil food-web characterisitics of the newly invaded sites included: (1) lower species richness and lower absolute numbers of fungi and invertebrates; (2) greater abundance of active bacteria; (3) similar species of bacteria and fungi as those found in soils invaded over 50 yr ago; (4) higher levels of silt (thus greater fertility and soil water-holding capacity); and (5) a more continuous cover of living and dead plant material (thus facilitating germination of the large-seeded *Bromus*). These results illustrate that (1) soil food-web structure can vary widely within what would generally be considered one vegetation type (semi-arid grassland), depending on plant species composition within that type, and (2) addition of a common resource can evoke disparate responses from individual food-web compartments, depending on their original structure.

Key words: *bacteria; biological soil crust;* Bromus tectorum, Hilaria, *and* Stipa*; desert soils; exotic-plant invasion; fungi; grasslands, semi-arid; microinvertebrates; nematodes; nutrient cycling; protozoa; soil food-web structure.*

INTRODUCTION

Understanding the relationship between invasive vascular plant species and native ecosystems is a high priority for ecologists and land managers worldwide. Examination of the dynamics of plant invasion, and the ecosystem response to these invasions, has recently been a focus for many researchers (Tilman 1997, Stohlgren et al. 1999). Most effort has been directed at visible components of ecosystems (e.g., native vascular plant communities and associated animal populations; Tilman 1997). Little attention has been paid to the role of soil food webs in the invasion process, or how their response to invasion may influence ecosystem function. As the structure of soil food webs is critical in regulating decomposition and subsequent nutrient mineralization rates, soil food webs can determine the form, timing, and amounts of nutrients available to vascular plants (Parker et al. 1984*b*, Zak and Freckman 1991). Given the microbial mediation of these processes, it is not unreasonable to expect soil food webs may influence or even determine invadability of a system and/or the response of an ecosystem to invasion by exotic plants.

Knowledge about what controls soil food-web struc-

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ture and function is extremely limited. Food-web theory has provided most of what little theoretical framework exists for understanding relationships within a given soil food web. Soil food webs have been considered classic examples of donor-controlled (bottom-up) food webs, (i.e., the density of the resource controls the density of the consumer, but not the reverse; Pimm 1982); thus, the flux from each component depends on the levels of that component, not on the level of the component that consumes it (DeAngelis 1992). This is based on the idea that soil organisms are unlikely to influence the short-term amount or quality of plant material input. However, there are multiple ways in which soil organisms can influence availability of their resource base in the short term, including: (1) increasing nutrient renewal rates or altering species composition of flora/fauna by predation and mineralization; (2) increasing substrate availability through detritus fragmentation; (3) increasing dispersal of soil organisms by faunal transport; (4) stimulating bacterial and fungal growth rates through grazing; and/or (5) influencing soil structure and moisture (Santos and Whitford 1981, DeAngelis 1992, Bengtsson et al. 1996, Polis and Winemiller 1996). Low input of resources may also generate a very different response than high inputs (DeAngelis et al. 1996). Thus, it is unlikely that any soil food web is completely donor-controlled. This debate is germane to understanding the influence of invasive plants on soil food webs, as the presence of exotic plants can alter the quantity, timing, quality, and/or spatial distribution of plant resources entering a given ecosystem.

Introduced annual grasses now dominate much of the western United States, currently comprising 50–85% of vascular plant cover in over two-thirds of western rangelands. *Bromus tectorum* alone dominates 40 $\times 10^6$ ha (100-million acres) (U.S. Environmental Protection Agency, Environmental Monitoring and Assessment Program [Las Vegas, Nevada, USA], *unpublished map*). *Bromus* can alter many soil and vascular plant community properties, including soil moisture, soil temperature, plant species diversity, primary productivity, timing of activity, root distributions, litter quality and quantity, and nutrient cycling (Walker and Smith 1997). As microbial diversity, biomass, and distribution depends on many of these same factors (McLaren and Skujins 1967, Dommergues et al. 1978), the presence of *Bromus* is expected to substantially alter the soil biota in many ways, including species composition, distribution, abundance, and the amount and timing of biotic activity. Such changes in these factors are expected to alter decomposition rates and nutrient availability; these alterations may then further affect soil biota and vascular plants (Rice et al. 1998).

Separating the effects of plant invasion from those of anthropogenic-related surface disturbances is often difficult or impossible in the western United States, as most lands have been grazed by livestock, chained, or burned at frequent intervals (Walker and Smith 1997). However, a few places have remained free of these influences, including a 100-ha grassland (Virginia Park) in southeast Utah. Surveys up to 1995 found a maximum *Bromus* cover of 0.4% in any given plot (Kleiner and Harper 1972; Canyonlands National Park [Moab, Utah, USA] Long Term Vegetation Monitoring program, *unpublished data*). After an extremely wet fall of 1994, surveys in spring 1995 found ~25 *Bromus*-dominated patches (~0.1 ha each) scattered throughout Virginia Park, although surface disturbance and fire regimes had not been altered. While some studies have documented soil food-web changes after annual-grass invasions into semi-arid perennial communities disturbed by livestock or fire (Bolton et al. 1993, Trent et al. 1994), we know of no studies in the absence of such disturbance. Accordingly, this study addresses the following questions: (1) Is soil food-web structure different between two grassland associations within a given vegetation type (semi-arid grassland) undisturbed by fire or grazing? (2) Does the addition of a common resource (*Bromus*) differentially affect vegetative and soil food-web communities in these two grassland associations? (3) What soil and plant characteristics are different between invaded and uninvaded sites? and (4) What controls soil food-web structure in this ecosystem?

Methods

Study sites

This study was conducted in Canyonlands National Park, 70 km south of Moab, Utah, USA. Three grassland sites were used: Virginia Park (VP), Chesler Park (CP), and Squaw Flat (SF). VP and CP are directly adjacent to each other, but separated by a 100-m-tall, 50-m-wide rock wall; SF is ~5 km away. Sites are at ~1700 m elevation. Annual average rainfall is 215 mm, with 35% occurring as summer monsoons (late July–August). Maximum average high temperatures are 28°C, while minimum average lows are −2°C, with evaporation exceeding precipitation most of the growing season (Fig. 1). Rainfall in November 1995 through April 1996 was 53 mm, well below average for this region. Rainfall in November 1996 through April 1997 was 104 mm, average for this region. Soils at all three sites are immature, alkaline, well-drained, fine sandy loams derived from calcareous sandstone.

Grasslands in this region contain two distinct perennial grassland associations: one dominated by the predominantly spring-active C_3 grasses *Stipa comata* and *Stipa* (*Oryzopsis*) *hymenoides* (hereafter referred to as "*Stipa*"), and one dominated by the predominantly fall-active C_4 grass *Hilaria jamesii* (referred to as "*Hilaria*") (Kleiner and Harper 1977, Ehleringer 1978, Welsh et al. 1993). It is important to note that all perennial grasses in this region show some activity

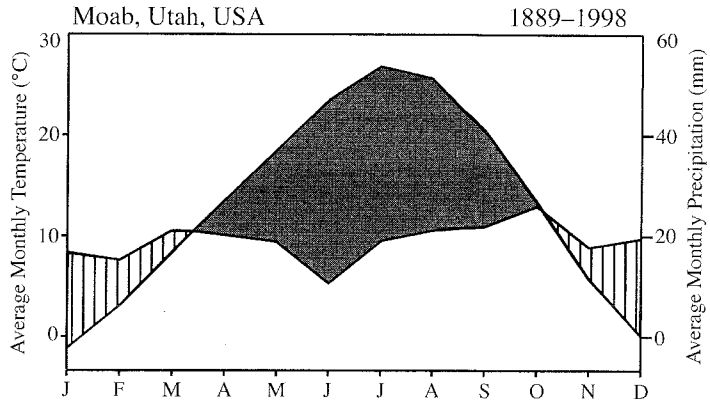

FIG. 1. Walter diagram of climatic conditions for Moab, Utah (USA), from 1889 to 1998. This climate station is 70 km northeast and at approximately the same elevation as the three study sites.

throughout the March to October growing season (e.g., the C_4 *Hilaria* puts out new leaves in spring and late summer, while the C_3 *Stipa* puts out new leaves in spring and with the late-summer rains). *Bromus* is a C_3 grass that germinates in September, overwinters as an appressed rosette, grows upwards in February, and is active until June.

CP and SF were invaded by *Bromus* sometime after 1900, and it was well established by 1940 (R. Redd, *personal communication*). VP, although surrounded by areas dominated by *Bromus,* escaped invasion until fall 1994. In spring 1996, permanent 1.0-ha plots were randomly located in the two grassland types, with and without *Bromus*. Plots were labeled *Stipa* (S), *Stipa–Bromus* (SB), *Hilaria* (H), and *Hilaria–Bromus* (HB). The four plot types were replicated three times in VP (total of 12 plots); in CP, S and SB plots were replicated three times (6 plots) and in SF, HB plots were replicated three times (three plots), resulting in a total of 21 plots. Lines were marked every 5 m within each plot, and random points selected along these line for vegetation and soil sampling.

Sampling procedures

Sites were sampled in spring (predetermined to be the time of maximum activity for soil biota) 1996 for vascular and non-vascular vegetation, soil chemistry, bacteria, soil fungi, protozoa, and invertebrates. Live and dead plant-infecting fungi were sampled in spring and fall 1997. Active (defined as green aboveground shoots) vascular plant cover was estimated with a 0.25 m^2, nested-frequency quadrat frame and Daubenmire cover classes. A 0.1-m^2 frame, with 16 point hits, was used to estimate cover of soil biological-crust components. For soil chemical, physical, and biological analyses, 30 subsamples of the surface 0–10 cm soils were collected randomly and composited into a 1200 g sample; three samples were collected per plot. After thorough mixing, each sample was split into four parts: 600 g were sent to the Brigham Young University Soil Laboratory (Provo, Utah, USA) for chemical analyses, 300 g to Soil Food Web, Inc (Corvallis Oregon, USA) for bacteria and nematode analyses, and 300 g to A. Moldenke (Department of Entomology, Oregon State University, Corvallis, Oregon, USA) for invertebrate analyses. Abundance estimates were done with direct counts after extraction and/or staining (Babiuk and Paul 1970, Ingham 1993, Moldenke 1994). Invertebrates were identified to either the genera or functional-group level, depending on difficulty of identification. Jack States (Department of Botany, University of Wyoming, Laramie, Wyoming, USA) collected and analyzed 50 g soil for fungal analyses from the same plots. Soil fungi were identified using the dilution plate method (States 1978). Plant and litter fungi were isolated by growing fungi on plant fragments from the soil samples (Bills and Polishook 1994).

Data were arc-sine transformed where required. Vascular and non-vascular vegetative cover, and bacteria and nematode numbers were analyzed using *t* tests or ANOVA and Tukey's HSD multiple-range test, if data had a normal distribution, or the equivalent nonparametric tests for data that were not normally distributed. Fungal-community similarity was determined using Sorenson's index. A Wilcoxon signed-rank test was used to analyze invertebrate data. Principal components analysis (PCA) was used to analyze similarities between the different community components.

RESULTS

Vascular and non-vascular vegetation

Plant architecture among the four community types was very different (Fig. 2). *Stipa* (S) plants grow upright, are widely spaced (up to 1.5 m apart), and dead leaves remain standing or curl inside the grass clump. Surface roots and litter are sparse. Thus, S communities were characterized by discrete grass clumps separated by large interspace areas barren of plant material. In contrast, *Hilaria* (H) is a rhizomatous, mat-forming, closely-spaced (<0.3 m apart) grass with many surface roots. H communities had fairly continuous above- and belowground plant cover. Native perennial grass and total vascular cover were higher in S than H (Table 1).

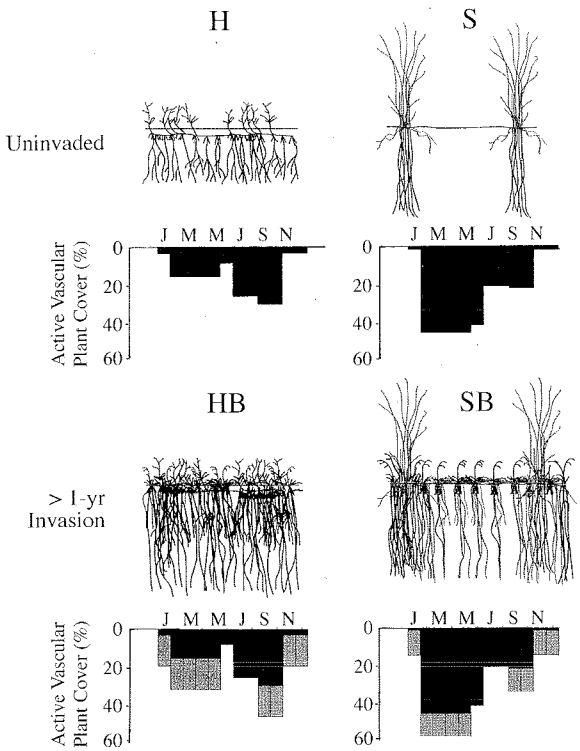

FIG. 2. Diagram of plant community architecture and activity times in four kinds of grassland plots. *Hilaria* (H) is a closely spaced, shallow-rooted, predominantly fall-active C_4 grass with homogenous litter and plant cover. *Stipa* (S) is a widely spaced, deeply rooted, predominantly spring-active C_3 grass with litter-free plant interspaces. Additions of *Bromus* (B) filled in plant interspaces. The bars below the plant diagrams represent estimates of active vascular plant cover during the year: black = native cover; grey = *Bromus* cover. Note that *Bromus* affects both timing and distribution of active plant material.

Moss and *Collema* lichen cover were similar in both H and S communities, ranging from 18% to 21%.

In the invaded plots, *Bromus* cover in spring 1996 was much higher than the 1967 values (Table 1). Architecture of S communities was the most altered by the *Bromus* invasion. The barren interspaces were filled with *Bromus* shoots and roots, and the once highly clumped distribution of live and dead plant material was replaced by a more continuous cover. Active plant material increased in HB greatly in spring, and increased in both SB and HB in winter, relative to the uninvaded plots. Architecture in the H communities was less affected, as *Bromus* invaded more or less uniformly and reinforced the already fairly continuous distribution of root and shoot material present in the H community (Fig. 2). The area occupied by dead perennial-grass clumps was not statistically different in H relative to HB or S compared to SB, indicating that *Bromus* presence did not immediately increase native grass mortality (Table 1). SB plots had lower *Stipa* cover than S communities, so despite much higher *Bromus* cover in the SB plots, overall plant cover was slightly higher in S than SB. Moss and *Collema* lichen cover were similar in HB and SB.

Ground litter (mostly *Bromus*) also increased in invaded plots: litter in HB was 2.2 times that of H, while SB litter was 2.8 times that of S. Qualitative observations found a large increase in plant root density in the top 20 cm of soil in the invaded plots relative to the uninvaded plots, as would be expected with the large increase in annual plants.

Soil chemistry

In H and S plots, soil texture and macronutrients were very similar, with the exception of nitrogen forms (Table 2). H had much lower NH_4, and much higher mineralizable N than S plots. Silt was significantly higher, and sand significantly lower, in the invaded plots relative to the uninvaded plots in both S and H.

TABLE 1. Cover values for vascular and nonvascular plants in Virginia Park (southeast Utah, USA) in spring 1996 (means with 1 SE in parentheses) and in 1967 (data are from Kleiner and Harper [1977]).

	H		HB	S		SB
Vegetation cover	1967	1996	1996	1967	1996	1996
Bromus	0.4	3.4^{a} (0.8)	18.7^{b} (4.0)	0	1.3^{a} (0.5)	13.7^{b} (1.5)
Perennial grass	22.1	22.3^{b} (1.2)	15.4^{a} (1.1)	17.6	27.8^{c} (1.6)	19.7^{ab} (1.8)
Forbs + Cacti		3.7^{ab} (0.9)	1.4 (0.4)		4.6^{b} (0.8)	3.4^{ab} (0.7)
Total vascular plant		39.8^{a} (2.6)	40.2^{a} (4.1)		59.0^{b} (3.0)	51.8^{ab} (3.5)
Shrubs		3.5 (1.5)	1.5 (1.2)		1.6 (1.0)	2.5 (1.6)
Dead grass clumps		5.3^{b} (1.0)	0.5^{a} (0.3)		4.1^{ab} (1.2)	7.3^{b} (1.1)
Ground litter (g/m^2)		2.4^{a} (0.1)	5.5^{b} (0.1)		3.1^{a} (0.1)	8.7^{c} (0.4)
Moss	21.1	18.5 (2.8)	12.1 (1.9)	19.2	17.6 (3.4)	12.0 (2.6)
Collema	19.5	19.6 (2.0)	19.6 (2.0)	17.9	19.1 (3.0)	18.7 (2.9)

Note: Within a row, means with different superscript lowercase letters are significantly different between plots for the 1996 values at $P < 0.05$, as determined using ANOVA and Tukey's HSD or Dunnett T3 (n = 30 quadrats).

TABLE 2. Soil chemistry values (means ± 1 SE) in four types of grassland plots, Virginia Park, Utah, USA, in spring 1996 using 600-g dry soil.

Parameters	H	HB	H:HB	S	SB	S:SB	H:S
P (μg/g)	5.1 ± 0.3	5.7 ± 0 .7		4.4 ± 0.7	4.9 ± 1.2		
K available (μg/g)	165 ± 11	172 ± 9		141 ± 5	176 ± 18		
pH	7.6 ± 0.1	7.6 ± 0.0		7.6 ± 0.0	7.5 ± 0.0		
Sand (%)	64.3 ± 1.3	59.0 ± 0.9	*	67.7 ± 1.5	60.0 ± 1.6	*	
Clay (%)	13.7 ± 0.3	14.7 ± 0.7		13.8 ± 0.4	14.3 ± 0.3		
Silt (%)	22.1 ± 1.5	26.3 ± 0.5	*	18.5 ± 1.7	25.6 ± 1.4	*	
CEC	10.6 ± 0.8	11.2 ± 0.7		9.1 ± 0.9	10.7 ± 0.5		
Zn (μg/g)	0.19 ± 0.02	0.24 ± 0.01		0.21 ± 0.04	0.25 ± 0.01		
Fe (μg/g)	1.8 ± 0.1	1.8 ± 0.2		1.4 ± 0.0	1.8 ± 0.1	*	*
Mn (μg/g)	4.7 ± 0.6	4.5 ± 0.3		3.1 ± 0.2	5.4 ± 0.2	*	*
Cu (μg/g)	0.38 ± 0.01	0.43 ± 0.05		0.32 ± 0.01	0.38 ± 0.01	*	*
Ca exchangeable (μg/g)	4143 ± 838	3893 ± 744		5260 ± 925	3163 ± 347	*	
Mg exchangeable (μg/g)	206 ± 17	210 ± 37		188 ± 6	226 ± 15		
Na exchangeable (μg/g)	12.2 ± 1.7	11.6 ± 0.8		11.2 ± 1.0	13.0 ± 1.3		
N (μg/g)	352 ± 35	378 ± 11		354 ± 40	455 ± 77		
NH_4-N (μg/g)	9.5 ± 0.8	12.2 ± 4.2		17.0 ± 3.1	15.3 ± 3.6		*
Mineralizeable N (μg/g)	8.5 ± 1.3	4.5 ± 4.5		0.8 ± 0.5	2.3 ± 2.3		*
NO_3 (μg/g)	8.3 ± 1.1	8.5 ± 2.2		9.8 ± 0.9	9.2 ± 0.8		

Notes: B = *Bromus*, H = *Hilaria*, and S = *Stipa*; CEC = cation exchange capacity.
* $P < 0.05$, as determined by Mann-Whitney U test; $n = 3$ plots.

Active and total bacterial biomass

Active bacterial biomass was significantly higher in H compared to S, and in SB relative to S (Fig. 3; Appendix A). However, it was significantly lower in HB relative to H. Total bacterial biomass was significantly higher in S than H.

Fungal communities

Coefficients of fungal community similarity were 60% for H and S; 53% for S and SB; and 48% for H and HB. Fungal species found in the different soils are listed in Appendix B. H soils had nine species, while S soils had 12 species. With invasion, HB soils gained three new fungal species, and one was lost (compared to H soils). Compared with S soils, SB soils gained two species (different from those added to HB soils) and two were lost (one was the same as HB). Changes in abundance of individual species happened quickly: of the species that changed within 50 yr (CP and SF plots), >70% increased or decreased within two years in the direction that more closely approximated soils invaded for >50 yr (Appendix B). Although the newly invaded soils had a similar number of species as the soils that had been *Bromus*-dominated for 50 yr, individual species composition varied, especially in HB vs. SB soils (Appendix A).

Appendix B presents the fungal species found infecting live plants. All species found on live *Bromus* were also on live *Hilaria* and *Stipa*; however, there were fewer species on *Bromus* than on native grasses. With invasion, the abundance of all generalist saprophytic fungal species increased, while abundance of almost all specialized facultative pathogens decreased.

The numbers of soil fungi and soil fungal species tended to be lower in H than S, while relative frequency of live-plant infection tended to be higher in H than S in both spring and fall (Fig. 3, Appendices A and B); however, fungal relationships were not tested statistically. The numbers of soil fungi, soil fungal species, and frequency of live-plant infections tended to increase in invaded soils (HB, SB) relative to uninvaded soils (H, S). In the newly invaded plots (HB, SB), infection of dead *Hilaria* tended to decline, while infection of dead *Stipa* increased. Plots dominated by *Bromus* for 50 yr in Chesler Park (CP) and Squaw Flat (SF) showed an intermediate response relative to uninvaded and newly invaded plots (Appendix A). Principal-components analysis (PCA) of the soil fungal community shows that S was different from H and the newly invaded sites. CP and SF were grouped along the Component 1 axis, while widely separated along the Component 2 axis. SB, H, and HB were similar (Fig. 4A).

Nematodes

Nematode numbers were low in all plots. Numbers of bacterial-feeding nematodes were significantly higher in H than S, and in HB than H (Fig. 3, Appendix A). No significant differences were seen in fungal or root-feeding nematodes. Total nematode numbers were significantly higher in H vs. S plots.

Protozoa

Protozoa numbers were also very low (Appendix A), being orders of magnitude lower than in forested soils (Coleman and Crossley 1996). Though differences in population averages were large, so was the variation; thus, no differences were statistically significant. However, a few trends were noteworthy (Fig. 3). Flagellates and ciliates tended to be higher in S than H, and higher

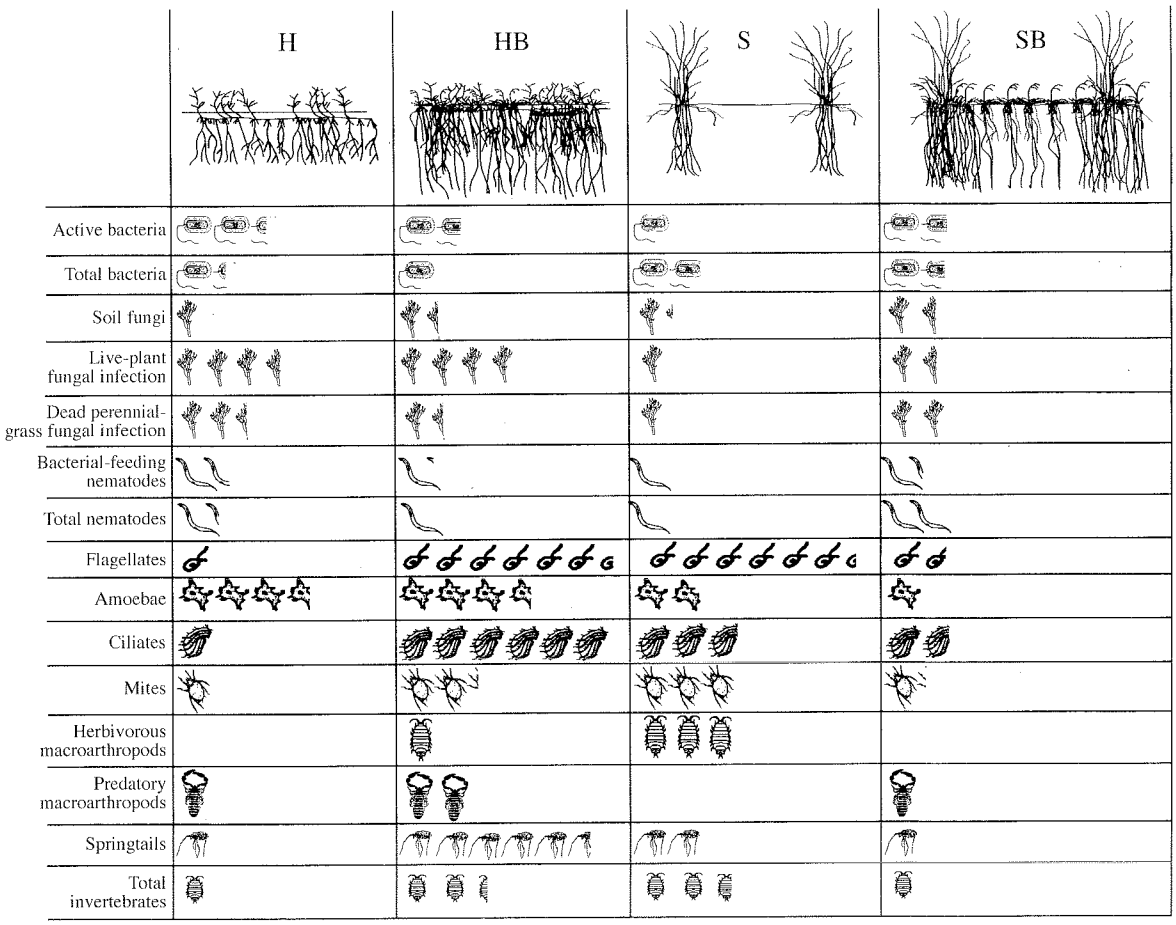

FIG. 3. Diagram of soil food-web structure in the four different grassland communities, showing the relative abundance within a given functional group. The numbers of icons on a given line are relative to each other; thus, twice as many icons indicates that organisms are twice as abundant. B = *Bromus*, H = *Hilaria*, S = *Stipa*.

in HB than H. In contrast, all protozoa tended to decrease in SB relative to S.

Soil invertebrates

As with protozoa, soil invertebrates numbers were extremely low (Table 3), again being several orders of magnitude less than in forested soils (Coleman and Crossley 1996). Combined, the total numbers of invertebrates, numbers of groups, and number of unique groups significantly increased in HB relative to H ($P < 0.05$), and decreased in SB relative to S ($P < 0.08$). Low numbers precluded statistical analyses within individual functional groups; however, some trends were present. Fungivorous mites heavily dominated the invertebrate community in all vegetation types (Fig. 5). However, the response of these mites to invasion was different: most species increased in HB relative to H, while most decreased in SB relative to S, in spite of increased fungal abundance in both HB and SB. Detritivore numbers showed little difference between invaded and uninvaded communities, in spite of plant litter increasing greatly with invasion. PCA of functional groups (Fig. 4B) showed H and SB were very similar, while other plot types were quite different.

As with functional groups, individual invertebrate species were similar between H and SB, and surprisingly different among the other plot types (Fig. 4B). S soils had 19 genera/groups, with 11 unique to the S community (Table 3); SB soils had 8 genera/groups (1 unique). In the transition from a S to a SB community, 15 genera/groups were lost, 4 retained, and 4 new gained. The H community had 9 genera/groups (3 unique); with *Bromus* invasion (HB), this increased to 16 genera/groups, with 7 unique groups. The transition from H to HB involved gaining 11 new groups and retaining 4 groups. The four grass communities had only three invertebrate genera/groups in common. The two native (H, S) and the two invaded (HB, SB) communities both had only one additional group in common.

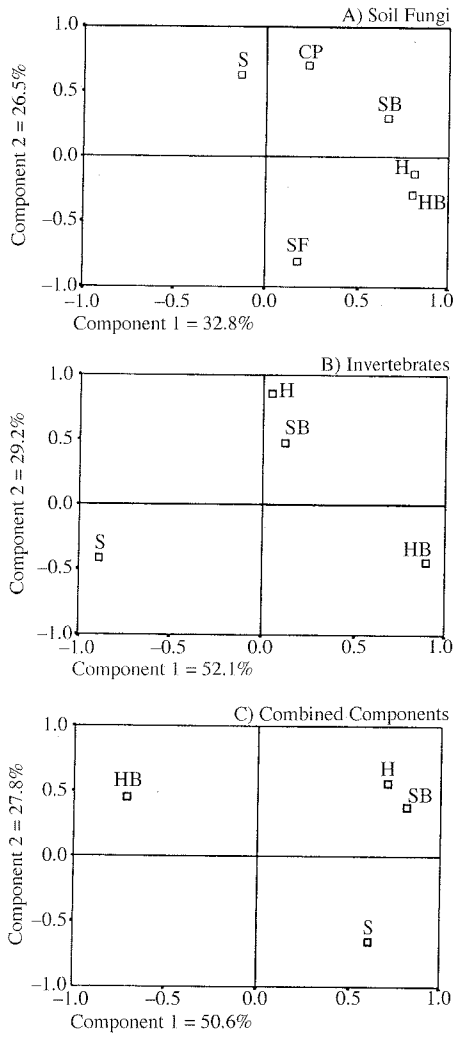

FIG. 4. PCA analyses of different soil food-web components. Percentage variance of eigenvalues is noted along component axes. Grassland types: B = *Bromus*, H = *Hilaria*, and S = *Stipa*; sites: CP = Chesler Park, SF = Squaw Flat. All panels are in Vari-Max rotated space (SPSS 1999). (A). Soil fungi; species most influencing eigenvalues are listed in Appendix B. (B). Invertebrates; individual species most influencing eigenvalues are listed in Table 3. (C). Combined food-web components. Component 1 positive space is most influenced by detritivores, total bacteria, and live-grass infecting fungal abundance, while negative space is most influenced by algivorous and predatory mites, springtails, and ciliates. Component 2 positive space is most influenced by number of live-grass infecting fungal species and abundance, and predatory macroarthropods.

DISCUSSION

How and why were soil food webs different between the different adjacent, uninvaded grassland associations?

Soil food-web structure was very different in the two native grassland associations, especially at higher trophic levels (Figs. 3 and 4). Differences in bacterial and

TABLE 3. Number of invertebrates found in uninvaded (*Hilaria* [H] or *Stipa* [S]) and *Bromus* (B)-invaded (HB, SB) soils in Virginia Park (Canyonlands National Park, Utah, USA). All samples were collected in spring 1996, using 300-g soil; n = 36 samples.

	Grassland sites				
Taxon	H	HB	S	SB	PCA†
Detritivores					
Beetle	16	0	0	16	2+
Sciarid	0	0	16	0	1−
Algivores					
Liposcelis	0	16	0	0	1+
Fungivorous mites					
Acarid	16	0	0	0	2+
Carabodoid	64	16	208	80	
Ceratozetes	0	0	16	0	1−
Endeostigmata	32	112	0	32	
Jacotella	0	0	32	96	
Nanorchestes	0	16	32	0	
Paratydaeid	208	160	224	112	
Propelops	0	176	352	0	2−
Scheloribates	16	112	32	32	
Speleorchest	0	0	16	0	1−
Tydaeid	0	0	16	0	1−
Tyrophagus	0	0	48	0	1−
Herbivorous meacroarthropods					
Curculionid	0	16	0	0	1+
Lygaeid	0	0	16	0	1−
Pseudococci	0	0	32	0	1−
Predatory macroarthropods					
Bembidion	0	16	0	0	1+
Dermestid	0	0	0	16	
Gnaphosid	0	16	0	0	1+
Micryphantid	16	0	0	0	2+
Predatory mites					
Cyta	0	16	0	0	1+
Galumna	0	0	16	0	1−
Gamasida	0	48	32	0	2−
Gamasidayel	0	0	16	0	1−
Rhodacarid	0	64	0	0	
Springtails					
Entomobrya	0	128	16	0	
Folsomia	0	0	16	0	1−
Hypogastrura	0	32	0	32	1+
Isotoma	16	0	0	0	2+
Isotoma, black	0	16	0	0	1+
Tullbergia	16	0	32	0	
Totals‡					
No. of individuals	400	960	1168	416	
No. of groups	9	16	19	8	
No. of unique groups	3	7	11	1	

† The principal components analysis (PCA) column identifies the species most influencing PCA components 1 and 2 in Fig. 4B; 1+, 1−, 2+, and 2− = Component 1 or 2, positive or negative space, based on factor loading values computed in PCA analysis. Wilcoxon signed-rank test showed that the numbers of individuals, groups, and unique groups were statistically distinct for H vs. S, H vs. HB, and for S vs. SB ($P < 0.06$).

‡ Totals are on a mass, not an area, basis.

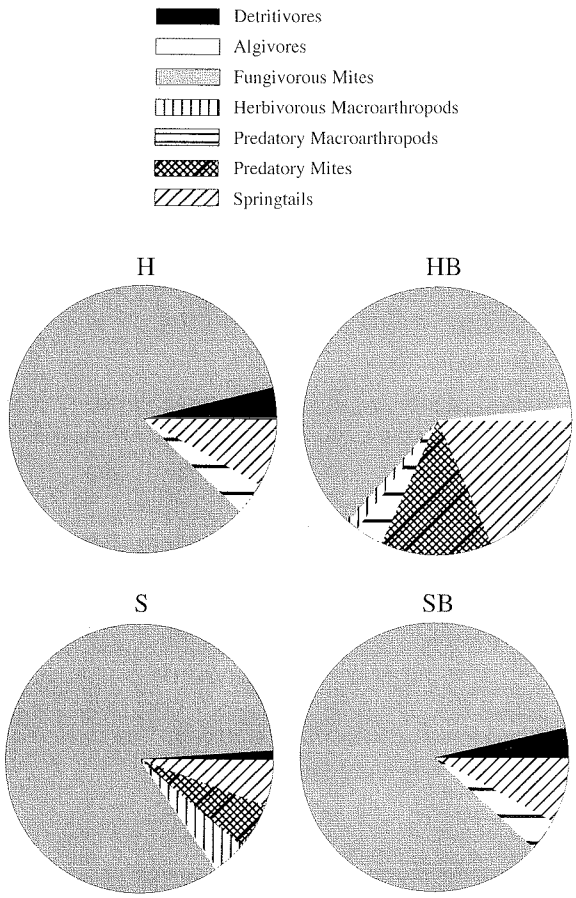

FIG. 5. Abundance of different invertebrate functional groups in the three kinds of grassland sites (B = *Bromus*, H = *Hilaria*, S = *Stipa*). Fungivorous mites dominate all plot types. Note the similarity between H and SB.

fungal abundance were variable when *Hilaria*, H, was compared to *Stipa*, S: active bacterial biomass and live-plant fungal infection were higher, while total bacteria, soil fungal numbers and species, and dead grass infections were lower or not different. Nematode abundance was higher in H than S. However, both abundance and richness of most invertebrates were lower in H compared to S. Species composition of the fungal and invertebrate communities was very different. Fourteen species of soil fungi were recorded in H and S, but only seven occurred in both communities. Of the 24 invertebrate genera/groups occurring in H or in S, only four were found in both grassland types (Table 3).

Direct comparisons of these results with studies done in other deserts is difficult or impossible, due to different methods used over the years. Bacterial and fungal numbers in the Mojave (Rundel and Gibson 1996) are up to four times higher than those in this study. While there is no way to directly compare nematodes from Mojave studies, proportions of organisms in the different functional groups were very different. Both sites had a similar proportion of bacterial feeders. However, in our study, most nematodes were fungivores, with almost no root feeders, while in the Mojave, nematodes were more evenly distributed among the three functional groups, with bacterial-feeders dominant (Freckman and Mankau 1977). Bamforth (1984) reported similar ranges of flagellates, amoebae, and ciliates in the Sonoran as are seen in our study. No comparisons for invertebrates could be found.

Most soil characteristics were similar between the two grassland associations, with the notable exception of mineralizable N being higher and NH_4 being lower in H relative to S (Table 2). Cover of *Bromus* and ground litter were not significantly different (Table 1). The largest differences were seasonal variation in plant cover, and amount and spatial distribution of plant resources (Fig. 2). Two points are notable about activity times in these plots: first, during the spring, S plots had far more active plant cover than did H plots. Second, although fall-active *Hilaria* was dominant in H plots, there was spring plant and soil biotic activity in the H plots. Analysis of the fungal community showed higher, or equal, spring activity compared to fall (Appendix A). Thus, if the fungal community is an indicator of food-web activity, spring was still the most active time in the H community. This may be due to rainfall being higher and more reliable in winter and spring than fall in this region (Fig. 1), as well as to C_3 plant activity.

The amount and distribution of plant resources probably played a decisive role in the observed differences between soil food-web structure in H and S. While both communities had similar amounts plant litter, S had more live plant material and a more clumped distribution of both live and dead plant material. Thus, resources in the S community were much more concentrated into a fewer, richer patches, in contrast to a more homogenous distribution of resources in the H community (Fig. 2). In desert areas where plant materials are sparse, such concentrations may be necessary for the development of more complex food webs or a more diverse invertebrate community. In addition, the ability to exploit diffuse vs. concentrated resources undoubtedly differs between species; thus, large differences in resource distribution are likely to foster divergent soil food-web structures.

*How did the addition of a common resource (*Bromus*) differentially affect vegetative and soil food-web communities in the two grassland associations?*

Most aspects of the vegetative and soil food-web communities changed with the addition of *Bromus*. As native grasses are dormant during winter, native-dominated plots only have green aboveground shoots March through October. However, *Bromus* has green aboveground shoots all winter; thus, plant activity in *Bromus*-

invaded plots increases to year-round (Fig. 2). HB (*Hilaria–Bromus*) plots had increased spring activity relative to H plots, while SB (*Stipa–Bromus*) plots had increased spring and fall activity relative to S plots. The amount of plant roots, shoots, and litter increased over pre-invasion levels, and distribution became more continuous in both HB and SB, as reported for *Bromus* invasion in other locations (Cline et al. 1977, Dobrowolski et al. 1990, Rundel and Gibson 1996). All these factors can influence soil food webs (Ingham et al. 1989, Zak and Freckman 1991, Whitford 1996).

Although *Bromus* greatly increased plant litter, it is currently debated if additions from aboveground material are significant in deserts. In this study, soil organic matter in S and H averaged 0.32%, significantly lower than the 0.54% recorded for HB and SB, indicating some litter was entering the soil. However, Whitford et al. (1995) assert most energy for desert soil organisms comes from live and dead roots, rather than from incorporation of aboveground plant litter. In support of this, Moorhead and Reynolds (1989) showed that at least 50–75% of total annual litter loss in deserts is from abiotic processes (e.g., wind and ultraviolet radiation). In contrast, Dormaar (1992) suggests low organic matter in desert soils is due to high rates of biogenic processes and biochemical reactions with high soil temperatures. *Bromus* litter has a C:N ratio of 150:1, while *Stipa* and *Hilaria* litter has a C:N of 50–60:1 (Evans et al. 1999). Thus, regardless of quantity, the lower quality *Bromus* litter should take longer to decompose than native grass litter (Wedin 1995).

Given that a common resource (*Bromus* roots and shoots) was added in similar quantities to H and S, and that in terms of plant inputs (activity times, quantity, and distribution), *Bromus* made the invaded plots more similar to each other, it was expected that changes in soil food webs between H vs. HB and S vs. SB would be of similar magnitude and direction. However, PCA (principal-components analysis) showed that this was not the case for overall soil community structure (Fig. 4C). HB and SB were very different from each other, and changed in opposite directions from H and S, respectively. Interestingly, SB was very similar to H. This further supports the idea that the distribution of plant material is very important in determining the structure of these soil food webs, as the addition of annual plants to the otherwise barren interspaces of the S community made it architecturally much more similar to HB (Fig. 2).

When the response of individual soil food components was examined, measured fungal components did show a similar response to invasion, as both HB and SB showed increases in soil and plant-infecting fungi. Fungal increases have been documented with other invasions of *Bromus* (Bolton et al. 1993) and of the annual grass *Taeniatherum* (Trent et al. 1994) into other perennial desert communities. In addition, both SB and HB showed a decline of fungal specialists relative to generalists with invasion. This was also expected, as perennial plants generally support higher numbers of specialists than annuals, due to a higher proportion of structural biomass and secondary plant metabolites and lower amounts of soluble nutrients; thus they provide greater substrate diversity for fungi. In addition, generalist fungi species grow faster than specialist species, and generally can more quickly occupy newly available substrate (Cooke and Whipps 1993).

However, the common responses to invasion seen in fungi was the exception, rather than the rule, for the rest of the soil food web. When the response of other components to invasion were compared (H vs. HB and S vs. SB), strikingly opposite responses were observed throughout the different trophic levels (Figs. 3 and 4). For instance, in spite of root biomass increasing in both invaded plots relative to uninvaded plots, active bacterial biomass increased in SB vs. S plots and decreased in H vs. HB plots. Previous studies have shown bacterial populations increase with increases in root biomass (Dommergues et al. 1978, Trent et al. 1994). In addition, bacterial-feeding nematode numbers were lower in HB than H, and higher in SB than S. While this may have reflected active bacterial biomass (lower in HB than H and higher in SB than S), fungal-feeding nematodes did not increase along with observed increases in fungal abundance. In direct contrast to this study, Ekschmitt and Griffiths (1998) reported a positive correlation between fungal biomass and fungivorous nematodes, and a negative relationship between bacterial biomass and bacteria-feeding nematodes. As microbivorous nematodes have preferred prey species (Coleman and Crossley 1996), it is possible that *Bromus* differentially altered the abundance and/or availabililty of the preferred prey.

Although root biomass increased with invasion, no significant response was detected in root-feeding nematodes, in spite of other studies showing a clear and positive relationship between root biomass and nematode numbers (Rice et al. 1998). The observed decline in total nematodes in HB relative to H may reflect the decreased bacterial biomass in HB, or the increased presence of nematode predators (see below); however, the trend in SB relative to S was an increase in total nematodes.

As protozoa prey on bacteria and fungi (Bamforth 1995), changes in these populations were expected to be reflected in protozoan populations; however, in this study, protozoans declined while bacteria and fungi increased in the S vs. SB plots. The opposite occurred when H and HB plots were compared. For invertebrates, Whitford et al. (1995) reported that abundance of soil invertebrates depended on the availability of prey such as fungi and nematodes. No such pattern was seen in this study. Comparing HB to H, invertebrate populations increased while active bacteria and nem-

atode numbers declined. The exact opposite was seen when comparing SB to S: invertebrates decreased, while active bacteria and nematodes increased.

HB had higher numbers of fungi, nematodes, and protozoans than H plots, which may explain why invertebrate numbers were also higher in HB plots. Unexpectedly, SB plots had lower numbers of invertebrates relative to S. The addition of spring-active *Bromus* to an already spring-active *Stipa* community, and the increase of both bacterial and fungal components was expected to increase the abundance of higher trophic-level organisms. The observed response may result from (1) lack of suitable habitat for larger organisms (in spite of increased food supply), perhaps due to changes in soil-crust organisms, soil temperatures, and/or plant material distribution; (2) changes in abundance of key predators; (3) changes in soil nutrients; and/or (4) changes in bacterial and/or fungal species that decreased or eliminated preferred prey (Parker et al. 1984*a*, Whitford 1996, Ekschmitt and Griffiths 1998). Our study did show that *Bromus* invasion altered the species composition and abundance of both the fungal and invertebrate community. S soils lost 15 genera/groups of invertebrates when compared to SB (see Table 3), six of which were fungivorous mites (in spite of fungal increases in SB). In addition, specialist pathogenic fungal species decreased, while generalist saprophytic fungal species increased. Among the invertebrates lost may have been those that preferred pathogenic over saprophytic fungi, or those that otherwise affected the availability of fungi or bacteria (Polis and Winemiller 1996).

Do food webs in these grasslands fit the classic "donor-controlled" model?

In general, the striking dissimilarity of response in these two native grassland communities to *Bromus* invasion is contrary to expectations in a classic "donor-controlled" system. In response to a large increase in plant inputs, HB had a mixed response in both lower and upper trophic levels, while SB, on the other hand, showed an increase in lower trophic levels and a decrease in higher trophic levels. These results suggest that while certain food-web components may respond directly to the addition of plant resources, neither resource-control nor internal dynamics alone can adequately explain the pre- or post-invasion food-web structures of these grass communities. Instead, as documented in numerous other studies (Polis and Winemiller 1996), both drivers appear important. Nematode numbers, for instance, were low when invertebrate numbers were high, and vice versa, indicating a top-down control on their numbers. This has been observed in several deserts (Parker et al. 1984*a*). As seen in our study, other studies report a decoupling between bacteria and bacterial-feeding nematodes (Ekschmitt and Griffiths 1998). The uninvaded S plots had lower numbers of bacteria and fungi than the invaded community (SB), yet supported higher numbers of invertebrates, clearly indicating that top-down drivers at least partially structure this soil food web.

What makes an ecosystem invadable?

In our study, communities and soils more susceptible to *Bromus* invasion were characterized by (1) higher levels of silt; (2) a more continuous cover of living and dead plant material; (3) lower species richness and lower numbers of invertebrates and protozoa; (4) greater numbers/biomass of active bacteria and fungi, and more fungal species; and (5) similar fungal species composition in invaded and uninvaded communities. In addition, preliminary genetic analyses of these soils show that bacteria in soils dominated by *Bromus* for 50 yr were much more closely related to bacteria in soils susceptible to invasion than bacteria in invasion-resistant soils (C. R. Kuske, L. O. Ticknor, U. M. Dunbar, U. A. Davis, M. Miller, S. M. Barns), and J. Belnap, *unpublished data*).

Little is known regarding the possible role of soil biota in helping or hindering invasion of native ecosystems. Harper et al. (1996) showed fungi associated with the invasive annual *Halogeton glomeratus* killed native perennial shrubs. A large, region-wide shrub die-off was partially explained by pathogenic fungal infections (Nelson et al. 1990). As nutrient availability is mediated through microbial processes, soil biota may also influence the long-term persistence of an invasion. Trent et al. (1994) show that invasion of the annual grass *Taeniatherum* resulted in decreased potential N mineralization (both aerobic and anaerobic) and total N in soils when compared to an adjacent native shrubland. This was also seen by Rimer and Evans (1997) with the *Bromus* invasion in Virginia Park (VP) (Canyonlands National Park, Utah, USA).

Most studies examining vulnerability of ecosystems to invasion have focused on vascular plants and/or soil total N and P. Plant studies have shown that vascular-plant species richness is both positively (Stohlgren et al. 1999) and negatively (Tilman 1997) associated with exotic-plant invasion. In this study, soils with lower soil fungi and invertebrate species richness were the most susceptible to invasion. While soil nutrients can be important in determining where plants invade, the discussion has generally focused on nitrogen and phosphorus (Wedin and Tilman 1993, McClendon and Redente 1994, Stohlgren et al. 1999). In this study, soils more susceptible to *Bromus* invasion did not have higher soil total N or P. However, these soils had high pH, Ca, Mg, and Fe, all which can make P seasonally unavailable. Thus, adequately characterizing P availability in desert soils may require multiple sampling times (Lajtha and Schlesinger 1988, Knight 1991, Paul and Clark 1996). There are other nutrients that can, individually or collectively, influence the composition of

a plant community, such as K, Mg, and additive "fertility indices" (Scott and Billings 1964, Woodward et al. 1984, McKnight et al. 1990). Chemistry of *Bromus*-invaded and uninvaded soils in the Canyonlands areas has been extensively sampled, and higher K and K/Mg have been the only consistent nutrients correlated with *Bromus* (J. Belnap, *unpublished data*).

The larger spaces between plants in the *Stipa* community might appear to offer greater invasion possibilities (e.g., greater availability of space, light, water, and nutrients). In desert communities, space and light are seldom limiting. On the other hand, water and nutrients are often limiting, and strongly tied to soil characteristics. In this study, higher silt and lower sand were found in soils invaded by the fall-germinating *Bromus*. Sandy soils drain quickly and have a limited ability to bind nutrients, thus allowing both water and nutrients to drain to deeper layers. In contrast, finer-textured soils hold both water and nutrients at the soil surface (Paul and Clark 1996). In deserts, evaporation of soil surface water is minimal in winter; thus, finer-textured soils, with increased water and nutrients at the soil surface, would benefit winter-active, surface-rooting plants such as *Bromus*. Sandy soils, with less water and fewer nutrients at the surface, would be less favorable for plant growth in winter. (It is interesting to note that there are no native, winter-active herbaceous plants in the flora of this region, regardless of soil type.) On the other hand, the high surface evaporation rates of late spring and summer generally result in sandy soils having greater water available at depth, favoring plants that germinate in early spring and quickly develop deep roots.

Other site characteristics, such as litter cover or soil stability, can also determine plant establishment success. *Bromus,* with large seeds, has repeatedly been shown to favor sites with increased litter cover (Young et al. 1969), as observed in this study.

Why is documenting changes in soil food webs so difficult?

Soil food webs are extremely complex, and yet we have only crude tools with which to analyze them. Large numbers of different organisms are grouped into categories such as "bacteria," "flagellates," "amoebas," and "ciliates" because of our inability to easily distinguish between species or similar taxonomic groupings (Eckschmitt and Griffiths 1998), Whitford 1996). This level of identification is analogous to only distinguishing plants from animals when characterizing ecosystems. Clearly, a finer level of resolution is needed to understand processes and relationship in these soils. This issue is highlighted by the invertebrate community observed in this study. By looking at total numbers of individuals per square meter present in each community type (H = 400, HB = 960, S = 1168, and SB = 416 individuals/m^2, Table 3), one could say that H, once invaded, "looks" more like an S community. However, examination of individual genera/groups reveals that the transition from an H to an HB community involved losing 5 species and gaining 12 new ones, only one of which was found in the S community (see Table 3). As each of these groups was very different, the resultant structure and function of the food web was expected to be very different. However, the level of detail available for most soil food-web studies precludes such analyses.

Other issues exist beyond species identification. While there are various techniques for assessing biomass or relative abundance, almost all have problems that are difficult to overcome (Coleman and Crossley 1996). In addition, researchers have often ignored soil and/or vascular plant community characteristics except on a very large scale (e.g., forests vs. grasslands, or coarse vs. fine-textured soils). Our data would indicate that fairly subtle differences in these variables may define the response of a given soil food web to perturbation.

Conclusion

It is not known which of the changes observed with *Bromus* invasion will have large-scale and/or long-term consequences for the native plant community or for nutrient cycles in this ecosystem. While some changes appear to be reversible in the short term (such as those observed in the fungal and invertebrate community), many of these changes may be difficult or impossible to reverse. As such, changes are likely to have major consequences for these ecosystems. Management efforts spent in preventing invasion or eliminating new invasions are more likely to be effective than efforts spent in trying to restore pre-invasion conditions.

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APPENDIX A

Observed values for soil food-web components in four kinds of grassland plots (B = *Bromus*, H = *Hilaria*, S = *Stipa*) at three grassland sites in Canyonlands National Park (Utah, USA), measured spring 1996 using 300-g soil.

Food-web component†	n‡	Uninvaded and 2-yr *Bromus* invasion§				Statistical analysis			>50-Yr Bromus‖	
		H	HB	S	SB	H: S	H: HB	S: SB	CP/ HB	SF/ SB
Active bacteria biomass (μg/g)	36	11.2 ± 1.0	7.9 ± 0.9	4.9 ± 0.8	8.3 ± 1.1	**	**	**		
Total bacteria biomass (μg/g)	36	90.2 ± 10.1	72.8 ± 11.1	135.7 ± 11.1	115.5 ± 5.9	**				
Soil fungal numbers/g soil × 10^3	100	32.7	48.5	38	55.8					
Soil fungal species/g soil × 10^3	100	21	25	25	32					
Live-grass fungal infection, Spring (%)	15	72	80	20	30					
Live-grass fungal infection, Spring (no./m^2)	15	14	9	6	10					
Live-grass fungal infection, Fall (%)	15	58	63	28	36					
Live-grass fungal infection, Fall (no./m^2)	15	15	9	14	9					
Dead-grass fungal infection (%)	15	33	47	38	56					
Dead-grass fungal infection (no./m^2)	15	21	27	25	32					
Dead-*Stipa* fungal infection (%)	15	...	...	30	60				...	50
Dead-*Stipa* fungal infection (no./m^2)	15	...	...	5	14				...	5
Dead-*Hillaria* fungal infection(%)	15	70	40	...	...				50	...
Dead-*Hillaria* fungal infection (no./m^2)	15	8	6	...	...				4	...
Dead-*Bromus* fungal infection (%)	15	...	20	...	30				10	10
Dead-*Bromus* fungal infection (no./m^2)	15	...	5	...	7				2	2
Root-feeding nematodes (μg/g)	36	0.02 ± 0.02	0.03 ± 0.02	0.01 ± 0.01	0.06 ± 0.03					
Fungal-feeding nematodes (μ/g)	36	2.76 ± 0.23	2.34 ± 0.42	2.39 ± 0.36	2.24 ± 0.32					
Bacterial-feeding nematodes (μg/g)	36	2.16 ± 0.21	1.47 ± 0.29	1.43 ± 0.25	1.99 ± 0.28	**	*			
Total nematodes (μg/g)	36	5.23 ± 0.31	4.03 ± 0.66	4.01 ± 0.55	4.49 ± 0.48	*				
Flagellates (μg/g)	36	10.9 ± 3.5	70.1 ± 44.2	68.4 ± 42.1	20.0 ± 6.4					
Amoebae (μg/g)	36	200.4 ± 114.9	195.7 ± 56.7	104.5 ± 34.9	55.0 ± 12.3					
Ciliate (μg/g)	36	3.3 ± 1.6	19.9 ± 12.6	9.7 ± 6.5	6.0 ± 3.5					

* $P < 0.05$; ** $P < 0.01$. Statistical differences were determined by t test or Mann-Whitney U. Fungi and inventebrates were not analyzed statistically.

† Measurement units: μg/g = μg/g dry soil; % = percentage relative frequency; no./m^2 = number of individuals or functional groups/m^2.

‡ No. of samples measured.

§ Data are means ± 1 SE.

‖ Cp/HB = the ratio of Chesler Park values to Virginia Park HB values for those components; SF/SB = the ratio of Squaw Flat values to Virginia Park values for these components.

¶ The value represents the (no. of nematodes in 1 g soil) × 10^3.

APPENDIX B

Frequency of occurrence of soil fungal species at three grassland sites in Canyonlands National Park, Utah, USA (Virginia Park, Squaw Flat, and the nearby grasslands of Chesler Park), and fungal species from live native (*Hilaria* [H] and *Stipa* [S]) and *Bromus* [B] dominated grass crowns in Virginia Park. All collections were made in spring 1996; $n = 10$ (10-g soil samples).

Fungal species, by functional type	Soil source							On live plants, Virginia Park	
	Virginia Park				Squaw Flat	Chesler Park			
	H	HB	S	SB	HB	SB	PCA†	H and S	B
Specialists									
Alternaria spp.	0	40	0	0	10	0		90	83
Bipolaris sp.	0	0	0	0	0	0		22	0
Bipolaris spicifera	20	10	30	0	0	0		35	3
Cladosporium herbarum	0	0	0	0	0	0		9	7
Cladosporium spp.	0	0	0	0	0	0		14	30
Epicoccum nigrum	10	30	0	30	0	10	2+	17	10
Fusarium cf. *gibbosum* gp.	0	0	20	20	0	50	1−	...	...
Fusarium cf. *oxysporum*	20	10	10	10	20	30		...	...
Fusarium cf. *moniliforme*	10	0	70	0	0	0	1−	...	...
Fusidium sp.	0	0	0	0	0	0		27	0
Phoma spp.	80	70	40	60	60	70	1+	36	10
Platyspora permunda	0	0	0	0	0	0		20	3
Stagonospora sp.	0	0	0	0	0	0		18	0
Ulocladium spp.	0	0	0	0	0	0		10	3
Generalist saprobes									
Acrophialophora sp.	0	0	10	10	0	30	1−	...	...
Aspergillus fumigatus	100	100	20	40	70	50	1+	...	...
Aspergillus leporis	0	0	50	10	20	0		...	...
Aspergillus spp.	0	0	0	0	0	0		3	10
Chaetomium cv. *aureum*	70	20	100	20	0	80	2+	...	...
Chaetomium spp.	0	0	0	0	0	0		5	10
Mortierella sp. (sterile)	50	30	10	20	20	20	1+	...	...
Penicillium cf. *citreo-nigrum*	0	0	0	0	30	0		...	...
Penicillium cf. *confertum*	0	10	70	60	10	20	2−	...	...
Penicillium cf. *neocanescens*	0	0	0	10	70	0	2−	...	...
Penicillium cf. *raistrickii*	0	0	0	0	60	0	2−	...	...
Penicillium spp.	0	0	0	0	0	0		3	40
Rhizopus oryzae	0	0	0	0	0	0		22	53
Nonparasitic									
Aureobasidium pullulans	30	60	0	0	10	10		16	13
Bispora sp.	0	0	0	0	0	0		3	17
Nematode feeder									
Arthrobotrys sp.	0	0	0	0	0	0		10	0
Epiphyte									
Acremonium spp.	0	10	10	10	50	0		39	43

† The principal-components analysis (PCA) column identifies the species most influencing the PCA components 1 and 2 in Fig. 4A; 1+, 1−, 2+ and 2− denote component 1 or 2, and positive or negative space.