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Comparison of Ground Beetle (Coleoptera: Carabidae) Assemblages in Rocky Mountain Savannas Invaded and Un-invaded by an Exotic Forb, Spotted Knapweed

Abstract

We compared ground beetle (Carabidae) assemblages between spotted knapweed (*Centaurea maculosa* Lam.) -invaded (invaded) and un-invaded (native) habitats in Rocky Mountain savannas. Carabids play important roles in biotic communities and are known as a good indicator group of environmental change. Carabid species activity-abundance and diversity were estimated, and environmental measurements were taken at four transects at each of six study sites in 1999 and 2000. Data on carabid trap captures were analyzed at both the species and functional group level. We found that species belonging to specialist predator and omnivore functional groups were more abundant on transects at invaded sites, whereas generalist predator species were more abundant within native sites. Carabid species richness was similar between invaded and native sites; however, evenness was greater at invaded compared to native sites. Greater species evenness in invaded versus native sites was primarily due to an increase in activity-abundance of species in the omnivore and specialist predator functional groups and a decrease in activity-abundance of dominant species belonging to the generalist predator functional group. Our results suggest that spotted knapweed invasion results in an alteration of carabid community structure and leads to the homogenization of carabid assemblages in Rocky Mountain savannas. Biotic homogenization, the increase in taxonomic similarity of once-diverse communities, is often a direct outcome of exotic invasions and an important concern currently facing biodiversity conservation.

Introduction

Biological invasions of nonindigenous organisms into novel habitats are becoming increasingly common worldwide (Hanfling and Kollmann 2002). Exotic organisms can influence biotic community structure and composition, as well as cause direct and indirect alterations to the physical environment (Williamson 1996, Pimentel et al. 2005). Exotic species may influence species richness and abundance of indigenous organisms, either directly through competition (Smith 2005), predation (Grosholz et al. 2000), and parasitism (Prenter et al. 2004), and/or indirectly through effects on trophic cascades and habitat (Crooks 2002, Gratton and Denno 2005, Groot et al. 2007).

Spotted knapweed (*Centaurea maculosa* Lam.), a Eurasian perennial forb, is considered to be one

of the most ecologically harmful invasive plants in western North America (Duncan 2001). Currently, over seven million acres in the U.S. and Canada are invaded by spotted knapweed (Duncan 2001), producing strong negative effects on native grassland communities (Tyser 1992, Ortega et al. 2006). In the northern Rocky Mountains, spotted knapweed primarily threatens mixed bunchgrass and forb communities of prairies and savannas. Once established, spotted knapweed forms dense, near-monoculture stands. Direct and indirect effects of spotted knapweed invasion on ecosystem processes and functions include alterations in soil chemistry (LeJeune and Seastedt 2001), changes in fire and hydrological regimes (Randall 1996, Jacobs and Sheley 1998), and increased soil erosion, sedimentation, and water run-off (Lacey et al. 1989). Effects of spotted knapweed invasion on plant communities include a reduction in native plant diversity (Tyser and Key 1988, Tyser 1992, Ortega and Pearson 2005), and a decrease in native forb, graminoid, and cryptogam cover

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(Tyser 1992). Few studies have examined effects of spotted knapweed invasion on animal communities (Ortega et al. 2006), although bottom-up effects are likely to result due to impacts of spotted knapweed on native plant-dependent species. One group of animals that are likely to be strongly affected, both directly and indirectly, by exotic plant invasions is insects (McEvoy 2002). Insects play critical roles in determining ecosystem structure and function (Wilson 1990, Wilson 1992), and consequently alterations in important invertebrate groups may influence ecosystem integrity.

We examined the response of carabid (ground) beetles to exotic plant invasions because these beetles play important roles in biological communities, especially as predators (Thiele 1977, Lövei and Sunderland 1996). Also, carabids are good indicators of environmental change. They are ubiquitous, abundant, easy to sample, and have well-known life histories so that changes in their diversity and activity-abundance can be related to observed changes in the environment (Lövei and Sunderland 1996, Niemelä et al. 2000). In addition, carabids exhibit distinctive species and/or genus-specific habitat requirements, short generation times, high fecundity relative to many other organisms, and high sensitivity to environmental change (Lindroth 1961-1969, Thiele 1977, Grum 1986, Lövei and Sunderland 1996, Niemelä et al. 2000).

The primary objectives of our research were to: 1) determine how spotted knapweed invasion influences carabid species diversity and activity-abundance, and functional group activity-abundance within Rocky Mountain savannas, 2) determine how carabid community (i.e., carabid assemblage) composition and structure varies between invaded and native habitats, and to 3) relate carabid community composition and structure to the relative abundance of spotted knapweed and other environmental variables.

Methods

Study Sites

Six study sites were established on the Lolo National Forest in Missoula and Mineral Counties, Montana, U.S.A. Three sites were moderately invaded with spotted knapweed (>25% mean cover) and three sites were invaded by only trace amounts of spotted knapweed (<1% mean cover)

(hereafter referred to as native sites). GPS derived Universal Transverse Mercator (UTM) coordinates for invaded sites were (Iv1=695961E, 5210032N, Iv2=694742E, 5209493N, Iv3= 699071E, 5205189N), and UTM coordinates for native sites were (N1=696891E, 5204085N, N2=287985E, 5184438N, N3=289279E, 5182267N).

Each study site consisted of sparsely forested grassland (ponderosa pine [*Pinus ponderosa* Laws.] and Douglas-fir [*Pseudotsuga menziesii* Douglas]) savanna located within a matrix of denser Douglas-fir dominated forest. Common native bunchgrasses occurring within these grasslands were bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg's bluegrass (*Poa sandbergii* Vasey), and June grass (*Koeleria cristata* Pers.). Dominant native forbs occurring at the sites were arrowleaf balsamroot (*Balsamorhiza sagittata* Pursh (Nutt.)), lupine (*Lupinus* spp.), yarrow (*Achillea millefolium* L.), and blue-eyed Mary (*Collinsia parviflora* Lindl.). Sites were chosen that possessed similar disturbance history and physiographic characteristics including elevation (between 1300 m and 1700 m), soils, slope (30% average), and aspect (southwest), to control for confounding factors. Previous analysis of plant communities at these study sites showed that vegetative differences between invaded and native habitats were primarily driven by knapweed invasion (Ortega and Pearson 2005).

Collection and Identification of Carabids

We deployed pitfall traps at each of the six sites in 1999 and 2000 to sample the relative activity-abundance of carabids. Traps were placed at equidistant spacing (20 m) along four 250 m transects with a total of 13 traps per transect (52 per site). Transects ran perpendicular to the slope and were located 50 m apart. Four collection periods, each lasting for two-weeks, were chosen for sampling from mid-May (snow-melt) until mid- August (seasonal drought). Pitfall traps were made from 2 L colorless plastic soda bottles, cut in half with the upper portion inverted into the lower to act as a funnel. Traps were placed even with the soil surface. A 1% formalin solution was added to each trap to retard decay of trapped insects during each two-week trapping period.

Carabids were sorted from samples, counted, and identified to species based on Lindroth (1961-

1969). Species identifications were verified by Dr. George E. Ball of the University of Alberta. For functional group analysis, all species that were not rare (occurring in more than 5% of pitfall traps) were placed into functional groups based on taxonomy, life history, and general trophic level (Table 2). These traits were chosen to categorize carabids because previous studies reveal that carabid species do not respond to environmental change in the same manner; instead results from these studies suggest that certain carabid species groups, based on taxonomy, life history, and trophic level (which we term here as functional groups), respond differentially to ecosystem change and disturbance (Richardson and Holliday 1982, Grum 1986, Mader 1986, Szyszko 1986, Casale 1990, Mossakowski et al. 1990, Rushton et al. 1990, Holliday 1991, Michaels and McQuillan 1995, Niemelä et al. 1996, Beaudry et al. 1997). Carabids from our trap captures were categorized into three functional groups: specialist predators (prey on Lepidoptera), generalist predators (prey on a wide range of soil animals), and omnivores (feed on plant materials such as seeds, rosettes, and pollen). We categorized carabid species into functional groups because exotic plant invasion may have differential effects on arthropod species depending on their dietary preferences. This approach has been used in many studies examining effects of exotic plant invasion on arthropods (e.g., Groot et al. [2007] and Gratton and Denno [2005]). We also statistically considered each carabid species separately to provide detailed natural history information.

Vegetation Measurements

Understory vegetation was measured in 5 m radius fixed plots established around each pitfall trap at each site. Visual estimates (after Pearson et al. [2000]) were made of percent cover for the following plant functional groups: shrubs, native forbs, bunchgrasses, spotted knapweed, and the exotic species cheatgrass (*Bromus tectorum* L.). Overstory vegetation was measured as numbers of trees per plot.

Physical Environmental Measurements

Because soil characteristics can influence carabid distribution (Luff et al. 1992), soil moisture retention at five matrix potentials was estimated for all sites in June of 2004. Soil moisture retention at a particular matrix potential relates soil moisture

content to the soil's matrix potential (the amount of energy required to remove water from soil pores). Available soil moisture (amount of water released between -0.3 and -15 bar) is largely dependent on soil properties such as texture, structure, and organic content (Klute 1986). Soil moisture retention at a range of matrix potentials (Klute 1986) was determined for each site to allow comparisons of soil moisture availability among sites. To do this, a soil probe was used to extract 3 cm diameter soil cores from the mineral soil line to a depth of 15.24 cm at each site. Two cores were randomly extracted along each of the four transects per site for a total of eight cores per site. Soil cores were oven dried for 24 hours at 80°C , and individually sieved through a 2.0 mm screen. Each individual core was divided into five sub-samples for measuring soil moisture retention at five soil matrix potentials (-0.3 , -1 , -5 , -10 , and -15 bar). A cellulose membrane pressure cell was used to measure water retention from -1 bar to -15 bar and a ceramic plate pressure cell was used to measure water retention at -0.3 bar. Moisture retention values (in g) found for each soil matrix potential (five in total) per core were averaged by transect resulting in four sample units per site. Each sample unit yielded five continuous variables (g of soil moisture for each soil matrix potential) for use in nonparametric multivariate analyses.

Soil type at each site was classified to family using the Lolo National Forest Land Systems Inventory (Sasich and Lamotte-Hagen 1989). Soils at all sites were Inceptisols weathered from metasedimentary bedrock parent material. Twelve families of soil types, in total, were found to occur across sites. The presence or absence of the various soil types was used as a set of binary variables in nonparametric multivariate analysis.

Additional environmental variables were measured for each pitfall trap station in 1999 and 2000. Percent bare ground (un-vegetated open ground), rock (surface rocks of fist size or larger), and woody debris, were estimated (after Pearson et al. 2000) to the nearest 5% within a 5 m radius circular plot, and litter was measured in depth to the nearest 0.5 cm. Percent slope was estimated with a clinometer.

Data Analysis

Total activity-abundance for each carabid species and functional group was calculated by pool-

ing trap captures for each individual pitfall trap over all four sampling periods per year. For all analyses, total activity-abundance of carabids from pitfall traps were pooled by transect resulting in four sample units per study site. Transects were treated as the independent sampling unit because carabids are very sensitive to microenvironment changes (Lövei and Sunderland 1996), and because transects were separated by large distances and were stratified by elevation (approx 12 m elevation gain with each transect), both of which resulted in large differences in environmental conditions (e.g., see standard errors in Table 1, representing within site variation). Accordingly, we limited inferences to the transect (i.e., microhabitat or within-site) scale, except in diversity analyses where transect data were summarized at the site level to allow examination of broader-scale patterns (i.e., alpha diversity and beta diversity). Data for 2000 were incomplete for two transects at each of two native and one invaded site due to missing samples from one sampling period. Therefore, data for 2000 were excluded from analyses of diversity and community patterns, i.e., where statistical methods could not account for imbalanced samples. All statistical analyses were set at a significance level of $\alpha = 0.05$.

Carabid Diversity and Activity-Abundance

Alpha diversity of carabids for 1999 was estimated for each site using two metrics, richness and evenness. Because patterns of richness and evenness are likely to be influenced by different mechanisms (Stirling and Wilsey 2001), assessing each separately allows for a better discrimination of the processes that lead to alterations in community composition and structure. To determine whether species richness had been adequately sampled at each of the study sites, species accumulation curves were developed for each site (Magurran 2004). Species accumulation curves indicated that sampling was sufficient to capture species richness at five of the six sites. The first order jackknife estimate (Heltshe and Forrester 1983) was used to assess estimated species richness for each site. The first order jackknife estimate is a non-parametric re-sampling method for estimating species richness and is resistant to bias caused by contagious distributions (Magurran 1988).

Evenness of carabid species at each site was estimated using Simpson's measure of evenness ($E_{1/D}$), which is simply the reciprocal form of Simpson's dominance index (D) (Simpson 1949) divided by the number of species in the sample

TABLE 1. Average and standard deviation of percent cover of vegetation and abiotic variables for transects per site (n= 4 transects per site, 13 pitfalls per transect) for the years 1999 and 2000. BASA (balsam leaf arrowroot), KNAP (spotted knapweed), SHRB (shrubs), BUNCH (bunchgrass), BRTE (*Bromus tectorum*), BARE (bare ground), ROCK (rock), WD (woody debris), LITTER (litter), (TPP (Trees per plot). Inv1, Inv2, and Inv3 represent invaded sites; N1, N2, and N3 represent native sites; n= 4 transects per site (13 pitfalls per transect).

Site	Year	BASA	KNAP	SHRB	BUNCH	BRTE	BARE	ROCK	WD	LITTER	TPP
N1	1999	10.53 (3.36)	0.01 (0.02)	4.17 (3.46)	20.79 (1.20)	1.48 (1.90)	41.54 (6.58)	8.84 (3.28)	4.14 (1.18)	0.77(0.26)	0.59 (0.28)
	2000	15.54 (4.57)	0.01 (0.01)	10.25 (5.17)	29.36 (6.46)	1.44 (1.13)	40.4 (10.42)	6.06 (2.85)	5.29 (2.11)	1.67 (0.43)	0.59 (0.28)
N2	1999	19.39 (3.25)	0.38 (0.59)	4.53 (4.26)	20.1 (2.21)	4.54 (4.16)	34.08 (4.84)	6.05 (2.78)	0.77 (0.69)	0.52 (0.21)	0.18 (0.26)
	2000	19.44 (4.77)	0.20 (0.30)	5.17 (3.73)	29.33 (1.93)	4.83 (1.96)	35.66 (6.67)	5.42(3.86)	0.68 (0.45)	0.94 (0.39)	0.18 (0.26)
N3	1999	19.232 (6.37)	1.68 (2.67)	2.49 (2.75)	15.31 (3.04)	0.93 (1.01)	36.12 (6.41)	2.04 (1.04)	4.76 (1.51)	0.58 (0.09)	0.5 (0.07)
	2000	22.16 (5.14)	1.06 (1.74)	6.426 (3.4)	36.56 (11.98)	0.30 (0.25)	29.53 (10.59)	0.40 (0.37)	4.63 (1.62)	1.01 (0.59)	0.5 (0.07)
Inv1	1999	13.81 (7.91)	30.9 (6.89)	6.56 (4.28)	10.76 (6.41)	5.26 (4.61)	39.33 (20.43)	7.01 (5.37)	3.58 (2.24)	0.65 (0.34)	0.25 (0.17)
	2000	16.15 (2.59)	26.96 (5.26)	5.59 (2.56)	5.28 (3.25)	2.78 (1.87)	11.33 (4.07)	3.15 (1.39)	3.13 (1.96)	0.81 (0.25)	0.25 (0.17)
Inv2	1999	9.35 (6.02)	17.51 (14.30)	1.03 (2.03)	10.69 (3.39)	11.91 (12.8)	26.2 (4.11)	9.05 (4.4)	0.4 (0.77)	0.52 (0.6)	0.04 (0.08)
	2000	13.75 (3.13)	16.55 (16.63)	2.36 (4.43)	15.04 (7.22)	7.53 (5.63)	14.63 (12.35)	7.54 (6.36)	0.27 (0.24)	0.84 (0.72)	0.04 (0.08)
Inv3	1999	7.01 (3.56)	16.66 (5.0)	7.33 (10.88)	11.74 (4.44)	6.23 (4.91)	31.39 (3.01)	1.38 (0.61)	1.52 (1.15)	0.37 (0.26)	0.2 (0.19)
	2000	5.37 (2.65)	18.83 (5.78)	7.79 (11.05)	19.33 (5.6)	11.13 (6.14)	25.94 (2.61)	0.588 (0.58)	1.258 (0.71)	1.14 (0.39)	0.2 (0.19)

(Smith and Wilson 1996, Magurran 2004). $E_{1/D}$ ranges from 0-1 (one represents maximum evenness) and is one of the best evenness measures available that is truly independent of species richness and weighs rare and dominant species equally (Smith and Wilson 1996, Magurran 2004).

All diversity indices and confidence intervals were calculated using Species Diversity and Richness version 2.65 (Pisces Conservation, Ltd, UK). Bootstrapping was used to generate standard errors and 95% confidence limits. A two-tailed paired-sample t-test was used to define the mean population difference between observed and estimated species richness within sites. Two-sample t-tests were used to test mean differences of carabid species richness and species evenness between knapweed invaded and native sites (SPSS Inc. 2001).

Beta diversity, the amount of variation in species composition and structure among sites (Whittaker 1972), was obtained using two estimators. First, we used average within group distance (D), as a descriptor of compositional and structural change in n-dimensional hyperspace. D is a dissimilarity proportional coefficient based on Sorensen (Bray-Curtis) distance (Czekanowski 1913) and was calculated by Multi-Response Permutation Procedures (MRPP) (described below). The second calculation of beta diversity, average half-changes β_D , uses D by linearizing its relationship with Beta diversity half changes, thereby improving the scale of dissimilarity (McCune and Grace 2002). One half-change is the amount of compositional and structural change resulting in 50% dissimilarity among habitats.

To compare species and functional group activity-abundance between invaded and native transects for 1999-2000, we used mixed linear models (PROC MIXED, SAS Institute 1999), treating year as a repeated measure and site as a fixed factor (to account for broad-scale similarity in environmental conditions). The interaction of invasion (invaded vs. native site) and year was also included in the models. Data from 2000 were included in this analysis for transects with complete data since PROC MIXED adjusts for imbalanced samples across model factors. For all dependent variables, we inspected scatterplots of residuals and found no large deviations from assumptions of normality and homoscedasticity.

Indicator species analysis (ISA) (Dufrene and Legendre 1997) was used to identify the species

that best described differences between invaded and native transects based on two independent measurements of species distribution, specificity and fidelity (i.e., a species was specific to a particular group [specificity] and widespread in all samples of that group [fidelity]). The typology used for this analysis was *a priori* based on invaded and native sites. Potential indicator values (IndVal) that can result from ISA range from 0-100 where values > 25 signify a good indicator (Dufrene and Legendre 1997). Significance of indicator values was estimated using Monte Carlo randomization set at 1000 permutations.

Community Patterns

Non-parametric multivariate analyses using PC-ORD, version 4.25 (McCune and Mefford 1999) were used to detect patterns in species and functional group activity-abundance for 1999. Rare species (occurring in less than 5% of pitfall traps) were not included in multivariate analyses to reduce noise and enhance the detection of community patterns (McCune and Grace 2002). MRPP (Mielke 1984) was used to test for differences among *a priori* groups of knapweed-invaded and native sample units by soil type, carabid functional group, and carabid species composition. Sorensen's dissimilarity measure was chosen for MRPP to calculate the average distance within each group since this measure is robust for community data (McCune and Grace 2002). The weighting used for MRPP to calculate Delta (weighted mean within group distance) was $n/\text{sum}(n)$ (Mielke 1984).

Nonmetric multidimensional scaling (NMS) (Kruskal 1964, Mather 1978) was used to compare carabid species assemblages among sample units in invaded and native sites. NMS was also used to relate soil moisture retention values among all sample units in invaded and native sites for use in correlation analyses with carabid NMS axes. Kruskal's least squares monotonic transformation (Kruskal 1964, Mather 1976) was used to minimize stress. Sorensen's dissimilarity measure was used to calculate distances between sample units. Stress versus iteration number was plotted to assess the stability of the solution with 0.00001 as the stability criterion. Monte Carlo permutations were used to assess the probability that a similar final stress could be expected by chance for a particular dimension. Pearson's r^2 was used to correlate sample unit distances in a reduced

TABLE 2. Activity-abundance of carabids captured in pitfall traps on transects in spotted knapweed-invaded and native savanna sites in western Montana (1999-2000), analyzed using mixed model analysis (PROC MIXED) (df= 1,18). Least squares means of transects $\pm$ SE are presented to adjust for unbalanced samples by year and site. Numbers in bold represent significant differences between site types at $P \leq 0.05$. GP, generalist predator; SP, specialist predator; O, omnivore.

Species	Functional group ^a	<u>Native</u>	<u>Invaded</u>	<i>F</i> (<i>P</i>)
		Mean (SE)	Mean (SE)	
<i>Amara latior</i> (Kirby)	O	8.5 (1.19)	10.5 (1.15)	1.5 (0.24)
<i>Amara obesa</i> (Say)	O	2.2 (1.54)	8.6 (1.46)	9.0 (0.008)
<i>Amara idahoana</i> (Casey)	O	4.2 (1.16)	8.1 (1.09)	6.0 (0.025)
<i>Amara interstitialis</i> (Dejean)	O	1.7 (0.33)	2.7 (0.3)	5.0 (0.038)
<i>Amara ellipsis</i> (Casey)	O	1.4 (0.34)	1.5 (0.32)	0.0 (0.84)
<i>Amara littoralis</i> (Mannerheim)	O	0.3 (0.36)	1.4 (0.34)	4.2 (0.05)
<i>Amara aurata</i> (Dejean)	O	0.4 (1.3)	12.5 (1.26)	45.2 (<.0001)
<i>Harpalus fraternus</i> (Leconte)	O	0.7 (1.05)	6.3 (0.98)	15.8 (0.001)
<i>Harpalus cautus</i> (Dejean)	O	121.6 (16.95)	93.2 (16.48)	1.5 (0.24)
<i>Harpalus innocus</i> (Leconte)	O	0.8 (0.51)	1.6 (0.49)	1.1 (0.3)
<i>Anisodactylus binotatus</i> (Fabricius)	GP ^b	4.1 (1.29)	4.6 (1.25)	0.1 (0.77)
<i>Calleida viridis amoena</i> (Leconte)	GP	0.2 (0.28)	1.3 (0.26)	8.6 (0.009)
<i>Carabus taedatus</i> (Fabricius)	GP	41.4 (4.75)	18.4 (4.69)	11.8 (0.003)
<i>Pterostichus protractus</i> (Leconte)	GP	3.9 (0.77)	<0.1 (0.77)	13.2 (0.002)
<i>Pterostichus sphodrinus</i> (Leconte)	GP	1.7 (0.25)	0.8 (0.23)	6.6 (0.02)
<i>Pterostichus adstrictus</i> (Eschscholtz)	GP	0.1 (0.22)	0.4 (0.21)	1.2 (0.3)
<i>Calosoma luxatum</i> (Say)	SP ^c	5.9 (5.92)	26.4 (4.88)	9.3 (0.007)
<i>Calosoma moniliatum</i> (Leconte)	SP ^c	1.8 (1.16)	2.1 (1.15)	0.0 (0.9)

^a Functional groups classified by trophic group at the genus level (Lindroth, 1961-1969)

^b Exotic species from Europe

^c Specialize on Lepidoptera larvae and pupae (Lindroth, 1961-1969)

dimensional space with distances in the original dimensional space to describe the percent of variation explained by the ordination.

To determine how carabid community structure related to environmental variables, Pearson product correlation analyses were performed. Environmental measurements taken at each pitfall trap were averaged by transect and correlated to carabid NMS axes. Prior to analysis, the constant 1 was added to all values to accommodate for zeros in the data set. Values were then log transformed.

Results

Vegetation

Mean vegetative cover between native and invaded sites differed significantly (Ortega et al. 2004; Table 1). Knapweed cover on knapweed transects averaged >25% in 1999 and 2000 compared to <1% on native transects across years (Ortega et al. 2004). Cover of balsamroot, bunchgrass, and bare ground was significantly higher relative to other habitat components on native transects,

whereas each was reduced on knapweed transects (Ortega et al. 2004).

Carabid Diversity and Activity-Abundance

Eighteen species of carabids were collected over all sites and years (Table 2). These species were divided into three functional groups (see methods): generalist predators, specialist predators and omnivores, with two, six, and ten species falling within each group, respectively (Table 2).

Neither observed nor estimated species richness differed significantly between invaded and native sites (two sample t-test [$t_{d.f.}$): $t_4 = -0.981$, $P=0.382$ and $t_4 = -2.417$, $P=0.341$, respectively; Table 3). Species evenness was significantly higher in invaded versus native sites (two sample t-test: $t_4 = -2.743$, $P=0.05$; Figure 1; Table 3). Beta diversity was lower among invaded sites compared to native sites in terms of both D (0.41 and 0.49, respectively) and β_D (a 0.76 half-change versus about 1 half-change, respectively) (Table 3).

Activity-abundance and species distributions differed substantially between invaded and native

TABLE 3. Carabid diversity in spotted knapweed-invaded vs. native savanna sites in western Montana in 1999.

		Species Diversity			Beta Diversity	
Sites	n_1	Observed Richness	Estimated ₂ Richness (SD)	Evenness $E(1/D)_3$	Ave w/in Group Distance	Average Half-changes ₄
<i>Native</i>						
N1	4	20	23.0 (2.12)	0.2119		
N2	4	17	18.5 (1.5)	0.1735		
N3	4	16	18.3 (0.75)	0.1692		
Mean		18	20.0 (2.67)	0.1849		
Overall	12				0.49	0.97
<i>Invaded</i>						
Inv1	4	21	24.8 (1.44)	0.3306		
Inv2	4	20	23.0 (1.22)	0.2532		
Inv3	4	17	19.3 (1.44)	0.2356		
Mean		19	22.0 (2.81)	0.2731		
Overall	12				0.41	0.76

¹ n = number of transects (13 pitfalls per transect)

² Estimated richness was calculated using the 1st order Jackknife estimator

³ $E_{(1/D)}$ = Simpson's evenness index

⁴ Average half-changes = $\log(1 - \text{average w/in group distance}) / \log(0.5)$

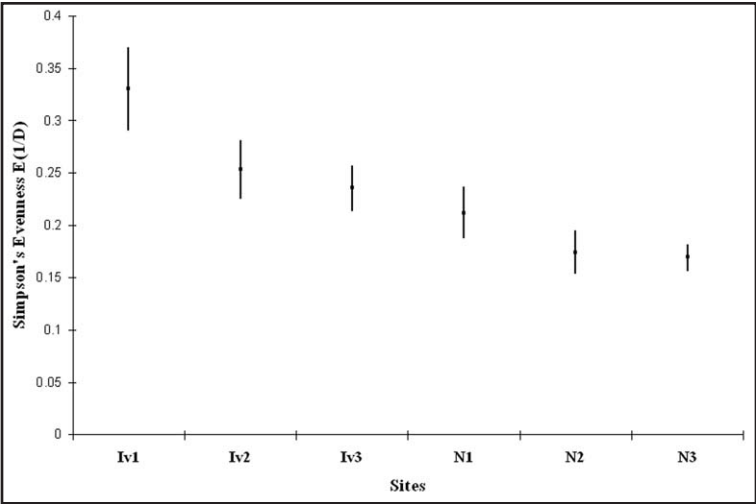


Figure 1. Simpson's Evenness values with 95% bootstrap confidence intervals for carabid species trapped at six savanna sites in western Montana, 1999. Iv1, Iv2, and Iv3 represent invaded sites; N1, N2, and N3 represent native sites; n = 4 transects per site (13 pitfalls per transect).

transects. The specialist predator functional group was 3.7 times more abundant on invaded compared to native transects for both 1999 and 2000 ($df=1,18$; $F=8.85$ and $P=0.008$; Figure 2), whereas, the generalist predator functional group was 2 times less abundant on invaded compared to native transects in both years ($df=1,18$; $F=13.46$ and $P=0.002$; Figure 2). There was no significant difference in omnivore activity-abundance ($df=1,18$; $F=0.11$,

$P=0.74$) between invaded and native transects for both years (Figure 2). ISA detected two generalist predator species as good indicators of native sites and one specialist predator and three omnivore species as good indicators of invaded sites (Figure 3).

Three of the six generalist predator species (*Carabus taedatus*, *Pterostichus protractus*, and *P. sphodrinus*) were significantly less abundant

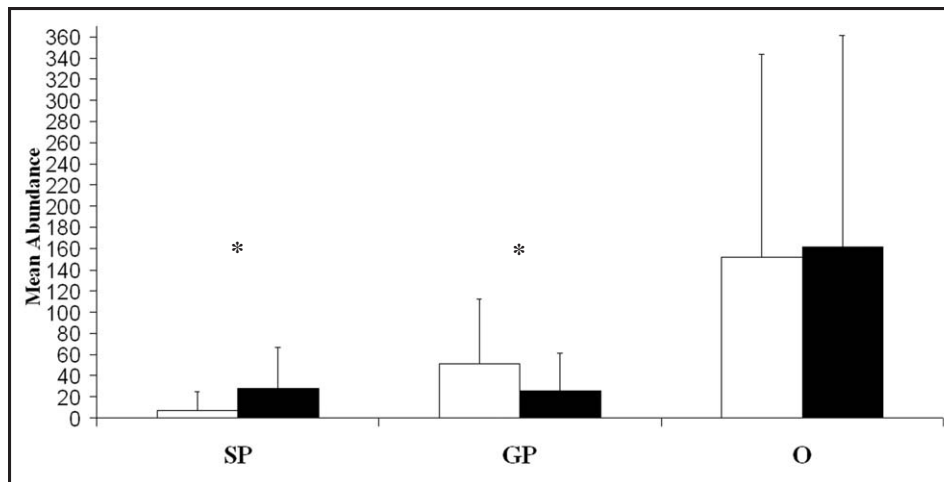


Figure 2. Mean activity-abundance of carabids by functional group on transects in spotted knapweed-invaded (black bars) and native savanna sites (white bars) in western Montana (1999-2000), analyzed using mixed models (PROC MIXED). Least squares means of transects (error bars indicate 95% confidence intervals) are presented to adjust for unbalanced samples by year and site. SP, specialist predator; GP, generalist predator; O, omnivore. * indicates $P \leq 0.05$.

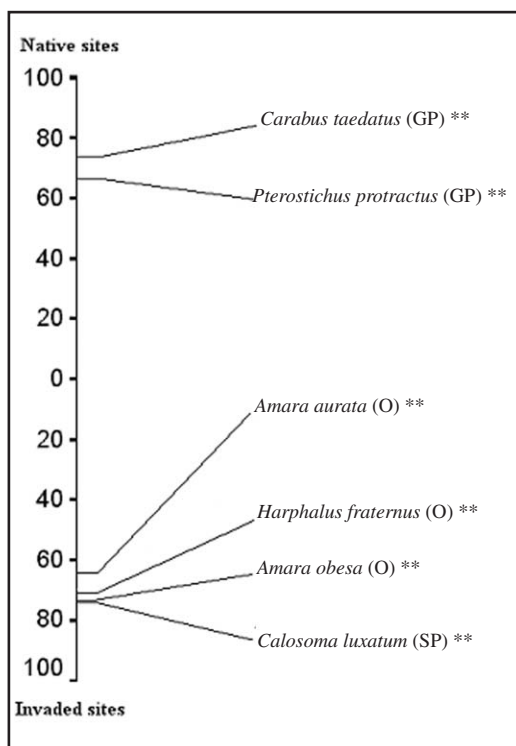


Figure 3. Indicator values (indicator species analysis) of carabid species found to best characterize native and spotted knapweed-invaded savanna sites in Montana, 1999. GP, generalist predator; O, omnivore; SP, specialist predator. ** indicates $P \leq 0.01$.

on invaded transects than native transects in both years (Table 2). Only one of the six generalist predator species (*Calleida viridis amoena*) was significantly more abundant in invaded than native transects (Table 2). There was no significant difference in species activity-abundance of the other two generalist predators (*P. adstrictus*, and an exotic species, *Anisodactylus binotatus*) between invaded and native transects in either year (Table 2).

In the omnivore functional group, five of seven *Amara* species (*A. obesa*, *A. idahoana*, *A. interstitialis*, *A. littoralis*, *A. aurata*) and one of three *Harpalus* species (*H. fraternus*) were significantly more abundant on invaded transects than native transects in both years (Table 2). For one of these species (*A. obesa*), there was a stronger effect of knapweed invasion in 1999 compared to 2000 (invasion $\times$ year: $df=1,16$; $F=9.9$, $P=0.007$). There was no significant difference in activity-abundance of two of the seven *Amara* species (*A. ellipsis* and *A. latior*) and of two of the three *Harpalus* species (*H. cautus* and *H. innocuus*) between invaded and native transects for both years (Table 2).

One of the specialist predators, *Calosoma luxatum*, was significantly more abundant on invaded than on native transects in both years (Table 2), whereas there was no difference in the activity-abundance of the other, *C. moniliatum*, between native and invaded transects (Table 2).

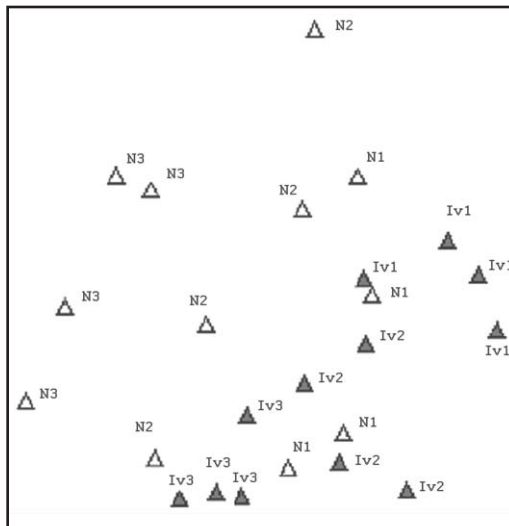


Figure 4. NMS ordination of carabid assemblages within spotted knapweed-invaded and native savanna sites in western Montana, 1999. Dark triangles are invaded sites and white triangles are native sites. Iv, invaded transects; N, native transects. $n = 24$. Final stress= 13.6.

Community Patterns

Carabid community composition and structure analyzed by species was significantly different for transects in invaded versus native sites (MRPP: $T=-3.87$, $A=0.06$, $P=0.004$). Carabid functional group composition and structure was also significantly different between invaded and native transects (MRPP: $T=-3.04$, $A=0.07$, $P=0.016$).

A NMS ordination of carabid species composition and structure yielded a 2-dimensional solution that explained 86% of the variation in the raw data with a final stress of 13.6, and a final instability of 0.00017 ($P=0.020$) (Figure 4). Invaded sample units separated from most of the native sample units in species space except for some sample units in one of the native sites (N1) (Figure 4). Separation of carabid species composition and structure between invaded and native transects was significant (MRPP, $T=-3.87$, $A=0.06$, $P=0.0042$). In addition, invaded sample units clustered more tightly together in ordination space than native sample units, suggesting that species composition and structure is more homogenous in invaded sites compared to native sites (Figure 4). These ordination results were supported by MRPP results where native sample units had a higher within group dissimilarity distance (D) than invaded sites (Table 3).

Effects of Abiotic and Biotic Variables

Soil type was not significantly different between invaded and native transects (MRPP: $T=-1.32$, $A=0.189$, $P=0.10$). A NMS ordination of soil moisture retention values yielded a 2-dimensional solution that explained 97.4% of the variation in the raw data with a final stress of 8.158, and a final instability of 0.0000 ($P=0.020$). Based on carabid NMS axis scores, carabid community composition and structure among sample units in invaded and native sites had a strong relationship to spotted knapweed cover, trees per plot, rock, litter, woody debris, and soil-moisture NMS axes (Table 4).

TABLE 4. Pearson correlation coefficients for comparisons of environmental variables and carabid ordination axis scores for invaded and native transects in western MT. Bold numbers represent significant correlations at $P \leq 0.05$, two-tailed test, $n=24$. Variables are spotted knapweed cover (Knap), Trees per plot (TPP), percent rock (Rk), percent litter (Lit), percent woody debris (WD), soil-moisture retention ordination axes scores (Soil 1, Soil 2), and carabid ordination axes scores (Carabid 1, Carabid 2).

	Knap	TPP	Rk	Lit	WD	Soil 1	Soil 2	Carabid 1	Carabid 2
Knap	1								
TPP	-0.332	1							
Rk	-0.032	0.148	1						
Lit	-0.272	0.372	0.513	1					
WD	-0.168	0.527	-0.156	0.308	1				
Soil 1	-0.106	-0.152	0.435	-0.021	-0.243	1			
Soil 2	0.724	-0.216	0.041	0.135	-0.179	-0.171	1		
Carabid 1	0.489	-0.405	0.327	0.027	-0.256	0.439	0.611	1	
Carabid 2	-0.135	0.393	0.457	0.471	0.424	-0.044	-0.166	0.166	1

Discussion

Carabid functional group structure shifted significantly between spotted knapweed invaded and native habitats. This was due to an increase in activity-abundance of some omnivore and specialist predator species, and a decrease in activity-abundance of some generalist predator species within invaded versus native sites (Figure 2; Table 1). Similar findings of shifts in arthropod functional groups have been found in *Phragmites*-invaded *Spartina* salt marshes versus native *Spartina* salt marshes (Gratton and Denno 2005), and invaded *Solidago* patches versus semi-natural vegetation patches in Europe (Groot et al. 2007). In both these studies there was a decrease in activity-abundance of generalist predators in invaded relative to native sites. Gratton and Denno (2005) and Groot et al. (2007) postulated that such shifts in arthropod functional groups between invaded and native sites is likely to be due to the loss of native vegetation and a modification of vegetative structure in invaded sites.

In our study, shifts in the relative dominance of species within particular functional groups between spotted knapweed invaded and native habitats may be due to altered food availability and other environmental changes induced by spotted knapweed. For example, three of six generalist predators were lower in activity-abundance within invaded relative to native sites. A reduction in generalist predator activity-abundance within invaded sites may be associated with a reduction in herbivore prey density. Spotted knapweed significantly reduces native plant diversity and abundance (Tyser and Key 1988, Tyser 1992, Ortega and Pearson 2005), and in turn may lower the availability of host plants of specialist herbivores. Additionally, a reduction in generalist predator activity-abundance may be due to alterations in environmental conditions associated with invaded habitats. Spotted knapweed is known to alter soil properties (Lacey et al. 1989, LeJeune and Seastedt 2001), fire and hydrological regimes (Randall 1996, Jacobs and Sheley 1998), decrease the amount of bare ground (Pearson et al. 2000), and alter vegetation structure by reducing native plant diversity and cover (Tyser and Key 1988, Tyser 1992, Ortega and Pearson 2005). Such modifications of environmental conditions may result in lower generalist predator abundance, because the invaded habitat may no longer optimally support generalist predator habitat requirements.

One of the two specialist predators (*Calosoma* species specializing on Lepidoptera [Lindroth 1961-1969]) was significantly more abundant in invaded relative to native sites. An increase in the activity-abundance of this predator may indicate that spotted knapweed supports an increase in the availability of its prey. Large numbers of native Noctuidae larvae have been observed within spotted knapweed root balls (D.L.S., personal observation), potentially supplementing food availability for this predator at invaded sites.

Amara and *Harpalus* species, classified as omnivores in this study, possess the ability to consume a wide variety of plant materials including seeds, pollen, and rosettes of weedy vegetation (Thiele 1977). Consequently, spotted knapweed invasion may provide a more favorable environment for some *Amara* and *Harpalus* species by increasing food availability. *Harpalus* are known to feed on exotic weed seeds even in preference to readily available protein resources (Brust and House 1988). Therefore, the increase in some *Amara* and *Harpalus* species we observed in knapweed-invaded sites may be due to their use of spotted knapweed as a food source. Spotted knapweed reaches superabundant densities relative to the native species that it displaces (Ortega and Pearson 2005), maintaining green leaves throughout most of the year and producing massive amounts of flowers, as well as seeds that remain in the seedbank for many years (Jacobs and Sheley 1990). Furthermore, the seeds of this plant produce eliasomes (Pemberton and Delilah 1990), nutrient rich nodes that are often targeted as food by carabids (Ohara and Higashi 1987, Ohkawara et al. 1996, Ohkawara et al. 1997).

Based on the carabid species NMS ordination and beta diversity, we found carabid assemblages to be more diverse and heterogeneous within native compared to spotted knapweed-invaded habitats (Figure 4; Table 2). In contrast, species evenness was greater at invaded versus native sites. However, this increase in evenness appeared to be largely due to an increase in the activity-abundance of several species belonging to the omnivore functional group, and a decrease in activity-abundance of a relatively few species belonging to the generalist predator functional group. Collectively, these results indicate that invasion of Rocky Mountain savannas by spotted knapweed may lead to the homogenization of carabid communities by increasing opportunistic species, particularly

omnivores. A similar increase in opportunistic generalist ground-dwelling arthropods also was found in *Arundo*-invaded versus native southern California riparian habitats (Herrera and Dudley 2003). The reason for the homogenizing effects of invasive plants is not known but may be tied to tolerance of some species to rapid environmental change. Magurran (2004) hypothesized that homogenization of species assemblages can result when a site is disturbed because only a particular subset of opportunistic species in the community can tolerate rapid changes in abiotic and biotic conditions. Our results, along with Herrera and Dudley (2003), indicate that not only disturbance, but invasion and subsequent dominance of a native habitat by an exotic plant can also result in community homogenization. With invasion, however, homogenization is likely to be long-lasting.

Several environmental variables, including the presence and relative abundance of spotted knapweed, were significantly correlated with carabid assemblage structure at our invaded and native sites. Although soil types were not statistically different between invaded and native habitats, soil-moisture retention (which is a function of soil texture, structure, and organic matter) was unique for each type. NMS axes derived from soil-moisture retention values showed a strong relationship with carabid community structure (Table 3). In addition, spotted knapweed cover, litter, rock, woody debris, and number of trees per plot also exhibited strong relationships with carabid community structure (Table 3). Interestingly, cover of spotted knapweed and one of the NMS soil-moisture retention axes were highly correlated. Whether soil characteristics determine spotted knapweed distribution or spotted knapweed influences soil

characteristics cannot be determined from our data. However, spotted knapweed is known to alter the organic matter and structure of soil (a function of soil moisture retention) (Lacey et al. 1989), which may in turn influence carabid distribution and community structure. Most likely several environmental variables interact to determine carabid community structure, and each of these would need to be manipulated independently to conclusively associate an environmental parameter with community structure.

In summary, spotted knapweed not only influences plant community structure, but it also appears to affect heterotroph community structure, and thus, food webs. Simplification of community composition as a result of biological invasions (i.e., biotic homogenization) has been reported in several systems (Olden et al. 2004). Changes in ecologically important arthropod community composition and structure underscore the need for studies to include examination of functional groups and beta diversity, and not just species richness and evenness when investigating impacts of exotics on native communities.

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