Biol Fertil Soils (2003) 38:72–77
DOI 10.1007/s00374-003-0638-x

ORIGINAL PAPER

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Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*

Received: 17 April 2001 / Accepted: 23 March 2003 / Published online: 14 June 2003
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Abstract Various biotic and abiotic components of soil ecology differed significantly across an area where *Halogeton glomeratus* is invading a native winterfat, [*Krascheninnikovia* (=*Ceratoides*) *lanata*] community. Nutrient levels were significantly different among the native, ecotone, and exotic-derived soils. NO_3, P, K, and Na all increased as the cover of halogeton increased. Only Ca was highest in the winterfat area. A principal components analysis, conducted separately for water-soluble and exchangeable cations, revealed clear separation between halogeton- and winterfat-derived soils. The diversity of soil bacteria was highest in the exotic, intermediate in the ecotone, and lowest in the native community. Although further studies are necessary, our results offer evidence that invasion by halogeton alters soil chemistry and soil ecology, possibly creating conditions that favor halogeton over native plants.

Keywords *Krascheninnikovia lanata* · Great Basin Desert · Halogeton glomeratus · Invasive plant species · Soil chemistry modification · Soil microbial communities

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Introduction

Increased globalization over the past 200 years has resulted in an artificial and unprecedented translocation of species across the globe (Mack et al. 2000). These exotic species often rapidly invade an area to the detriment of native communities. Ecological effects of these invasions range from local effects at the population level to ecosystem effects at regional and ecoregional levels. Many of these changes to ecosystems and their functioning are detrimental, some irreversibly so (Vitousek 1990). Invasive species also present an economic problem, costing the United States as much as U.S. $137 billion annually in lost ecosystem services, control measures, and public health (Pimentel et al. 2000; Wilcove et al. 1998).

There is a wide array of species and habitats involved in this crisis, with each region facing unique problems. In the Intermountain west of North America, the replacement of native perennials by annual weeds leads to a loss of genetic and species diversity, reduced forage production, decreased soil and food web stability, increased fire frequency, and a decline in mineral cycling (Randall 1996; Vitousek et al. 1996; Gordon 1998; Huxel 1999; Stohlgren et al. 1999). Despite a long history of scientific study and public concern, there is remarkably little known about the mechanisms by which alien annual plants displace native perennial vegetation.

Halogeton glomeratus (Chenopodiaceae), an annual currently invading rangelands of 13 western states, originated in Central Asia and was accidentally introduced into the United States in 1934 (Dayton 1951 Pemberton 1986; USDA-NRCS 1999). Halogeton rapidly

invades saline soils (Mack 1986), typically following disturbance events associated with overgrazing, road construction, and agriculture (Tisdale and Zappetini 1953; Eckert 1954; Frischnecht 1967). Consequently, it is often found along anthropogenic rights-of-way, grazing allotments, and fallow fields. Halogeton possesses many of the biological characteristics associated with successful invasive plant species (Westbrooks 1998): it germinates early in the growing season, produces prodigious numbers of long-lived, dormant seeds (Cronin 1965), possesses adaptations for wide seed dispersal (Frischknecht 1968), resists predation by vertebrates (Kingsbury 1964), and has an ability to survive harsh conditions. The bimorphic seeds of halogeton are produced in abundance (Tisdale and Zappetini 1953), providing a high innate capacity for increase that allows halogeton to dominate recently disturbed areas.

Here, we document soil characteristics of an area where a large monoculture of halogeton is steadily spreading into a cold desert community in western Utah dominated by the long-lived shrub, *Krascheninnikovia* (=*Ceratoides*) *lanata*. We measured soil and tissue nutrient concentrations of plants harvested from the native community, the invading halogeton monoculture, and the ecotone between them. Also, we estimated the functional diversity of the soil bacterial community to determine if vegetative changes were accompanied by changes in soil ecology.

Materials and methods

Study area

The Desert Experimental Range (DER), operated by the U.S. Forest Service, is a 22,533-ha facility where the effects of livestock grazing have been studied since 1935 (Clary and Holmgren 1982; Emlen et al. 1989; Freeman and Emlen 1995; Harper et al. 1996). The DER occupies a typical Great Basin valley with elevations ranging from 1,547 to 2,656 m. Seventy-five percent of the DER is composed of gently sloping, coalescing alluvial fans and valley bottom, all draining into a large playa. Soils are mostly gravelly loams, sandy loams, and gravelly sandy loams (Aridisols and Entisols; Tew et al. 1997). Vegetation occurs as a mosaic of cold desert vegetative communities, dominated primarily by shrub *(Atriplex confertifolia, K. lanata, Artemisia spinescens, Chrysothamnus greenei, Ephedra nevadensis*) or shrub-grass *(Pleuraphis hymenoides, Hilaria jamesii, Sporobolis cryptandrus*) associations (Kitchen and Jorgenson 1999). Annual precipitation at the DER averages 15.8 cm $year^{-1}$, with 53% of the total occurring in the growing season (Harper et al. 1996). Moisture accumulates in the soil primarily during the winter, when evaporation and plant respiration is low (Blaisdell and Holmgren 1984).

Halogeton, first documented at the DER in 1969, typically occurs in low population densities as scattered individuals or patches in livestock paddocks, in or adjacent to washes, or adjacent to the gravel roads that crisscross the DER (J. J. Duda, unpublished data). We have focused our attention on a large monoculture of halogeton first observed at the site in 1970, following a flooding event in the previous year that resulted in an unexplained, large die-off of the native winterfat (*K. lanata*) community (Harper et al. 1996). After establishing itself in 1970, halogeton has moved into and replaced the winterfat community at different rates each year, averaging approximately 3 m $year^{-1}$ (S. Kitchen, personal observation).

Sampling design

In August of 1997, we used a stratified-random design to sample vegetative community composition, soil chemistry analysis, and soil microbial diversity. We stratified the halogeton invasion zone into three separate areas: the native winterfat community (NATV), the invading halogeton monoculture (EXOT), and the ca. 5-m-wide interface or ecotone between them (ECOT).

In order to estimate the size distribution of individual plants, we obtained Daubenmire cover estimates (Daubenmire 1959) by centering circular 0.2-m^2 quadrats around randomly located halogeton and winterfat individuals following the methods of Emlen et al. (1989) and Freeman and Emlen (1995). One hundred quadrats were centered around winterfat individuals in NATV (KRLA-NATV) and 100 were centered around winterfat individuals in ECOT (KRLA-ECOT). Similarly, 200 quadrats were centered around halogeton in the EXOT (HAGL-EXOT) and ECOT (HAGL-ECOT) communities. Because of the abrupt demarcation between the two communities, individual winterfat plants were not found in the EXOT area and individual halogeton plants were not found within the NATV area. We counted the number of flowers on all targeted winterfat individuals, but could not do this for halogeton because it was not flowering at the time of sampling.

Soil chemistry

Soil samples were taken at a depth of 0–10 cm within the rhizosphere of individual plants targeted for plant cover estimates. Twenty soil samples were taken within winterfat and halogeton quadrats in both of their parent areas (KRLA-NATV and HAGL-EXOT, respectively) and in the ecotone (KRLA-ECOT and HAGL-ECOT, respectively). We measured exchangeable and water-soluble levels of Ca, K, Mg, and Na, in addition to levels of NO_3^-, NH_4^+, and P. Soil chemistry analyses were conducted at the Soil and Plant Analysis Laboratory at Brigham Young University. Exchangeable Ca, K, Na, and Mg were extracted using a buffered neutral 1.0 normal ammonium acetate solution (Jackson 1958; Hesse 1971; Jones 1973). Soil P and N were determined using sodium bicarbonate and macro-Kjeldahl procedures, respectively (Jackson 1958, Olsen et al. 1954). Soluble salts, pH, electrical conductivity, and Na absorption ratio, were determined on a saturated paste (Rhoades 1982). We determined percentages of soil organic matter by using the Walkley-Black dichromate oxidation procedure (Walkley and Black 1934). We report all elemental soil concentrations in parts per million (ppm, $\mu g\ g^{-1}$).

Plant tissue chemistry

In July 1998, we collected samples from 12 additional quadrats per species in each area to measure the tissue and soil concentrations of Ca, K, P, Na, N, and Mg. Also, we measured the plant tissue concentration of Mn and Zn. We clipped approximately 10 g plant tissue from a single halogeton or winterfat individual. Tissue samples were digested using HNO_3-$HClO_4$ and then analyzed using inductively coupled plasma emission spectroscopy (Richards 1993). Analysis of N and P was performed with an autoanalyzer.

Bacterial functional diversity

We collected soils from NATV, ECOT, and EXOT in June 2000 to assess the impacts of halogeton on the potential bacterial diversity in each of these areas. We used the BIOLOG approach of Zak et al. (1994) to estimate the functional status of soil bacteria based on the ability of these flora to use a range of 95 different C substrates. Ten composite soil samples were collected to a depth of 15 cm from each area. Soils were kept cool and processed within 2 weeks of collection. For each soil sample, a 10 g dry wt equivalent was processed according to the procedures of Zak et al. (1994) using BIOLOG GN-2 microtiter plates. Plates were incubated at 25°C

and the plates were read at 24, 36, 48, 60, and 72 h. Color change was measured at 590 nm using an automatic plate reader (model EL 311; Bio-Tek Instruments). Each BIOLOG plate had a control well that was subtracted from all other wells to correct for background color. Wells that exhibited no growth and that had optical density values <0 were set to zero for the analyses. Optical density values obtained at 72 h incubation were used for the assessment of bacterial functional diversity and statistical analyses.

Two aspects of bacterial functional diversity were obtained from each BIOLOG micrometer plate: total substrate utilization, which is the total optical densities recorded for each microplate; and substrate richness, i.e., the number of substrates that produces an optical density >0.01 (Zak et al. 1994; Dobranic and Zak 1999).

Results and discussion

We used a principal components analysis (PCA) with varimax rotation analysis to reduce the total number of variables describing soil nutrient concentrations, retaining all PCs that had eigenvalues >1.0 and communalities >0.7 (Bryant and Yarnold 1995). Although the loading scores for the first principal component of the water-soluble and exchangeable concentrations were highly correlated (Spearman's rho=0.93, $P<0.001$), those for the second were not (Spearman's rho=0.53, $P=0.12$), so we present the results of the exchangeable concentrations separately from those describing the water-soluble concentrations.

For the water-soluble fraction, two principal components were extracted; the first accounted for 50.6% of the variance and the second accounted for 21.4% of the variance. This PCA clearly separated the parental communities from each other along the first axis (Fig. 1a). Water-soluble K and Na, NO_3, and electrical conductivity all loaded heavily upon the first principal component and very little upon the second axis (Table 1). Increases along the first axis corresponded with significant increases for each of these nutrients across the invasion area, with the highest values occurring in the EXOT area (Table 2). Furthermore, the multivariate soil nutrient scores of HAGL-derived soils in EXOT and ECOT were different, whereas KRLA soils were similar between ECOT and NATV. Additional separation of HAGL soils occurred along the second axis, which had factor loading coefficients mostly influenced by Ca and Mg. These nutrients were depressed in the ECOT (Table 1).

For the exchangeable fraction, three components explaining 80.9% of the variance were extracted, accounting for 50.6%, 17.3%, and 13.0%, respectively. As with the water-soluble-fraction PCA, there was clear separation, especially among HAGL and KRLA in the parental areas, along the first axis (Fig. 1b) which was dominated by elements associated with halogeton, i.e., Na, K, P, and NO_3 (Table 1). All of these nutrients had high positive loadings (Table 3) on the first axis. The soils associated with both species in ECOT were distinct from soils in either parental area, yet overall more similar in multivariate soil space to the NATV soils. As with the water-soluble-fraction PCA, most of the separation occurred along the second axis.

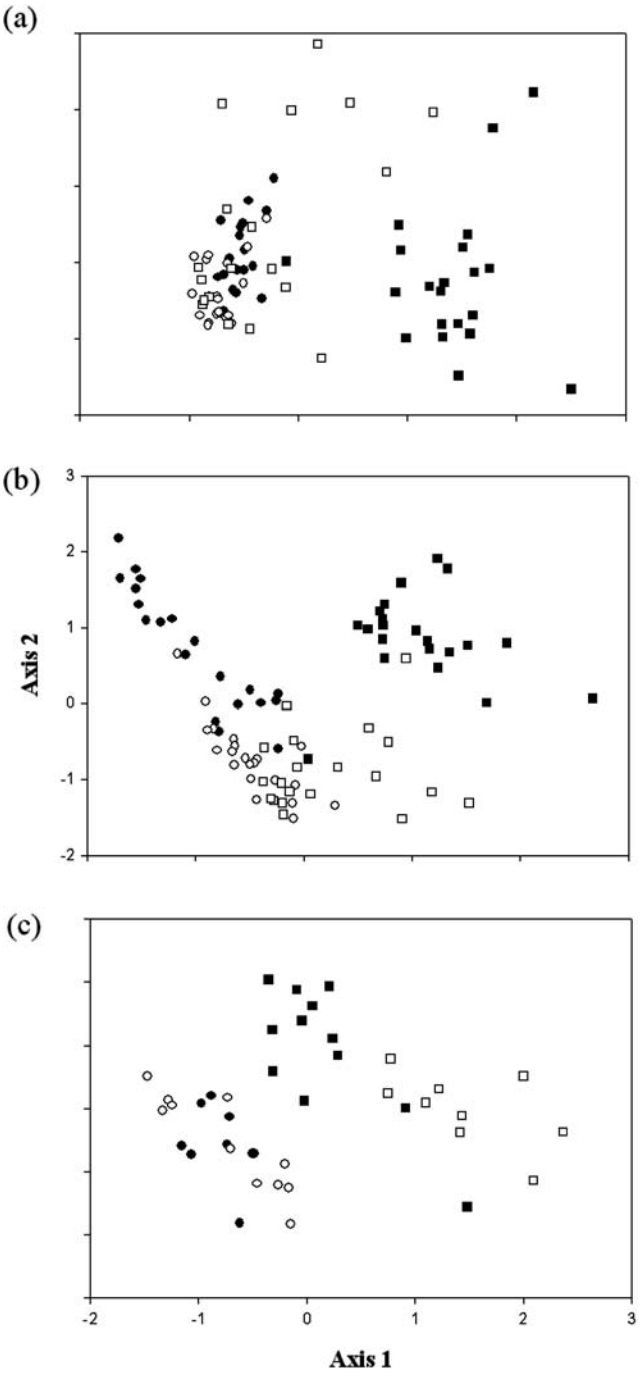

Fig. 1 Principal components analysis (PCA) ordination of (**a**) soil nutrients measured as water-soluble cations, (**b**) soil nutrients measured as exchangeable cations, and (**c**) plant tissue nutrient concentrations of *Halogeton glomeratus* (squares) and *Krascheninnikovia lanata* (circles). Soil rhizosphere samples and plant tissues were collected from *H. glomeratus* in the invading halogeton monoculture (■) and the ca. 5 m-wide interface or ecotone between the latter and the native community (ECOT; ❑) and from *K. lanata* quadrats in the native community (●) and ECOT (◯) areas of the Desert Experimental Range, Utah

Table 1 Factor loading coefficients of principle components (PCs) extracted from water-soluble (*SAR*) nutrients and physical properties of soils associated with *Krascheninnikovia lanata* and *Halogeton glomeratus* collected across an active halogeton invasion area, Desert Experimental Range, Utah. *EC* Electrical conductivity, *OM* organic matter

Variable	Factor 1	Factor 2
Ca (SAR)	–0.002	0.92
K (SAR)	0.93	0.04
Mg (SAR)	0.33	0.87
Na (SAR)	0.92	–0.20
NO_3	0.70	0.27
NH_4-N	0.36	0.02
P	0.85	0.21
EC	0.95	0.06
pH	–0.001	–0.74
OM	0.83	0.37

Table 3 Factor loading coefficients of principal components extracted from exchangeable nutrients and physical properties of soils associated with *K. lanata* and *H. glomeratus* collected across an active halogeton invasion area, Desert Experimental Range, Utah. For abbreviations, see Table 1

Variable	Factor 1	Factor 2	Factor 3
Ca (exchangeable)	–0.69	0.40	0.33
K (exchangeable)	0.85	0.34	0.12
Mg (exchangeable)	0.14	0.92	0.02
Na (exchangeable)	0.88	0.14	0.35
NO_3^-	0.79	–0.06	–0.08
NH_{4+}-N	0.12	0.74	0.01
P	0.76	0.32	–0.36
EC	0.94	0.22	0.01
pH	–0.01	0.04	0.95
OM	0.74	0.41	–0.36

The soil nutrient profile across this area of invasion, whether taken singly (Table 1) or in multivariate space (Fig. 1a, b), clearly suggests significant differences among the three areas. The three essential plant macronutrients (N, P, and K) were all higher in the EXOT area compared to the directly adjacent areas of ECOT and NATV. Furthermore, concentrations of Na were especially striking, increasing 22 and 49 times the levels in NATV for water-soluble and exchangeable fractions, respectively. Halogeton sequesters Na in high concentrations (Table 4). At the end of each growing season, plants senesce and leave an abundant litter layer that leaches Na into the soil following each precipitation event (Eckert and Kinsinger 1960). Although further studies, including manipulative and experimental approaches are necessary, we propose that over a period of years, repeated sequestration and leaching has drawn Na from deeper soils and deposited it on the surface, causing a dramatic change in soil chemistry, facilitating the invasion of halogeton. Harper et al. (1996) showed in the laboratory that winterfat seedlings can germinate and grow on halogeton-influenced soils at rates equal to those for winterfat-derived soils, but only provided that such soils have been sterilized. It is possible that the presence of halogeton, with the associated influences on soil chemistry, disrupts the microbial community (see below), which in turn could increase the pathenogenicity of soil microbes and explain the results of Harper et al. (1996). Studies are currently underway that examine this hypothesis and others.

Our PCA of plant tissue concentration, which extracted two factors explaining 74.4% of the variance among sites, might explain differences seen in soil properties and offer possible explanations of the mechanisms involved with this invasion of halogeton into NATV habitat. The two species were separated into two distinct groupings in multivariate tissue concentration space (Fig. 1c). Moreover, halogeton from the ECOT was fairly distinct from that of the EXOT community with clear separation occurring along the first axis. However, winterfat showed no differentiation based upon whether individuals were

Table 2 Average (SE *in parentheses*) nutrient concentrations ($\mu g\ g^{-1}$) and physical characteristics of rooting zone soils associated with *K. lanata* (***KRLA***) and *H. glomeratus* (***HAGL***) individuals sampled in three different areas of an active halogeton invasion area, Desert Experimental Range, Utah. Significant differences were assessed using a Kruskal-Wallis test and non-parametric post hoc tests. Means followed by a *different letter* are significantly different at$P$ =0.05. Nutrients were rated on relative importance to plant performance: essential and limiting (1), essential but not limiting (2), and non-essential (3) following Cross and Schlesinger (1999). Soil samples were taken under **KRLA** and **HAGL** individuals located in the native community (**NATV**), the monoculture of invading halogeton (**EXOT**), and the ca. 5 m ecotone between them (**ECOT**); for other abbreviations, see Table 1

Nutrient ($\mu g\ g^{-1}$)	Importance	KRLA-NATV	KRLA-ECOT	HAGL-ECOT	HAGL-EXOT	H	P
NH_4^+-N	1	11.4 (0.9) A	3.7 (0.5) B	5.8 (1.8) B	12.5 (0.6) A	44.3	<0.001
NO_3^-	1	3.3 (0.3) A	2.7 (0.3) A	5.2 (0.9) A	7.0 (0.7) B	34.7	<0.001
P	1	12.6 (0.4) A	12.9 (0.5) A	13.8 (0.7) A	24.7 (1.2) B	45.4	<0.001
K (exchangable)	1	511.0 (23.0) AB	475.1(30.0) A	638.4 (42.6) B	1,220.7 (35.2) C	51.1	<0.001
Ca (exchangable)	2	7,837.4 (144.9) A	7,371.9 (97.3) A	6,891.1(123.5)B	6,464.4 (96.5) C	42.8	<0.001
Mg (exchangable)	2	761.1 (42.1) A	459.6 (11.2) B	432.1(36.2) B	928.4 (32.4) A	57.5	<0.001
Na (exchangable)	3	7.3 (1.6) A	28.2 (4.6) B	76.6 (30.4) B	355.5 (40.4) C	56.3	<0.001
K (SAR)	1	49.0 (3.7) A	44.2 (2.0) A	59.5(8.6) A	139.0 (7.7) B	44.0	<0.001
Ca (SAR)	2	66.2 (3.6) A	41.7 (2.2) B	85.6 (11.1) A	50.6 (3.4) A	25.1	<0.001
Mg (SAR)	2	20.3 (1.0) A	12.9 (0.6) B	25.9 (3.9) A	23.1 (2.0) A	29.6	<0.001
Na (SAR)	3	8.2 (0.7) A	23.7 (3.4) B	53.2 (11.3) B	179.4 (7.0) C	61.1	<0.001
EC		0.5 (0.02) AB	0.4 (0.02) A	0.8 (0.1) B	1.7 (0.08) C	56.3	<0.001
pH		8.29 (0.04)	8.18 (0.04)	8.12 (0.06)	8.18 (0.1)	5.39	0.14
OM		0.6 (0.03) A	0.6 (0.03) A	0.8 (0.07) A	1.2 (0.06) B	40.9	<0.001

Table 4 Nutrient concentrations in tissue samples of *H. glomeratus* and *K. lanata* collected from three areas of an active halogeton invasion area at the Desert Experimental Range, Utah. Significant differences in mean nutrient concentrations between species-community types tested with Kruskal-Wallis ANOVA and pairwise comparisons with a distribution free multiple comparison test. Means followed by a *different letter* are significantly different at P=0.05. For abbreviations, see Table 2

Nutrient	KRLA-NATV	KRLA-ECOT	HAGL-ECOT	HAGL-EXOT	*H*	*P*
Ca (%)	1.48 (0.03) A	1.48 (0.06) A	1.42 (0.04) A	1.00 (0.08) B	19.9	<0.001
Mg (%)	0.46 (0.02) A	0.48 (0.02) A	0.66 (0.05) B	0.56 (0.03) AB	15.2	0.002
K (%)	1.59 (0.09) A	1.46 (0.03) A	2.71 (0.26) B	3.03 (0.17) B	26.4	<0.001
Na (μg g^{-1})	532 (54) A	728 (127) A	80,986 (4245) B	77,133 (2886) B	37.7	<0.001
N (%)	2.20 (0.8)	2.14 (0.08)	2.09 (0.11)	2.23 (0.10)	0.31	0.96
P (%)	0.141 (0.004) A	0.136 (0.003) A	0.166 (0.008) B	0.158 (0.004) B	16.5	0.001

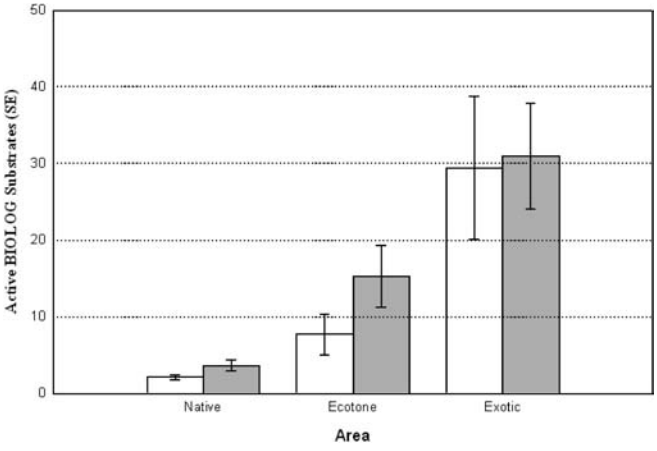

Fig. 2 Bacterial functional diversity of rhizosphere collected under *H. glomeratus* and *K. lanata* in the native, exotic, and ecotone areas of the halogeton invasion. *Filled bars* represent average (±SE) substrate richness and *open bars* average (±SE) total activity on BIOLOG substrates

collected in the NATV or ECOT areas. This suggests that winterfat is not losing nutrients in the presence of halogeton. Further, it is halogeton whose tissue concentrations differed between the ECOT and EXOT. The effects of this competition was seen in differences in the stature of individual KRLA and HAGL plants within the ecotone versus each parental area. A frequency distribution of cover values for 100 individuals of each species per area showed that HAGL plants were smaller in the ECOT than in EXOT (χ^2=54.8, P <0.001), whereas there was no difference in KRLA plants (χ^2=2.4, P>0.25). So, competition or other neighborhood effects apparently negatively affect halogeton fitness, but do not affect winterfat. Yet the halogeton monoculture has been expanding and displacing the native community for over 30 years.

The three areas also differed significantly in the functional diversity of soil bacteria. Total substrate activity, measured as the number of substrates promoting bacterial growth on BIOLOG plates, was 13.8 times higher in the EXOT area than the NATV area ($F_{2,27}$=14.0, P<0.001; Fig. 2). Similarly, substrate richness was highest in EXOT, intermediate in ECOT, and lowest in NATV ($F_{2,27}$=17.1, P<0.001; Fig. 2). Post-hoc Student-Newman-Keuls tests revealed that the total substrate utilization and substrate richness was significantly different among all sample locations (P<0.05). Differences in bacterial functional abilities were not due to soil moisture, which was found not to differ among the three areas at the time samples were taken. It is not clear whether the increase in microbial activity occurs as a result of or in spite of the increase in litter, soil organic matter, or soil chemistry. Other studies examining the microbial community dynamics as they relate to the halogeton invasion are currently underway.

In conclusion, our results clearly show significant differences in soil chemistry and microbial community structure among the three areas affected by the invasion of halogeton. We point out that our design was pseudoreplicated, because the halogeton invasion area was unique at the DER and replicates were unavailable. As such, generalizations about the results are limited. However, based on other KRLA soil samples taken from four different areas at the DER (data not presented), we believe that the soil chemistry profiles of the NATV area are representative and thus the possibility of pre-existing gradients fails to explain the patterns in our data. Furthermore, the halogeton invasion zone is not static, but has been expanding since 1970. These lines of evidence, coupled with data presented, suggest the hypothesis that the presence of halogeton alters both the physical soil environment and the soil microbial community in ways that are maladaptive for native species. Similar conclusions have been drawn by Talley and Levin (2001), based upon research showing both above-ground and below-ground habitat alterations associated with the salt marsh invasion by *Phragmites australis* and by Kourtev et al. (2002) who showed dramatic changes in microbial community structure and function associated with invasive stands of *Berberis thunbergii* and *Microstegium vimineum*.

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