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SOIL BIOTA CAN CHANGE AFTER EXOTIC PLANT INVASION: DOES THIS AFFECT ECOSYSTEM PROCESSES?

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Abstract. Invasion of the exotic annual grass *Bromus tectorum* into stands of the native perennial grass *Hilaria jamesii* significantly reduced the abundance of soil biota, especially microarthropods and nematodes. Effects of invasion on active and total bacterial and fungal biomass were variable, although populations generally increased after 50+ years of invasion. The invasion of *Bromus* also resulted in a decrease in richness and a species shift in plants, microarthropods, fungi, and nematodes. However, despite the depauperate soil fauna at the invaded sites, no effects were seen on cellulose decomposition rates, nitrogen mineralization rates, or vascular plant growth. When *Hilaria* was planted into soils from not-invaded, recently invaded, and historically invaded sites (all currently or once dominated by *Hilaria*), germination and survivorship were not affected. In contrast, aboveground *Hilaria* biomass was significantly greater in recently invaded soils than in the other two soils. We attributed the *Hilaria* response to differences in soil nutrients present before the invasion, especially soil nitrogen, phosphorus, and potassium, as these nutrients were elevated in the soils that produced the greatest *Hilaria* biomass. Our data suggest that it is not soil biotic richness per se that determines soil process rates or plant productivity, but instead that either (1) the presence of a few critical soil food web taxa can keep ecosystem function high, (2) nutrient loss is very slow in this ecosystem, and/or (3) these processes are microbially driven. However, the presence of *Bromus* may reduce key soil nutrients over time and thus may eventually suppress native plant success.

Key words: decomposition; desert grassland; ecological legacy; microarthropods; nitrogen; nutrient cycles; phosphorus; rangeland.

INTRODUCTION

Many studies have examined the effect of invasive plants on native plants and animals. However, only a handful of studies have focused on the effects exotic plants can have on soil food webs (e.g., Belnap and Phillips 2001, Ehrenfeld et al. 2001). Because many studies have found that different plants foster different soil food web organisms (Wardle 2002), it is to be expected that invasive plants would alter soil food composition and structure. These changes, in turn, are expected to alter soil process rates, and thus soil nutrient availability.

The types of changes in soil food webs that affect plant communities are currently of great debate: does a change in belowground biodiversity or richness alone affect ecosystem processes or plant community structure, or are changes in particular soil biota required for changes to manifest in vascular plants? Is there a functional redundancy within soil organisms sufficient to maintain normal ecosystem functions if the soil food web structure is altered?

Despite the significance of these questions, only a limited number of studies have directly addressed whether (or which) alterations in soil food webs can affect vascular plant communities (Wardle 2002). Several noteworthy studies have been published in this arena: some, for instance, have provided evidence that mycorrhizal fungi and microbial biomass can alter taxa composition and/or maintenance of aboveground biodiversity, nutrient capture, and productivity (e.g., van der Heijden et al. 1998). Modeling studies also suggest that altered soil food webs can have a substantial impact on plant growth and species composition (Bever et al. 1997).

Bromus tectorum L. (*Bromus*) is an exotic C_3 annual grass that currently dominates over 7×10^6 ha of the western United States and occurs as a subdominant in most low-elevation plant communities. It has resulted in the endangerment of many native taxa. Studies on how *Bromus* affects soil nutrients have been short-term and equivocal, with varying effects on soil phosphorus (P), nitrogen (N) cycles, and decomposition rates (reviewed in Ehrenfeld 2003). Few studies have addressed

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the effect of *Bromus* on soil biota (e.g., Belnap and Phillips 2001).

In this study, we asked three questions. Do soil food webs differ along a gradient of time since *Bromus* invasion? Are alterations in soil biota reflected in altered ecological process rates and does this affect native grass growth? Is there a relationship between the richness and abundance of plant taxa and soil biota? To answer these questions, we measured soil nutrients, decomposition rates, N mineralization rates, and richness and abundance or biomass of bacteria, fungi, protozoa, nematodes, microarthropods, and vascular plants in three naturally occurring soils with different invasion histories (not invaded, recently invaded, and historically invaded). Because *Bromus* preferentially invades *Hilaria jamesii* Torr. Benth. (hereafter referred to as *Hilaria*) communities at our study site (Belnap and Phillips 2001), we also documented the growth of *Hilaria* when grown in soils with varying invasion history.

Methods

Canyonlands National Park (~1500 m above sea level) is located in a cold semiarid desert in southeastern Utah (average annual precipitation 214 mm, average annual temperature 12°C; Miller 2000). This area has experienced substantial turnover of communities once dominated by *Hilaria* to communities now dominated by *Bromus*. In 1996, we laid out three replicate 30 × 30 m plots within three vegetation types: (1) not invaded, *Hilaria* dominated, and never grazed by livestock; (2) invaded in 1995, now dominated by a *Hilaria–Bromus* mix and never grazed by livestock; and (3) invaded over 50 years ago, *Bromus* dominated for 50+ years, and grazed by livestock until 1974. The not-invaded and recently invaded sites are directly adjacent to each other, with the historically invaded site about 2 km away. Soils at all three sites are Begay sandy loam and similar in texture, depth, and landscape position. Air temperatures and the timing and size of precipitation events show little difference among sites. Vegetation cover by species has been measured annually since 1996, using 25 0.25-m^2 quadrats within each of the nine plots and composite soil samples collected from the top 10 cm (30 subsamples per composite). Soils were gently mixed by hand, split into thirds, and sent moist over ice for immediate extraction to Soil Food Webs, Inc. (Corvallis, Oregon, USA) for microbe, protozoan, and nematode analyses, and to Oregon State University for microarthropod analysis. Dry and sieved soils were sent to Brigham Young University for soil texture and general chemistry analyses. In addition, acid-neutralizing potential (ANP) was determined. High ANP indicates high carbonate or oxide levels, thus indicating low P availability in these highly alkaline soils (pH 8.1).

Protozoa abundance was measured in 1996, nematode abundance in 1996 and 2002, fungal taxa in 1997, active and total bacterial and fungal biomass in 1996, 2001, and 2002, and microarthropods in 2001. In 2002, standardized cotton strips (Latter and Harrison 1988) were inserted to 30 cm in the soil. Cellulose decomposition rates were defined as percentage loss of tensile strength in 2-cm increments along the strips. Rates were similar among depth classes; therefore we present only one example from the surface (4–6 cm) and subsurface (18–20, 22–24 cm) depths.

Hilaria was grown in soils from the three sites in two 30-d trials. Seeds were planted in 10 pots and received deionized water when soils dried. Average minimum and maximum temperatures during Trial 1 were 21 and 27°C and for Trial 2, 16 and 27°C. Dried shoot biomass was determined after both trials, with root biomass determined only for the first trial.

Statistics were run using SPSS v.12 (SPSS, Inc. 2003) and PCOrd v.4.27 (McCune and Medford 1999). Data were tested for normality and equal variance with Kolmogorov-Smirnov and Levene's tests. Nonnormal data were arcsine transformed. Sorenson's similarity index, Spearman's rho, *t* tests, and ANOVA (with post-hoc Tukey's honestly significant difference test) were used to analyze differences in soil taxa and *Hilaria* growth. Nonmetric multidimensional scaling (NMS) ordination (400 iterations with a stability criterion of 0.0001 standard deviations in stress over the last 15 iterations, with a minimum of five separate runs) with Sorenson distance measures were used to delineate site relationships. Monte Carlo was used to test stress and strength of the NMS results and the Pearson *r* bivariate correlation statistic used to test the relationship between NMS scores and environmental variables. Statistical significance was defined as $P < 0.05$, unless otherwise noted in the text. The correlations discussed were statistically significant and had an R of at least 0.65.

Results

Soil chemistry; vascular plant cover; and richness, decomposition, and disturbance rates

During 1996–2002, soils at the recently invaded site had significantly higher levels of N, ammonium (NH_4), P/ANP, manganese (Mn), and organic matter than soils at the not or historically invaded sites (Table 1). All soils had similar levels of nutrients when collected for the *Hilaria* growth trials, although NH_4 and Mn levels appeared to drop and levels of nitrate (NO_3), zinc (Zn), and copper (Cu) increase somewhat at the recently invaded site relative to the other sites. There was no difference in N mineralization rates among the site types, nor any pattern relative to invasion status (Table 1). There was no difference in cellulose decomposition rates across years (Fig. 1). Total plant and *Bromus* cover varied with precipitation at all sites (Table 2). Plant taxa richness was always lowest, and plant cover generally lowest, at the historically invaded sites. During

TABLE 1. Values for soil chemistry mean ± SE at the not-invaded, recently invaded, and historically invaded sites.

Component	Soil chemistry 1996–2002			Soil chemistry at time of planting		
	Not invaded	Recently invaded	Historically invaded	Not invaded	Recently invaded	Historically invaded
Sand (%)	$64.9^{ab} \pm 0.9$	$62.1^{a} \pm 1.1$	$69.7^{b} \pm 3.0$	69	55	65
Silt (%)	$22.5^{a} \pm 0.8$	$25.6^{a} \pm 1.2$	$17.3^{b} \pm 1.7$	16.5	30.5	18.5
Clay (%)	13.0 ± 0.3	11.7 ± 0.8	13.2 ± 1.5	14.2	14.2	16.2
P (ppm)	$6.4^{a} \pm 0.3$	$7.0^{a} \pm 0.4$	$10.9^{b} \pm 0.6$	6.7	7.3	8.2
Organic matter (%)	$0.9^{a} \pm 0.1$	$1.3^{b} \pm 0.1$	$0.7^{a} \pm 0.1$	0.3	0.9	0.5
Zn (ppm)	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.2	0.6	0.3
Fe (ppm)	2.0 ± 0.2	2.0 ± 0.2	2.0 ± 0.3	2.1	2.1	1.7
Mn (ppm)	$4.9^{a} \pm 0.3$	$6.0^{b} \pm 0.4$	$4.7^{a} \pm 0.5$	5.9	5.2	5.9
Cu (ppm)	0.5 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.5	1.2	0.5
Ca exchangeable (ppm)	$3217^{a} \pm 159$	$2951^{a} \pm 150$	$4059^{b} \pm 286$	3404	2612	3268
Mg exchangeable (ppm)	181 ± 6	215 ± 6	192 ± 24	119	200	158
K exchangeable (ppm)	249 ± 13	265 ± 16	309 ± 45	275	517	437
Na exchangeable (ppm)	38 ± 3	40 ± 3	35 ± 3	69	59	59
N (ppm)	$385^{a} \pm 16$	$445^{b} \pm 22$	$385^{a} \pm 22$	352	484	344
Min. NH_4^+-N (ppm)	8.5 ± 1.3	4.5 ± 4.5	11.7 ± 2.1	0.3	0.7	0.3
NH_4^+-N (ppm)	9.5 ± 0.8	12.2 ± 4.2	9.7 ± 1.4	10.2	8.7	6.1
NO_3^--N (ppm)	8.3 ± 1.1	8.5 ± 2.2	7.7 ± 0.5	10.8	14.8	9.7
ANP (%)	ND	ND	ND	5.3	2.5	4.5
P/ANP	ND	ND	ND	1.3	3.0	1.8

Notes: Significant differences among sites are denoted by different superscript letters within rows. Although $N = 1$ in soils used for planting, relative levels of nutrients observed were similar to those seen during 1996–2002. "ND" indicates that data were not collected.

the drought years of 2001–2002, plant richness was highest at the not-invaded sites.

Greenhouse Hilaria *growth response*

Average aboveground *Hilaria* biomass was significantly different between trials ($F_{1,52} = 18.82$, $P = 0.01$) and among soils ($F_{2,52} = 12.32$, $P = 0.01$), with aboveground biomass consistently greatest in soils from the recently invaded site (Fig. 2). There was no difference in root biomass among soils ($F_{2,26} = 1.22$, $P = 0.31$), although the pattern of root biomass was similar to that of shoot biomass. We also found no differences in root/shoot ratios among the three site types.

Soil food webs

In 1996, biomass of active bacteria and fungi and active/total fungi was higher in the not invaded sites compared to the recently invaded sites (Table 3). In 2001, the historically invaded sites had the highest biomass of active bacteria and fungi and active/total bacteria and fungi ($P < 0.02$–0.10) compared to the other two sites. In 2002, active bacteria and active/total bacteria were again highest at the historically invaded site. Richness of fungal taxa found on *Hilaria* shoots appeared higher at the not-invaded sites (13 in spring, 15 in fall) than the recently invaded sites (10 in spring, 11 in fall), with the coefficient of similarity between *Hilaria* and *Bromus* shoots at 48% in spring. Richness of taxa on *Bromus* shoots appeared similar between the recently invaded (nine taxa) and historically invaded sites (eight taxa; Table 4; coefficient of similarity = 75%). It is interesting to note that more saprobic fungal species occur more commonly and total infection rates are higher on *Hilaria* shoots at the not-invaded sites relative to the recently invaded sites. When all site types were combined, active bacteria showed negative correlations with native plant cover ($R = -0.71$). No significant differences were seen in ciliates, flagellates, amoebae, or total protozoa abundance among the sites (Table 5). When all site types were combined, flagellate abundance was found positively correlated to native plant cover ($R = 0.73$).

Bacterial-feeding nematode abundance (Table 5) was higher at the not-invaded and historically invaded sites compared to the recently invaded sites in 1996. However, although abundance was still highest at the not-invaded sites in 2002, there was no difference between the recently and historically invaded sites. In 2002, there were more root/fungal feeders and total nematodes at the not-invaded sites than at the recently or historically invaded sites. Nematode taxa richness dropped from 14 at the not-invaded site to 12 at the recently invaded site and to eight at the historically invaded site. Combining all site types, nematode abundance was negatively correlated with *Bromus* and plant litter cover ($R = -0.72$ and -0.74, respectively).

The composition and abundance of microarthropods also showed large differences among the site types (Fig. 3). The not-invaded sites contained 16 taxa of microarthropods, the recently invaded sites had 12 taxa, and the historically invaded sites had only four taxa. Composition was quite different among the sites: whereas the historically invaded sites were generally a more depauperate version of the recently invaded sites, there was a large difference in composition between the not-invaded and recently invaded sites, with only six taxa in common. Where taxa were common across sites, the not-invaded sites always had the greatest

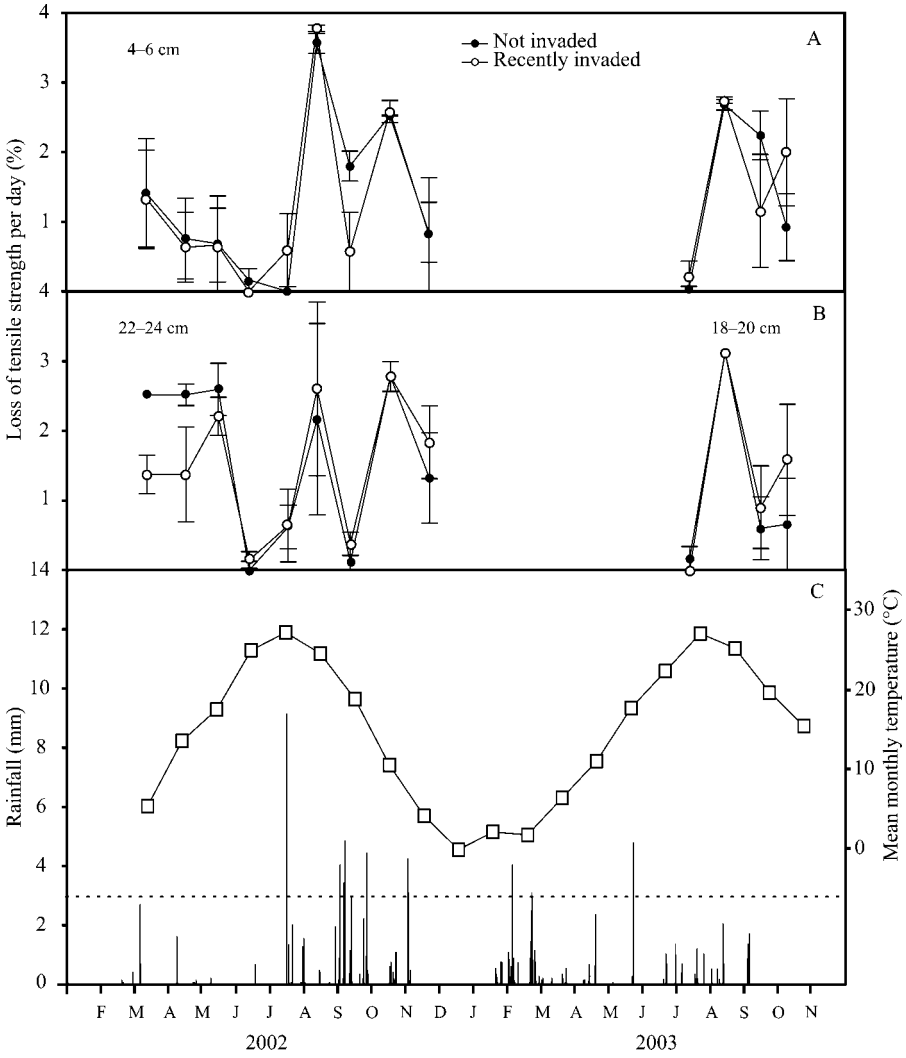

FIG. 1. (A, B) Decomposition rates of cellulose (mean ± SE) and (C) precipitation (bars) and temperature (open squares) over two years at soil depths of 4–6 cm, 18–20 cm, and 22–24 cm at the not-invaded and recently invaded sites. Maximum decomposition rates occurred with high air temperatures, not the presence of *Bromus*. The dotted horizontal line shows the precipitation required (3 mm) to wet soils to 1 cm.

abundance of a given taxon. Among all site types, there was a strong positive correlation between microarthropod taxa richness and abundance and plant taxa richness ($R = 0.70$ and 0.65, respectively) and native plant cover ($R = 0.77$ and 0.69, respectively). However, correlations with plant litter cover were negative ($R = -0.66$) for both microarthropod richness and abundance.

Several interactions between soil biotic components were interesting. When all site types were combined, active bacterial biomass showed negative correlations with microarthropod abundance and richness and nematode richness ($R = -0.72$, -0.69, and -0.83, respectively). Total bacterial biomass was negatively correlated with bacterial-feeding nematode richness ($R = -0.76$). The ratio of active/total bacteria was negatively correlated with nematode richness ($R = -0.81$).

NMS analysis of all soil food web groups combined showed a great similarity between soil food webs where *Bromus* was present (recently and historically invaded sites), whereas the not-invaded sites were quite distinct (Fig. 4). Environmental factors associated with axis 1 (which separated the not-invaded from the two invaded sites) included plant taxa richness ($R = -0.78$), *Bromus* cover ($R = 0.72$), native cover ($R = -0.71$), ANP ($R = -0.66$), Zn ($R = 0.60$), and P ($R = 0.59$). The major factor associated with axis 2 was *Bromus* cover ($R = -0.67$).

DISCUSSION

Distinctive patterns in our data include (1) a rapid decline in richness of fungi and richness and abundance/biomass of nematodes and microarthropods with *Bromus* presence; (2) a higher abundance of active mi-

TABLE 2. Values (mean and SE) for vascular plant species richness and cover of *Bromus*, total plant cover, and native plant cover from 1996 to 2002 at the three site types.

Year	Invasion status	Species richness			*Bromus tectorum* cover (%)			Total vascular plant cover (%)			Native plant cover (%)		
		Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*
1996	not invaded				3.3	1.5	0.35	46.0[a]	2.1	0.04	42.7[a]	2.2	0.0001
	recently invaded				18.7	10.9		45.0[a]	13.0		26.3[b]	2.1	
	historically invaded				10.2	4.5		11.1[b]	4.7		1.0[c]	0.6	
1997	not invaded				3.7[a]	2.9	0.005	64.6	9.8	0.79	60.8[a]	11.8	0.003
	recently invaded				41.6[b]	14.0		66.7	11.6		25.1[b]	2.7	
	historically invaded				70.7[c]	4.5		73.0	3.4		2.4[b]	1.5	
1998	not invaded	12.0[a]	1.0	0.004	6.8[a]	2.7	0.02	52.0[a]	10.2	0.096	45.2[a]	8.2	0.01
	recently invaded	10.7[a]	1.5		54.3[b]	13.4		77.6[b]	8.9		23.4[ab]	4.6	
	historically invaded	3.7[b]	0.9		38.7[b]	5.7		45.9[a]	7.5		7.1[b]	3.1	
1999	not invaded	12.0[a]	1.2	0.008	9.4[a]	1.9	0.058	56.7[a]	4.1	0.03	47.3[a]	3.2	0.0001
	recently invaded	10.3[a]	2.2		44.8[b]	11.4		67.4[a]	12.7		22.6[b]	2.4	
	historically invaded	2.3[b]	0.7		20.1[ab]	8.7		22.3[b]	8.3		2.3[c]	1.8	
2000	not invaded	10.3[a]	0.3	0.08	6.4[a]	2.7	0.003	67.2[a]	9.4	0.006	60.8[a]	10.3	0.002
	recently invaded	8.7[ab]	1.9		9.8[a]	0.2		24.7[b]	3.9		14.9[b]	3.9	
	historically invaded	5.7[b]	0.9		21.3[b]	1.9		29.7[b]	4.1		4.8[b]	1.8	
2001	not invaded	17.0[a]	0.0	0.0001	2.9	1.4	0.17	47.2	3.1	0.14	44.3[a]	4.5	0.001
	recently invaded	12.0[b]	0.6		31.2	11.5		48.6	7.6		17.4[b]	4.3	
	historically invaded	2.7[c]	0.9		27.7	6.1		28.8	5.9		1.1[c]	0.8	
2002	not invaded	6.7[a]	0.9	0.06	0.0	0.0		20.6[a]	2.3	0.013	20.6[a]	2.3	0.004
	recently invaded	3.7[b]	1.3		0.0	0.0		18.5[a]	2.2		18.5[a]	2.2	
	historically invaded	2.3[c]	0.9		0.0	0.0		5.0[b]	2.7		2.6[b]	2.2	

Notes: Average years, 1996 and 1998; wet years, 1997 and 1999; dry years, 2000, 2001, and 2002. Significant differences among site types within a given year are denoted by different letters.

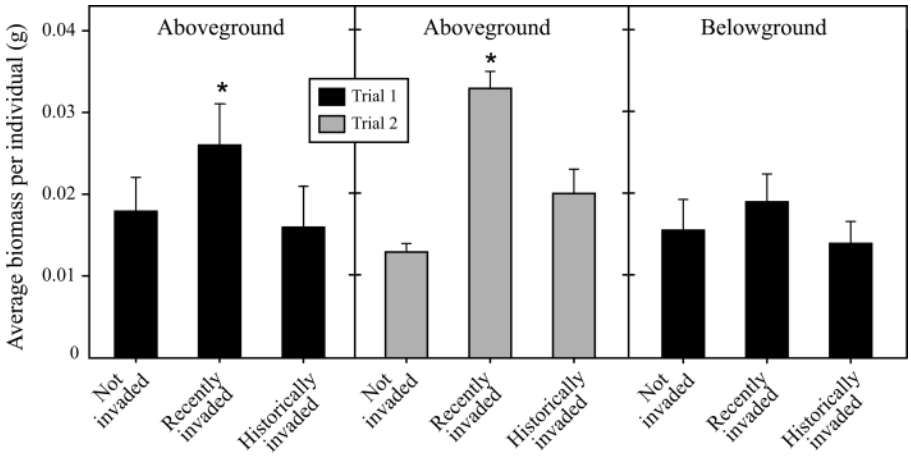

FIG. 2. Aboveground and belowground *Hilaria* biomass (mean + SE) for each of two 30-d trials. Soils were from the three site types. Aboveground *Hilaria* biomass is consistently higher when grown in soils from the recently invaded sites. Significant differences ($P < 0.01$) are denoted by an asterisks.

TABLE 3. Mean and SE of active and total bacterial and fungal biomass (μg/g soil) from the three site types.

Biomass measure	Invasion status	1996			2001			2002		
		Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*
Active bacteria (AB)	not invaded	11.17[a]	0.96	0.03	6.82[ab]	0.74	0.10	5.13[a]	0.61	0.01
	recently invaded	7.90[b]	0.90		6.38[a]	0.35		3.17[a]	1.33	
	historically invaded				8.33[b]	0.85		12.47[b]	1.56	
Total bacteria (TB)	not invaded	90	10	0.27	145	5	0.64	92	8	0.39
	recently invaded	73	11		152	6		113	8	
	historically invaded				147	3		130	24	
Active fungi (AF)	not invaded	3.1[a]	0.40	0.03	3.20[a]	0.93	0.05	0.21	0.21	0.39
	recently invaded	1.7[b]	0.40		3.47[a]	0.26		0.19	0.09	
	historically invaded				5.86[b]	1.25		1.41	0.99	
Total fungi (TF)	not invaded	18	3	0.62	188	37	0.22	20	2	0.14
	recently invaded	16	1		109	11		30	4	
	historically invaded				178	50		21	3	
TF:TB	not invaded	0.24	0.06	0.63	1.29[b]	0.24	0.10	0.22	0.04	0.39
	recently invaded	0.28	0.06		0.73[a]	0.09		0.27	0.03	
	historically invaded				1.24[b]	0.38		0.18	0.05	
AF:TF	not invaded	0.19[a]	0.03	0.03	0.021[a]	0.007	0.02	0.012	0.012	0.42
	recently invaded	0.11[b]	0.02		0.032[ab]	0.002		0.006	0.003	
	historically invaded				0.047[b]	0.014		0.077	0.059	
AB:TB	not invaded	0.13	0.01	0.91	0.047[ab]	0.005	0.08	0.057[ab]	0.012	0.04
	recently invaded	0.13	0.02		0.042[a]	0.003		0.027[a]	0.011	
	historically invaded				0.057[b]	0.006		0.101[b]	0.018	
AF:AB	not invaded	0.31	0.06	0.17	0.50	0.16	0.17	0.05	0.05	0.74
	recently invaded	0.20	0.04		0.55	0.05		0.05	0.03	
	historically invaded				0.74	0.16		0.10	0.06	

Notes: Significant differences among site types within a given year are denoted by different letters.

crobes at the recently or historically invaded sites compared to the not-invaded sites; (3) no apparent relationship between measured ecosystem processes and the structure and taxa richness of soil food webs or the performance of *Hilaria* in the greenhouse trials; and (4) a large temporal variability in bacterial and fungal biomass and nematode abundance.

We measured three soil processes to indicate the effect of soil biota on ecosystem processes: potential N mineralization, cellulose decomposition rates, and nutrient availability to native grasses. We saw no relationship between soil food web structure, abundance/biomass, or richness with potential N mineralization rates. While there were patterns in cellulose decomposition rates similar to those of microbial biomass (active bacterial and fungal biomass and active/total ratios), there was no apparent relationship to nematode or microarthropod richness or abundance. (Protozoa may have contributed to the ecosystem process patterns, although the huge variability made the data difficult to interpret.)

There is substantial literature on linkages among types and abundance of soil biota, especially upper trophic soil fauna and plant performance factors (e.g., net primary productivity, growth rates, leaf nitrogen contents), nutrient cycling and availability, and decomposition rates. These relationships are reported as both positive (e.g., Kuikman and van Veen 1989, Bonkowski et al. 2000) and negative (e.g., Wardle et al. 1997, Cole et al. 2004). We saw few such linkages in this study, especially with upper trophic level fauna. This suggests several possible interpretations of our data: (1) decomposition in this system is mostly microbially driven, with upper trophic levels being insignificant in this

TABLE 4. Frequency of infection by dominant fungal taxa (>10% frequency) on live *Hilaria* and *Bromus* shoots at the three site types.

Species	Fungal type	*Hilaria*				*Bromus*	
		Spring (N = 12)		Fall (N = 9)		Spring (N = 12)	
		Not invaded	Historically invaded	Not invaded	Historically invaded	Recently invaded	Historically invaded
Acremonium spp.	E	11	44	33	33	67	42
Alternaria spp.	FP	100	100	100	92	83	100
Arthrobotrys sp.	Z	⋯	⋯	⋯	17	⋯	⋯
Aureobasidium sp.	S	⋯	⋯	33	⋯	8	33
Bipolaris spicifera	FP	22	11	83	50	⋯	⋯
Bipolaris sp.	FP	33	⋯	25	8	⋯	⋯
Bispora sp.	FP	⋯	⋯	⋯	⋯	8	33
Chaetomium aureum	S	22	⋯	8	⋯	33	⋯
Cladosporium spp.	S	44	⋯	42	⋯	67	100
Embellisia spp.	FP	56	11	8	⋯	⋯	⋯
Epicoccum nigrum	S	56	⋯	⋯	17	33	⋯
Fusarium sp. #2	FP	11	33	⋯	⋯	⋯	⋯
Fusidium sp. ?	FP	11	11	50	⋯	⋯	⋯
Penicillium spp.	S	⋯	⋯	⋯	⋯	⋯	100
Phoma sp.	?	11	56	42	33	13	83
Platyspora permunda?	FP	⋯	⋯	8	33	⋯	⋯
Rhizopus oryzae	S	⋯	22	44	50	83	22
Sphaeropsidales spp.	?	22	⋯	25	17	⋯	⋯
Stagonospora sp.	FP	⋯	⋯	44	17	⋯	⋯
Ulocladium spp.	S	⋯	⋯	33	⋯	⋯	⋯
Sterile white-gray	?	44	11	⋯	⋯	⋯	⋯
Sterile white cottony	?	⋯	44	⋯	⋯	⋯	⋯
Total species		13	10	15	11	9	8

Notes: The coefficient of similarity between fungi on *Hilaria* and *Bromus* shoots in spring was 48%. The coefficient of variability between *Bromus* at the two sites was 75%. Fungal types: E, endophytic; Z, nematode associated; S, saprobic (generalist); FP, facultative parasite. Ellipses indicate that the species was not present. N is the number of plant shoots that were examined.

process and microbial abundance having a low threshold which, when exceeded, does not affect process rates; (2) upper trophic-level fauna are sufficiently abundant and/or redundant in function to maintain soil fertility, or only a few key taxa which are still present are required to maintain soil processes (as found by Bonkowski et al. 2000 and others); and/or (3) the threshold for N is very low for *Hilaria* and *Bromus* and thus even a depauperate soil biota can provide enough N for plants, at least under current conditions. We might have seen more evidence of linkages had we increased our sample size and/or measured all taxa in all years.

There was also no association between patterns in soil biotic abundance/biomass and/or richness and *Hilaria* biomass in the growth trials; instead, *Hilaria* biomass was highest where soil available P, Mn, and total N were highest. Many studies have found the cover of invasive plants in general, and *Bromus* in particular, positively correlated with these nutrients (e.g., Stohlgren et al. 1999, Miller 2000, Blank et al. 2002, Ehrenfeld 2003). We believe these soil nutrient differences were present before the invasion, as we saw little pattern in nutrient levels relative to time-since-invasion and most studies show nutrient changes due to *Bromus* invasion to be relatively small or transient (Evans et al. 2001, Ehrenfeld 2003).

One of the most striking results of this study was the rapidity of change seen in the nematode and microarthropod fauna, as most of the change that occurred over 50 years (historically invaded sites) actually happened within the first few years (recently invaded sites). Within a few years, three of the 14 nematode taxa were lost, while after 50 years, only three additional taxa were lost. The loss of mostly fungal/root-feeding nematodes may have been due to consistently lower plant cover over time at the historically invaded sites, resulting in less available root biomass. In contrast, the species composition of bacterial feeders (all Cephalobidae) appeared stable, regardless of invasion status, perhaps due to the active bacterial populations also being fairly stable across site types. It may also be that the broad distribution of the Cephalobidae shows high adaptability to changing conditions (Yeates 2003). Microarthropods showed a similar response: within one year, 10 taxa were lost and six appeared, while after more than 50 years of *Bromus*, only four more taxa had been lost and two gained. It is unlikely that these species actually emigrated, died, or immigrated so quickly. It seems more likely that at least some individuals were present and ''awakened'' from dormancy by the ''Prince Charming'' kiss (the Sleeping Beauty hypothesis, Lavelle and Spain 2001) of new plant taxa

TABLE 5. Protist and nematode abundance per gram of fresh soil (mean ± SE) at the three site types.

Taxa	Spring 1996			Spring 2002		
	Not invaded	Recently invaded	Historically invaded	Not invaded	Recently invaded	Historically invaded
Protozoa abundance						
Flagellates	12 ± 3	316 ± 249	15 ± 4			
Amoebae	294 ± 149	180 ± 54	486 ± 377			
Ciliates	3 ± 1	21 ± 14	10 ± 6			
Total	308 ± 149	518 ± 240	510 ± 376			
Nematode abundance						
Bacterial feeders						
Acrobeles				1.02 ± 0.44	0.26 ± 0.06	0.26 ± 0.08
Acrobeloides				0.21 ± 0.13	0.02 ± 0.01	0.29 ± 0.10
Acrobelophis				0.11 ± 0.06	0.02 ± 0.01	0.04 ± 0.03
Cephalobus				0.02 ± 0.02		0.03 ± 0.03
Chiloplacus				0.23 ± 0.06	0.03 ± 0.01	0.04 ± 0.02
Cervidellus				0.09 ± 0.04	0.03 ± 0.02	0.04 ± 0.01
Total	1.12[b] ± 0.15	0.74[a] ± 0.10	1.16[b] ± 0.17	1.67[a] ± 0.75	0.37[b] ± 0.11	0.72[b] ± 0.27
Fungal feeders						
Eurdorylaimus				0.04 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
Thonus				0.03 ± 0.01		
Thornia					0.01 ± 0.01	
Total	0.27 ± 0.05	0.25 ± 0.04	0.16 ± 0.04	0.07 ± 0.02	0.04 ± 0.02	0.03 ± 0.01
Fungal/root feeders						
Aphelenchus				0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02
Aphelenchoides				0.13 ± 0.06	0.02 ± 0.01	
Ditylenchus				0.19 ± 0.08	0.01 ± 0.00	
Tylenchus				0.36 ± 0.06	0.06 ± 0.03	
Total	0.45 ± 0.06	0.46 ± 0.08	0.28 ± 0.07	0.69[a] ± 0.20	0.10[b] ± 0.05	0.02[b] ± 0.02
Root feeders						
Helicotylenchus				0.05 ± 0.05		
Meloidogyne					0.01 ± 0.00	
Tylenchorhynchus				0.03 ± 0.03		
Total				0.09 ± 0.09	0.01 ± 0.00	
Total nematodes	1.84 ± 0.22	1.45 ± 0.19	1.60 ± 0.26	2.51[a] ± 1.05	0.52[b] ± 0.18	0.76[b] ± 0.30
Nematode generic richness				14	12	8

Note: Significant differences among site types within a given year for the nematodes are denoted by different letters.

(in this case, *Bromus*), thus facilitating a fast response to changes in plant composition.

The response of the soil taxa to changes in rainfall, *Bromus* cover and/or total plant cover was different among years and site types. Temporal variability in bacterial and fungal biomass and nematode abundance (the only taxa assessed over time) at a given site was greater than the variability due to invasion status for 1996 (an average rainfall year) and 2001 (a dry year). However, in 2002 (another dry year) variability among sites for bacterial-feeding, fungal-feeding, and total nematodes was higher than that due to invasion status, probably because all sites had a large drop in plant cover and *Bromus* was totally absent.

At the historically invaded site, patterns in active bacterial biomass and fungal-feeding nematode abundance were similar to rainfall patterns, while patterns in active fungal biomass were similar to that of *Bromus* and total plant cover. At the recently invaded site, patterns over time in biomass of total bacteria and abundance of all nematode groups were similar to those for *Bromus* cover, while patterns for nematodes were similar to those of total plant cover. At the historically invaded site, biomass over time in all taxa except active bacteria showed a pattern similar to that of *Bromus* and total plant cover. In addition, abundance of all nematode groups showed a pattern similar to that of rainfall. Therefore, we saw an increasing number of soil taxa respond as we progressed along the time-since-invasion gradient, indicating a drop in resistance to change with invasion. There was another indication that the not-invaded site was more resilient to large changes in climate and total plant cover: all nematode groups increased at this site in 2002, despite low rainfall and low plant cover, whereas they all declined dramatically at the other sites. In contrast, active and total microbial biomass was always equal to or higher at the invaded sites, regardless of changes in climate or plant cover.

This study also illuminates some currently debated hypotheses.

Hypothesis 1: Greater plant taxa richness results in greater soil biotic richness.—Plants influence factors that also affect soil biota (e.g., soil carbon, temperature, moisture). It has been hypothesized that greater plant

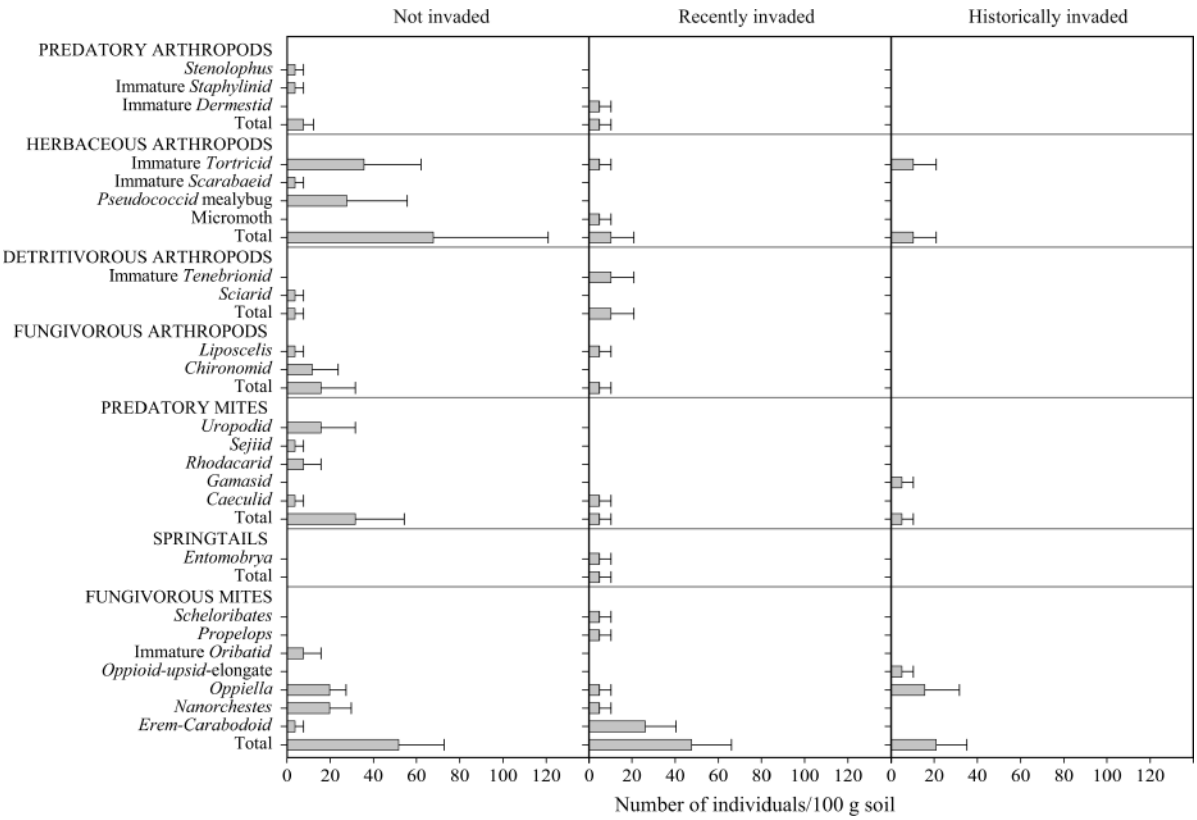

FIG. 3. Mean + SE microarthropod abundance at the three site types (2001). Note that there are 16 taxa at the not-invaded sites, 12 taxa at the recently invaded sites, and only four taxa at the historically invaded sites.

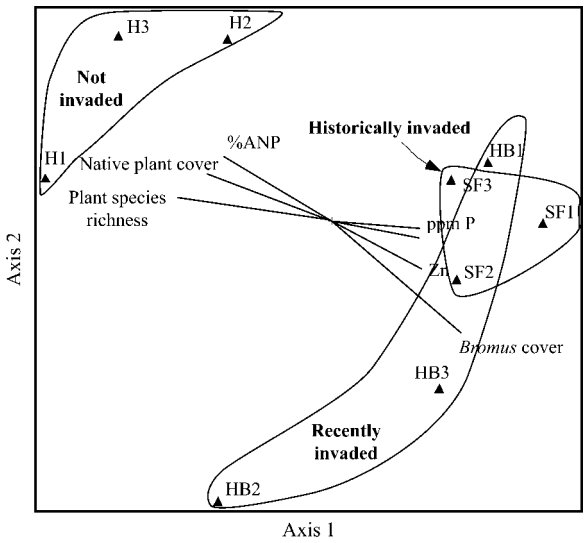

FIG. 4. Ordination of soil biota at the three site types, showing that the invaded sites are distinct from not-invaded sites. Vectors show correlations of site characteristics with ordination space.

richness will result in greater heterogeneity of soil resources, and thus, greater soil biotic richness (reviewed in Wardle 2002). Our study supports this hypothesis: sites with the greatest plant richness (not invaded) had greater richness in all soil groups analyzed (fungi, nematodes, microarthropods), whereas sites with the lower plant taxa richness (historically invaded) had the lowest taxa richness of these groups. Intermediate levels of disturbance (recently invaded plots) did not support higher richness of vascular plants or soil biota.

Other studies show mixed support for this hypothesis. Richness in cryptostigmatid mites (Anderson 1978), gastropods, and mites (Badejo and Tian 1999, Barker and Mayhill 1999, Hansen 2000) were positively related to plant taxa/litter richness. However, Hooper and Vitousek (1998) saw a relationship between soil biota and plant richness only when they had less than two plant taxa, indicating this was unlikely to be operative in most ''real world'' situations. Belnap and Phillips (2001) found lower soil biotic richness where plant richness was higher.

The large variability in the responses above suggests that the relationship between plant and soil biota richness is likely predicated on the specific plants involved, with no generalizable relationship between plant and soil biotic richness. This finding has been supported by multiple studies. Specific tree taxa support higher mite

diversity than other taxa. Badejo and Tian (1999), and David et al. (1999) showed that shrub communities had twice the macrofaunal taxa of forest sites. Eom et al. (2000) showed that arbuscular mycorrhizal fungal richness differed among specific grass taxa. There have also been studies showing that as plant taxa are added to the community, there are changes in microbes (Frankland 1998), arthropods (Paquin and Coderre 1997), and nematodes (Wasilewska 1994). At our site, Belnap and Phillips (2001) showed the addition of the same plant taxa (*Bromus*) to two different plant communities had the effect of increasing soil biotic richness in one community while depressing it in the other, adjacent community. Gremmen et al. (1998) observed that when *Agrostis stolonifera* entered into a shrub community, abundance in some soil groups was enhanced, whereas other groups were depressed.

Hypothesis 2: Higher levels of soil resources result in higher soil biotic richness.—There have been multiple studies showing a positive correlation between higher levels of soil resources (e.g., carbon, nutrients) and richness in soil groups. These include nematodes (Wright and Coleman 1993), chilopods and isopods (Paoletti 1988), and other groups (Schaefer and Schauermann 1990). Wardle (2002) reported seven studies that all showed decomposer richness increasing with soil resources. In this study, however, there was no relationship between the richness of any measured group (fungi, nematodes, microarthropods) and soil nutrient levels. Instead, richness was related to plant richness.

Hypothesis 3: Greater richness means maintenance of ecological processes and their rates.—It has been repeatedly suggested that greater biotic richness confers stability upon ecological processes (e.g., Grime 1998), with the idea that a greater number of taxa will mean a greater probability that the taxa necessary to carry out a specific function will ''match'' future conditions. A corollary hypothesis is that the taxa that may currently appear redundant could be critical under changed conditions (Andren et al. 1995). However, maintaining function may only require the right combination of taxa; richness per se may not assure these particular taxa will be present. This has been suggested for soil biota in a wide variety of habitats (Wardle 2002). Our data support the idea that lower biotic richness does not necessarily result in loss of processes or the slowing of their rates. Soil biotic richness clearly declined with time after *Bromus* invasion, yet the invaded systems appear as functional as the not-invaded systems, if function is defined in terms of decomposition rates, N mineralization rates, plant cover, plant growth, or soil nutrients.

There is some evidence that changing soil food webs can alter process rates (Griffiths et al. 2000). However, Wardle and others (reviewed in Wardle 2002) maintain that soil biotic richness or diversity in natural systems is not likely to be reduced to the point that the decomposer community as a whole is affected. Our data support Wardle's position, as we saw no changes in decomposition, rates despite large changes in soil organisms. Data from other studies also support these findings (reviewed in Wardle 2002).

Conclusion and Future Research Directions

Our goal was to evaluate whether short- or long-term dominance of a site by *Bromus* leaves behind a legacy of altered soil biota, such that future ecosystem processes or plant growth are affected. Our results indicate that the ecosystem parameters we measured did not respond to changes in soil biota, especially changes in the upper trophic levels. The exceptions were a correlation between plant richness and fungi, nematode and microarthropod richness, and the possible relationship of decomposition to microbial abundance.

Long-term dominance by *Bromus* is likely responsible for the low abundance/biomass and richness of the soil biota we saw at these sites. However, despite this reduction, plant-available nutrients are still present in sufficient quantity to support the once-dominant native plant taxa. We believe this supports the argument that taxa richness *per se* does not determine ecosystem process rates and community stability, but instead that the main biotic controls of ecosystem function are likely to be the interaction among the key traits of a few critical taxa, other taxa in the community, and the abiotic environment. Application of the intermediate disturbance hypothesis does not appear warranted in this study, as most measured variables in this and other soil food web studies show a monotonic decline with disturbance.

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