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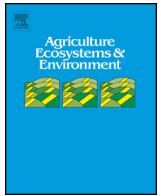
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# Responses of predatory invertebrates to seeding density and plant species richness in experimental tallgrass prairie restorations



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## ABSTRACT

In recent decades, agricultural producers and non-governmental organizations have restored thousands of hectares of former cropland in the central United States with native grasses and forbs. However, the ability of these grassland restorations to attract predatory invertebrates has not been well documented, even though predators provide an important ecosystem service to agricultural producers by naturally regulating herbivores. This study assessed the effects of plant richness and seeding density on the richness and abundance of surface-dwelling (ants, ground beetles, and spiders) and aboveground (ladybird beetles) predatory invertebrates. In the spring of 2006, twenty-four 55 m × 55 m-plots were planted to six replicates in each of four treatments: high richness (97 species typically planted by The Nature Conservancy), at low and high seeding densities, and low richness (15 species representing a typical Natural Resources Conservation Service Conservation Reserve Program mix, CP25), at low and high seeding densities. Ants, ground beetles, and spiders were sampled using pitfall traps and ladybird beetles were sampled using sweep netting in 2007–2009. The abundance of ants, ground beetles, and spiders showed no response to seed mix richness or seeding density but there was a significant positive effect of richness on ladybird beetle abundance. Seeding density had a significant positive effect on ground beetle and spider species richness and Shannon–Weaver diversity. These results may be related to differences in the plant species composition and relative amount of grass basal cover among the treatments rather than richness.

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## 1. Introduction

Predatory invertebrates play an important role in regulating insect pest populations within agroecosystems. Natural regulation of agricultural pests by invertebrate predators and parasites is an ecosystem service estimated to provide 5–10 times more control of pest species than industrially produced pesticides (Pimental et al., 1992) and is valued at \$4.5 billion annually in the United States (Losey and Vaughan, 2006). Invertebrate predators that may reduce the densities of herbivorous insects in cropland include spiders (Araneae) (Laub and Luna, 1992; Lang et al., 1999; Maloney et al., 2003), ground beetles (Coleoptera: Carabidae) (Lang et al., 1999; McCravy and Lundgren, 2011), ants (Hymenoptera: Formicidae)

(Way and Khoo, 1992; Choate and Drummond, 2011), and ladybird beetles (Coleoptera: Coccinellidae) (Obrycki and Kring, 1998).

In the Midwestern United States, there is a positive relationship between crop pest abundance and the proportion of cropland in a county (Meehan et al., 2011). Because patches of natural or semi-natural non-crop habitats (e.g., hedgerows, field margins, grassland and woodland) are recognized to be important sources of food, shelter, and overwintering habitat for predatory invertebrates in agroecosystems, restoring habitats on former cropland can increase local habitat heterogeneity, the abundance of predatory invertebrates, and the provision of pest control within an agroecosystem (Bianchi et al., 2006; Rusch et al., 2010; Pywell et al., 2011). One of the rarest habitats within North American agroecosystems is native (unplowed) northern tallgrass prairie, which since the late 1800s has been largely converted to cropland and covers less than 3% of its pre-settlement extent (Samson and Knopf, 1994). Thousands of hectares of tallgrass prairie have been restored in the central United States in the last few decades using mixtures of native grasses and forbs, with a focus on restoring ecosystem services such as soil retention, improved water quality, and

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provision of habitat for wildlife such as birds, butterflies, mammals, and herpetofauna (Dunn et al., 1993; Packard and Mutel, 1997). The predatory invertebrate communities of these restorations have received less attention even though restorations may provide a valuable ecosystem service of pest control.

Initial studies indicate tallgrass prairie can provide valuable habitat for some predatory invertebrates such as ground beetles. In a comparison of ground beetle assemblages in six different habitats (tallgrass prairie, oats, corn, soybean, old-field, and woods) at four sites in northeastern Iowa, tallgrass prairie hosted a significantly more diverse assemblage of ground beetles than was found in the other habitats (Larsen et al., 2003). Prairie also had a higher percentage of habitat specialists in its assemblage than did the less stable agricultural habitats, which were dominated by generalists.

In two recent studies, Davis and Utrup (2010) and Orlofske et al. (2011) assessed the invertebrate communities of tallgrass prairie restorations, including some predator families. Davis and Utrup found no difference in total invertebrate abundance, family richness, or richness of invertebrates between low- and high-richness plantings of varying sizes and ages in south-central Nebraska. Similarly, Orlofske et al. (2011) found no significant difference in invertebrate abundance and species richness among remnant and restored prairies in Iowa. In both studies, specimens were not identified beyond the family level. To our knowledge, no studies have compared the abundance of predatory invertebrates within experimental tallgrass restorations created with methods typically used to restore prairie in the region. Such an approach may help identify seed mixes that are most effective in attracting predatory invertebrates.

Determining the appropriate seeding density and plant species richness to use in seed mixes is important because these factors affect the plant community and soil characteristics of the restoration, which in turn influences the invertebrate community. For example, high plant species richness in grasslands has been associated with high plant biomass (Hector et al., 1999; Spehn et al., 2000) and greater diversity of plant structures, which increases the availability of microhabitats and limiting resources to invertebrates (Joern and Laws, 2013). In addition, the density of vegetation can affect the densities of invertebrates within a habitat by affecting food resources and the amount of bare ground cover, which influences microclimate (Arnan et al., 2007). Soil moisture has been found to affect oviposition, larval survival, and within-field distribution of ground beetles (Holland et al., 2007). However, the effect of the plant community on soil is not clear as studies have found no significant relationship between plant richness, soil moisture, and soil temperature in grasslands (Porazinska et al., 2003; Dias et al., 2010).

In this study we evaluated the effect of seeding density and plant species richness on grassland invertebrates. We compared the abundance and richness of predatory invertebrates in 55 m × 55 m-research plots seeded with a low richness tallgrass prairie seed mix commonly used in central Nebraska (15 species representing a typical Conservation Reserve Program (CRP) mix used by the Natural Resources Conservation Service, or NRCS, the CP25 mix), at low and high seeding densities, and a high richness mix (97 species typically planted by The Nature Conservancy), at low and high seeding densities. Although high richness seed mixes or high seeding densities can cost up to five to ten times as much as low richness or low seeding densities, little information is available on the benefits that may result from the added richness or seeding density.

We assessed the abundance and richness of four groups of predatory invertebrates: ants, ground beetles, spiders, and ladybird beetles that were identified to species or the lowest taxonomic level feasible and grouped into feeding guilds. Although both omnivorous and carnivorous invertebrates can be effective in pest control (Hunter, 2009) and are encompassed by the term “predatory

H1	C1	H2	C2	H1	C1
C2	H1	C1	H2	C2	H1
H2	C2	H1	C1	H2	C2
C1	H2	C2	H1	C1	H2

**Fig. 1.** Layout of the treatments applied to 55 m × 55 m plots in the study (C1 = low richness seed mix, low seeding density; C2 = low richness seed mix, high seeding density; H1 = high richness seed mix, low seeding density; H2 = high richness seed mix, high seeding density).

invertebrates” in this paper, feeding guilds may respond differently to habitat manipulation (Harvey et al., 2008). We tested three null hypotheses: (1) the abundance of ant, ground beetle, spider, and ladybird beetle feeding guilds will not differ among the four treatments; (2) the richness and Shannon–Weaver diversity of ant, ground beetle, spider, and ladybird beetle feeding guilds will not differ among the four treatments; and (3) there is no correlation between plant community characteristics and invertebrate abundance, richness, and Shannon–Weaver diversity.

## 2. Methods

### 2.1. Study area

The study area lies within the central Platte River ecosystem, which includes the Platte river channel and floodplain from mid-Dawson County to mid-Hamilton County in central Nebraska (NGPC, 2005). The Nebraska Game and Parks Commission has determined the central Platte River to be a biologically unique landscape (NGPC, 2005). The region has a continental climate, with warm, wet summers and cold, dry winters. Mean annual air temperature is 10.4 °C and mean annual precipitation is 63.9 cm (High Plains Regional Climate Center, 2010).

The study site is located approximately 10 km south of Wood River, Nebraska (Hall County; 40°44'41" N, 98°35'11" W) on a 7.3-ha field owned by TNC. Soils at the site are of loamy alluvium or sandy alluvium parent material and include Wann loam, rarely flooded; Caruso loam rarely flooded; and Bolent–Calamux complex, occasionally flooded (NRCS, 2010). The site is bordered to the south and east by county roads and TNC prairie restorations, to the west by a cornfield, and to the north by trees and the Platte river. The study site was under cultivation in a corn–soybean rotation in the decades prior to the experiment.

### 2.2. Treatments and experimental design

In late March and early April 2006, the 7.3-ha field was cultivated and divided into 24, 0.30-ha plots (55 m × 55 m). The plots were seeded from an all-terrain vehicle (ATV) and a John Deere drop spreader according to a 2 × 2 factorial design, in which two levels of richness (low plant richness and high plant richness) were applied using two different seeding densities (low and high seeding rates). The experiment was arranged in a systematic design, with six columns running west to east across the field and each column containing four plots assigned to the four treatments (Fig. 1). The treatments were applied systematically instead of randomly in order to facilitate seeding with the drop spreader. Treatments consisted of: (1) a low richness CRP tallgrass prairie seed mix (CP25 mix, 15 species) used by the NRCS seeded at half the recommended

seeding rate (grass, 148 pure live seeds (PLS)/m<sup>2</sup>; forbs, 16 PLS/m<sup>2</sup>; low richness/low rate mix); (2) the CP25 mix applied at the recommended seeding rate (grass, 297 PLS/m<sup>2</sup>; forbs, 31 PLS/m<sup>2</sup>; low richness/high rate mix); (3) a high richness tallgrass prairie mix typically used by the local TNC (97 species) seeded with a seeding rate typical for TNC grassland restorations in the region (grass, 129 PLS/m<sup>2</sup>; forbs, 43 PLS/m<sup>2</sup>; high richness/low rate); and (4) TNC mix applied at twice the seeding rate (grass, 258 PLS/m<sup>2</sup>; forbs, 86 PLS/m<sup>2</sup>; high richness/high rate) (seed mixes are listed in Appendices A and B). The second and fourth treatments were at half and double, respectively, NRCS or TNC normal seeding rates.

We designed the CP25 seed mix with the Grand Island, Nebraska NRCS District Conservationist. We purchased grass seed used in the mix from Arrow Seed in Broken Bow, Nebraska and forb seed was locally harvested from the Platte river area. TNC high-richness seed mix was harvested from local prairies.

Management of the plots was minimal. All of the plots were burned on March 20, 2008. In July 2008, *Achillea millefolium* and *Helianthus maximilliani* that had invaded the edges of plots where they had not been sown were sprayed with glyphosate and killed in order to reduce the edge effect on the spread of these aggressive species. We clipped the inflorescences of *Bromus inermis* that had naturally invaded the south row of plots from a road ditch and two plots in the northwestern corner of the field in order to limit the spread of *B. inermis* that had not been experimentally introduced into the plots. Following that effort no plants were intentionally killed or manipulated. Vegetation growing in unseeded 2-m lanes between the plots was mowed several times during the growing season.

### 2.3. Invertebrate community composition

We collected surface-dwelling invertebrates by randomly placing ten pitfall traps within each plot for a total of 240 samples, or 60 samples per treatment. We used a random number table to place two pitfall traps along each of five 55-m transects that were 9.1 m apart and ran north to south, with the random number representing the number of paces to walk along the transect before placing the pitfall trap. Each pitfall trap consisted of an 18-mm diameter glass test tube that was filled 2/3 full with Sierra antifreeze (Safe Brands Corporation, Omaha, Nebraska) and inserted into a polyvinyl chloride [PVC] sleeve in the ground. We left the traps open over a 3-day sampling period in late June or early July and in early September 2007–2009. The PVC sleeves remained permanently in the ground and were capped with cork stoppers when not in use, allowing repeated sampling at the same locations over time. Spiders, ground beetles, and ants were identified to species or the lowest taxonomic level possible.

Ladybird beetles were collected with a standard 38-cm diameter canvas sweep net along two 55-m transects within each plot. Ladybird beetles were collected in mid-June, mid-July, and mid-August 2007–2009. Sweep net samples were collected on sunny to partly cloudy days between 1000 and 1600 h when the vegetation was dry, the temperature was above 15 °C, and the wind speed was less than 24 kph. A total of 60 sweeps were conducted for each transect; after each set of 20 sweeps, contents of the sweep net were transferred to a sealable plastic bag and stored in a cooler in the field. The samples were then frozen until ladybird beetles were identified to species in the lab.

### 2.4. Plant community composition

Within each plot, we established five 55-m transects located 9.1 m apart. Each transect ran north to south and was marked on each edge with a 0.6-m rebar spray-painted orange. We assessed

the species composition of the plant community along three of the 55-m transects within each plot, the middle transect and the two end transects, in mid- to late June 2007–2009. We used the line-intercept transect method because it is an efficient method of collecting cover and species richness (Bonham, 1989). Starting at the end of each transect, we stretched a measuring tape to a length of one meter. The transect was broken up into these smaller one-meter segments, or “subtransects,” to keep the measuring tape from sagging in the wind. We measured the basal cover of any plant touching the top edge of the measuring tape by recording the distance that the plant covered along the tape to the nearest 0.2 cm (Elzinga et al., 1998). We took measurements along every twelfth meter and at the opposite end of the transect for a total of six one-meter subtransects along the transect (data at every 0, 12, 24, 36, 48, and 55 m were recorded).

### 2.5. Statistical analyses

Plots were the experimental units in this study. For analyzing the effects of plant species richness and seeding density on abundance, we sorted insect species into feeding guild based on literature reports of adults feeding only on animal material (carnivore), feeding only on seeds (granivore), or feeding on both animal and plant material (omnivore) (Nemeč, 2012). No species were reported to be herbivores, or feeding only on non-seed plant material such as leaves and stems. Because only two granivore species were collected they were not included in the analysis. Twelve other species were not included in analyses because there was no information available on their diet. Spiders are recognized to be largely carnivorous, feeding on insects and other arthropods (Foelix, 2010). Therefore, spiders were grouped into guilds based on foraging strategy and were either web-builders or hunters (Nemeč, 2012). The Shannon–Weaver diversity index ( $H'$ ) (Shannon and Weaver, 1949) was calculated using the BIO-DAP software program (Thomas, 2000) for plants and for each invertebrate taxon rather than each feeding guild within a taxon because of the low number of carnivorous species recorded for insects.

We tested normality in the response variables (abundance of predatory invertebrates by feeding guild, and Shannon richness and species richness of each invertebrate taxon) with the Kolmogorov–Smirnov normality test (PROC UNIVARIATE, SAS Version 9.2; SAS Institute, 2007). Because the residuals were not normally distributed, each set of data was fitted with a mixed-effects model using PROC GLIMMIX (SAS Version 9.2; SAS Institute, 2007). Mixed-effects models are appropriate for data that contains both fixed and random factors and the GLIMMIX procedure does not require the response to be normally distributed (Littell et al., 2006). Plant species richness, seeding density, sampling date, and their interactions were used as fixed effects and plot column was used as a random effect to account for observed spatial variation in soil fertility that generally ran from west to east across the field. We ran post hoc Tukey–Kramer tests comparing significant richness, density, and sampling date interactions. The covariance structure that was the best fit for each model covering multiple years of data was determined by comparing Akaike's information criterion (AIC) for the each model. Spearman rank correlations among plant and insect variables recorded in June or July of each year were conducted using SAS and *P*-values for the Spearman rank test and were adjusted using the Bonferroni method (Rice, 1989).

## 3. Results

A total of 30,320 ants belonging to 18 species, 4897 ground beetles belonging to 52 taxa [51 species, 1 identified to genus only], and 406 spiders belonging to 51 taxa [36 species, 12 families, 3 genera]

were collected from the pitfall traps (Appendix C). A total of 1273 ladybird beetles belonging to six species were collected from sweep netting (Appendix C).

Within each invertebrate group, three or fewer taxa accounted for more than 50% of the specimens collected. The dominant ant species was *Lasius neoniger*, which comprised 97.9% of ant specimens collected across all three years of the study. Ground beetles were dominated by *Notiobia terminata* and *Pterostichus permundus*, which together accounted for 58.7% of the ground beetle specimens. The most abundant spider taxa were Lycosidae, Linyphiidae, and *Agyreta unimaculata*, which accounted for 51.2% of the spider specimens, and the most abundant ladybird beetle species was *Hippodamia convergens*, which accounted for 78.3% of the ladybird specimens. The abundance of most species fluctuated and showed no clear trends over time. However, two species were abundant either early or late in the course of the study. The spider *Agyreta unimaculata* was only collected in June 2007 and comprised 25% of spiders in this sampling period. The ground beetle *Amara musculus* was only collected in September 2009 and comprised 25% of ground beetles in this sampling period.

### 3.1. Treatment effects on abundance of invertebrates within feeding guilds

Most ant, ground beetle, and ladybird beetle species were omnivores and most spiders were hunters. The number of ladybird beetles and ants collected increased during the three years of the study, while the number of ground beetles collected decreased after the first year (Fig. 2). The number of hunting spiders was generally similar among all three years but web-building spiders were most abundant in the first sampling period (Fig. 2).

The abundance of all invertebrate feeding guilds except for carnivorous ants varied significantly with sampling date (Fig. 2, Appendix D). Richness ( $P < 0.0001$ ) and the sampling date  $\times$  richness interaction ( $P < 0.0001$ ) were significant positive effects on omnivorous ladybird beetle abundance. The sampling date  $\times$  richness interaction ( $P = 0.0020$ ) was a significant negative effect on omnivorous ground beetle abundance. Seeding density was a greater factor in explaining spider abundance. For example, the richness  $\times$  seeding density interaction ( $P = 0.0368$ ) was a significant effect on hunting spider abundance. The sampling date  $\times$  seeding density interaction ( $P = 0.0156$ ) was a significant effect on web-building spider abundance, primarily because of the high abundance of web-building spiders in the high seeding density plots and low seeding density plots in June 2007 compared to later sampling periods.

### 3.2. Treatment effects on invertebrate richness and diversity

Because species richness of carnivorous taxa was small relative to omnivorous taxa for ants, ground beetles, and ladybird beetles, mean species richness and the Shannon–Weaver diversity index were calculated for all species within an invertebrate group rather than by feeding guild. Species richness and Shannon–Weaver diversity of all invertebrate taxa (Figs. 3 and 4, Appendix D) varied significantly with sampling date. Ground beetle richness ( $P = 0.0331$ ) and spider richness ( $P = 0.0186$ ) and ground beetle Shannon–Weaver diversity ( $P = 0.0215$ ) and spider Shannon–Weaver diversity ( $P = 0.0409$ ) were significantly higher in plots seeded at higher densities. In addition, there was a significant effect of plant richness on spider richness, with higher spider richness in the low plant richness plots ( $P = 0.0268$ ), and a significant effect of the richness  $\times$  seeding density interaction on spider richness ( $P = 0.0058$ ). There was also a significant effect of the date  $\times$  diversity interaction ( $P = 0.0261$ ) on ground beetle richness.

Total richness of ground beetles was highest in 2007, when 42 species were collected, compared to 25 species in 2008 and 24 species in 2009. The total richness of spiders was variable throughout the study, with the highest number of spider taxa, 38, collected in 2009. Total richness of ladybird beetles and ants did not vary appreciatively throughout the study, ranging from five to six for ladybirds and 11–15 for ants in each year of the study.

### 3.3. Correlation between plant community characteristics and invertebrate richness and abundance

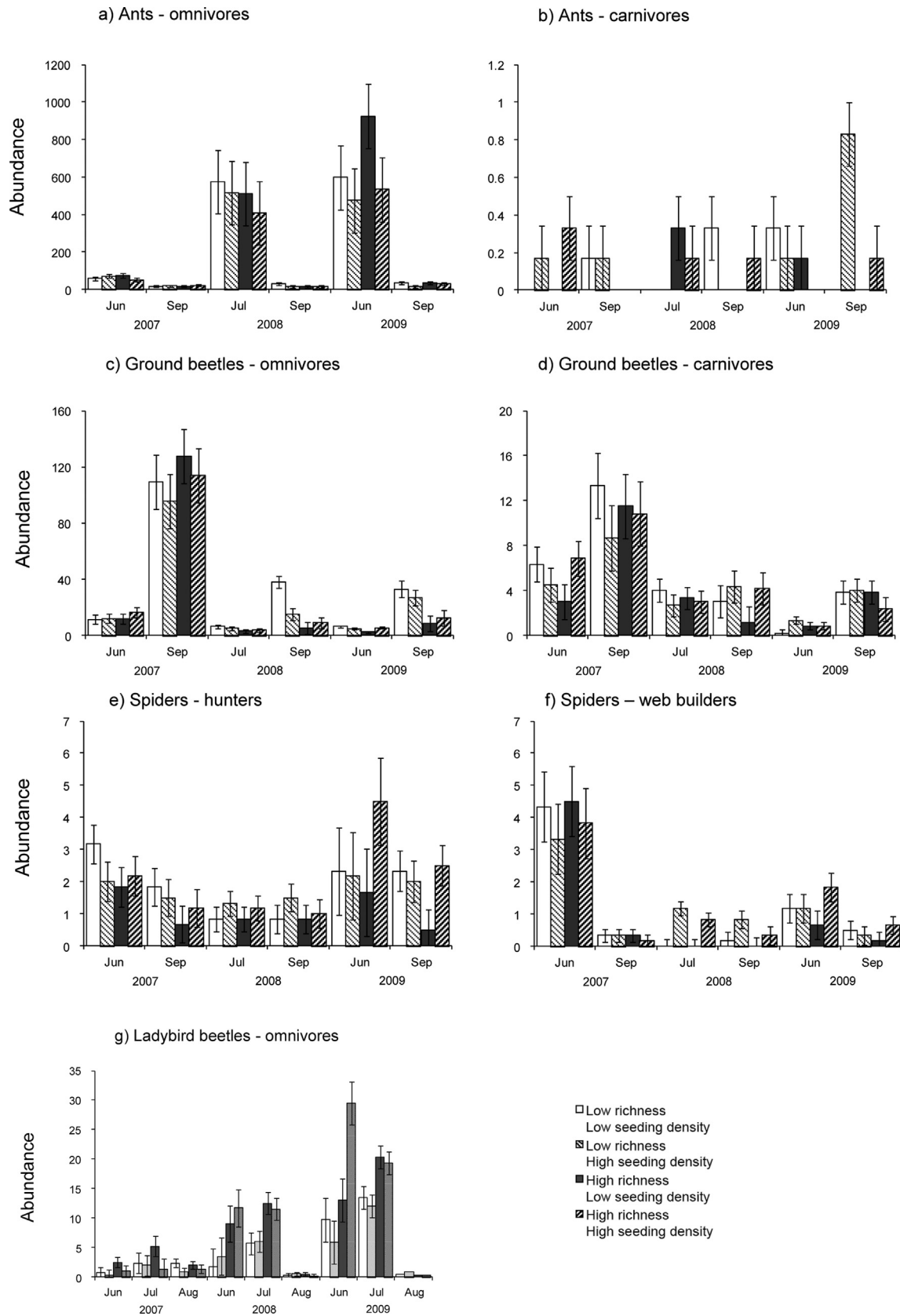
Recorded total seeded plant species richness was approximately twice as large in the high richness plots compared to the low richness plots. During three seasons of sampling from 2007 to 2009, we recorded a total of 27 seeded species, with 9 species observed in the low richness, low seedling density plots; 13 species observed in the low richness, high seedling density plots; 22 species observed in the high richness, low seedling density plots; and 22 seeded species observed in the high richness, high seedling density plots.

Although HZHH in 2007 mean species richness and mean Shannon–Weaver diversity of plants was higher in the plots that had been seeded with the high richness seed mix, by 2009 mean species richness and mean Shannon–Weaver diversity was higher in the plots that had been seeded with the low richness seed mix (Fig. 5). There was a significant negative correlation between plant richness and ground beetle richness in the high richness, high seedling density mix ( $r_s = -0.572$ ) and also a significant negative correlation between plant richness and ground beetle species richness in the low richness, low seedling density treatment ( $r_s = -0.761$ ) (Appendix E). Within each treatment, there was a significant negative correlation between forb basal cover and ant abundance (Appendix E), and a positive correlation between grass basal cover and ant abundance that was significant for the low richness/high density treatment ( $r_s = 0.637$ ). In contrast, there were significant positive correlations between forb basal cover and ground beetle abundance ( $r_s = 0.655$ , high diversity/high seedling density treatment) and spider abundance ( $r_s = 0.644$ , low diversity/low seedling density treatment). There were significant negative correlations between grass basal cover and ground beetle abundance in all but the low diversity/low seedling density treatment (Appendix E).

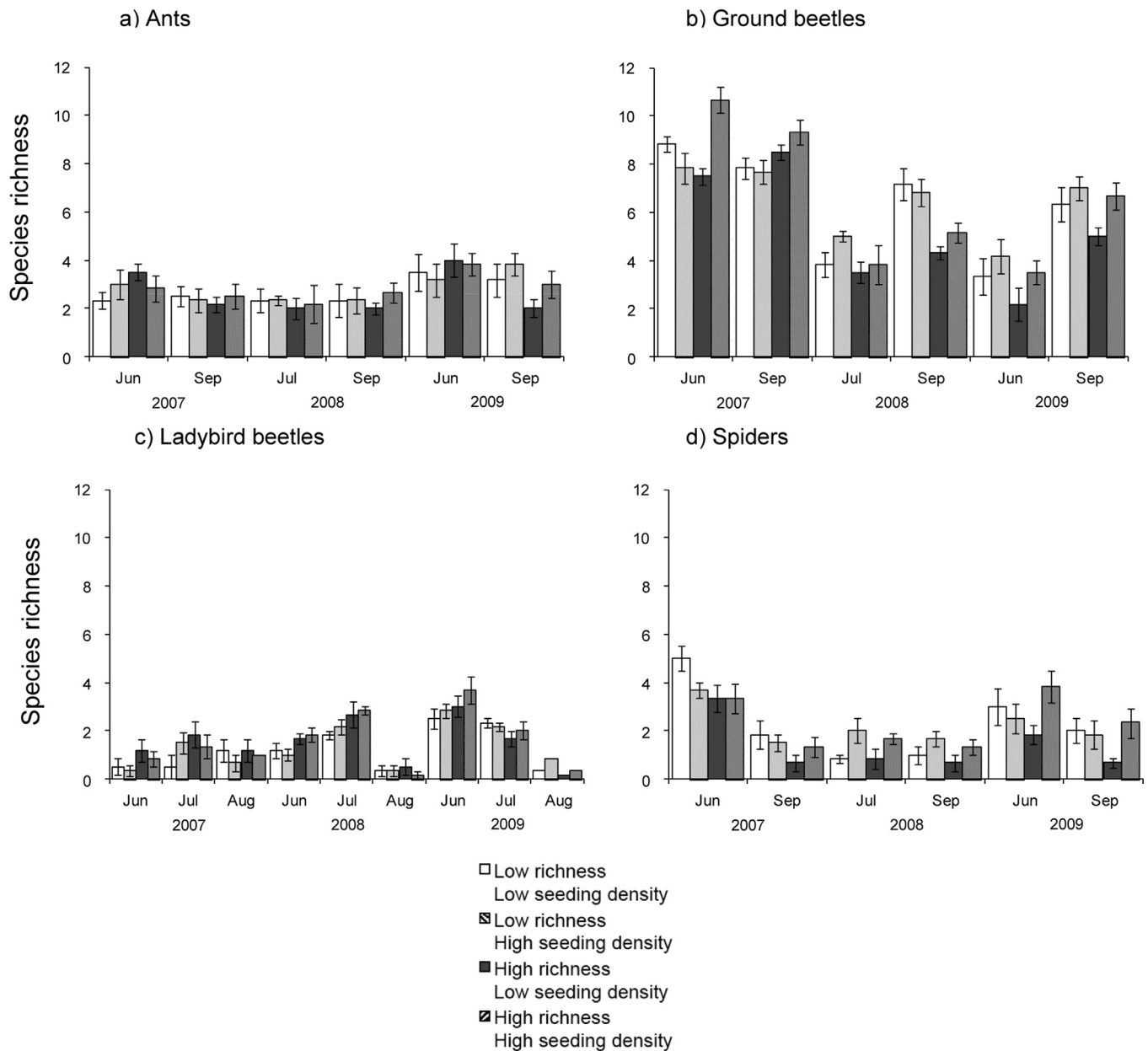
## 4. Discussion

The overall objective of our study was to determine the effect of low and high plant species richness as well as low and high seeding densities on predatory invertebrate richness, abundance, and Shannon–Weaver diversity in experimental tallgrass prairie restorations. We manipulated the structure of the plant community by altering seeding rates and the initial richness of the seed mix to create four restoration treatments. We failed to reject our null hypothesis that the abundance of ants, ground beetles, and spiders would not differ among the treatments, although we did reject the null hypothesis that ladybird beetle abundance would not differ. We also did not reject the null hypothesis that ant and ladybird beetle richness and Shannon–Weaver diversity would not differ among the treatments, but did find that seeding density had a significant positive effect on ground beetle and spider species richness and Shannon–Weaver diversity. We rejected the null hypothesis that there was no correlation between plant community characteristics and invertebrate abundance, richness, and Shannon–Weaver diversity.

In general, our results in young (second–fourth growing season) prairie restoration plots do not support ecological theory describing bottom-up forces in communities, in which a more diverse plant community is associated with a greater abundance and richness of



**Fig. 2.** Abundance of invertebrate species aggregated according to feeding guild during 2007–2009. Values are least-square means ( $\pm$ SE) from mixed-model analysis.  $N=6$  plots per treatment.



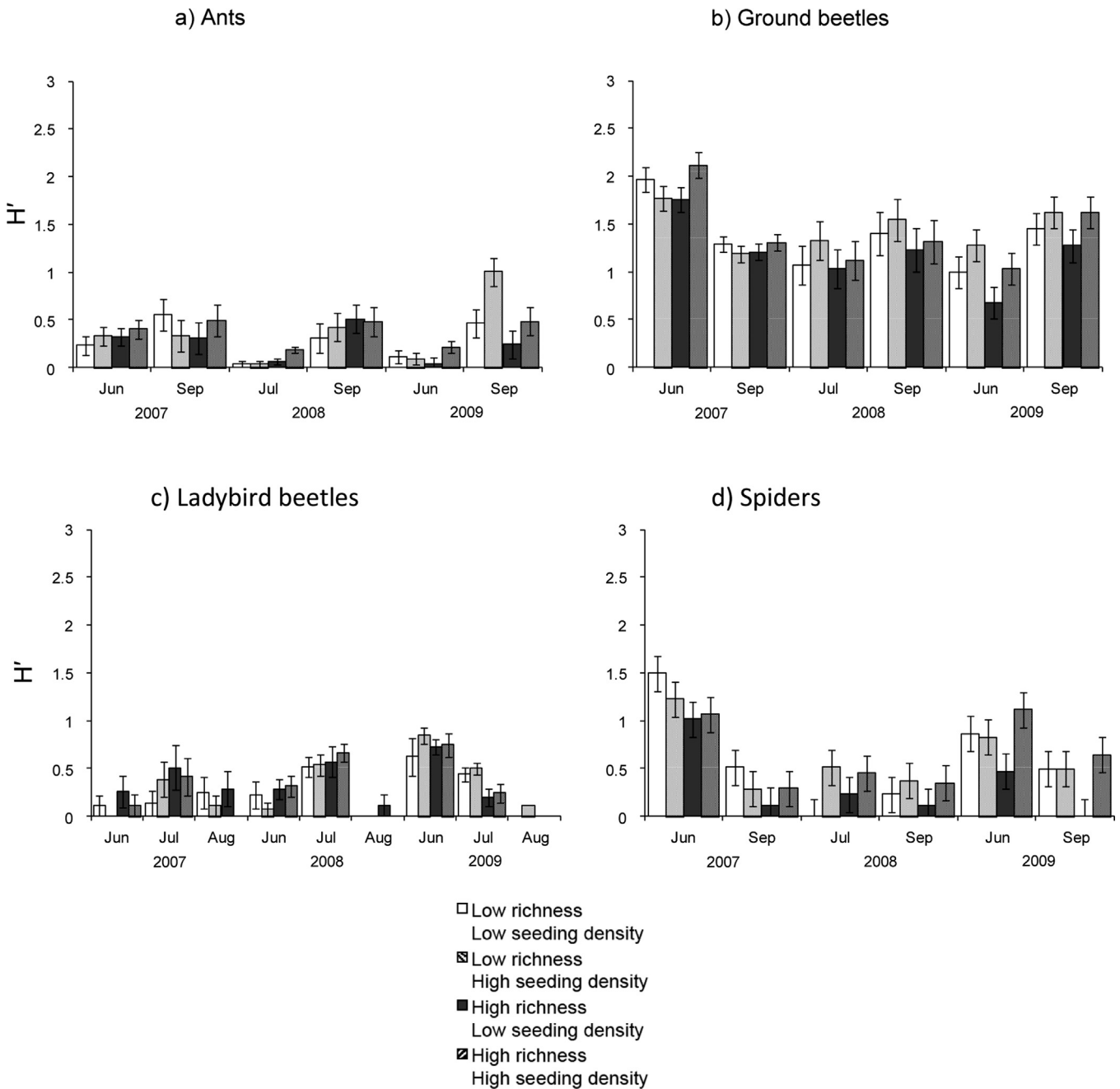
**Fig. 3.** Species richness of invertebrate species collected during 2007–2009. Values are least-square means ( $\pm$ SE) from mixed-model analysis.  $N = 6$  plots per treatment.

predators and parasites. According to theory and some experimental results, high plant species richness is associated with a high abundance and richness of predators and parasites that feed on the greater variety of herbivores that become available at different times during the growing season and in a variety of microhabitats, or due to the greater diversity of plant structure available in high plant richness habitats (Root, 1973; Haddad et al., 2001; Pywell et al., 2011).

However, other studies do not find a positive relationship between plant species richness and predatory invertebrate abundance. Asteraki et al. (2004) sowed different mixtures of simple grasses or complex grasses with or without forbs and found a positive relationship between plant species richness and spider abundance however predatory beetle abundance showed no relationship with the different mixtures. Davis and Utrup (2010) found no significant difference in the abundance of ground beetles and spiders collected from pitfall traps from 4- to 20-year-old prairie restorations in south-central Nebraska that had been sown with

low richness (4–5 prairie grasses) and high richness ( $\geq 25$  grass and forb species) seed mixtures. Their findings are similar to ours in that we did not find the richness of the seed mix alone to be a significant explanation for the abundance of ants, spiders, or ground beetles. However, there was a significant positive effect of richness on ladybird beetle abundance. Because ladybird beetles were collected by sweep netting, their numbers reflect differences in the aboveground cover rather than basal cover of plants. Adult ladybird beetles are frequent visitors to the extrafloral nectaries and pollen of various plants, as well as honeydew excreted by some Hemiptera (Lundgren, 2009). The greater number of ladybirds collected in our high richness treatments may have reflected a stronger preference for pollen and nectar from forb species that were more prevalent in the high richness plots, although little information is available on the relative attractiveness of the prairie forbs recorded in this study for ladybird beetles.

Many studies have found a positive relationship between plant species richness and predatory invertebrate richness as



**Fig. 4.** Shannon–Weaver diversity index ( $H'$ ) of invertebrate species collected during 2007–2009. Values are least-square means ( $\pm$ SE) from mixed-model analysis.  $N=6$  plots per treatment.

measured by species richness or diversity indices such as the Shannon–Weaver diversity index (Crisp et al., 1998; Siemann et al., 1998; Knops et al., 1999; Jonas et al., 2002). However, some studies have contradicted these results. Koricheva et al. (2000) found a significant negative relationship between plant species richness and spider and ground beetle activity in European grassland communities. We also found that plant species richness did not have a significant effect on predatory invertebrate species richness. However, seeding density had a significant positive effect in explaining the species richness and Shannon–Weaver richness index of ground beetles and spiders, and the total species richness of ground beetles was highest early in the restoration, in 2007. Many ground beetles are effective seed predators of weed species, and can influence plant richness and distribution within a habitat (McCravy and Lundgren, 2011). The response to seeding density treatments may reflect a

greater richness of ground beetle species being attracted to the higher density of sown seeds in the higher seeding rate treatments.

The recorded total plant richness of the high plant richness treatments was approximately twice that of the low plant richness treatments, a similar result to Carter and Blair's (2012) study conducted in the same plots. The main difference in vegetation characteristics between the low and high richness treatments was the higher basal cover of grasses in the low richness treatments, which was expected because grass seed comprised 90% of the low richness seed mix compared to 75% of the high richness seed mix. In addition, although many unsown weedy species such as mare's tail (*Conyza canadensis*), dandelion (*Taraxacum officinale*), and common ragweed (*Ambrosia artemisiifolia* var. *eliotior*) were common among all the treatments, the species composition recorded in low and high richness treatments differed. Therefore, the abundance



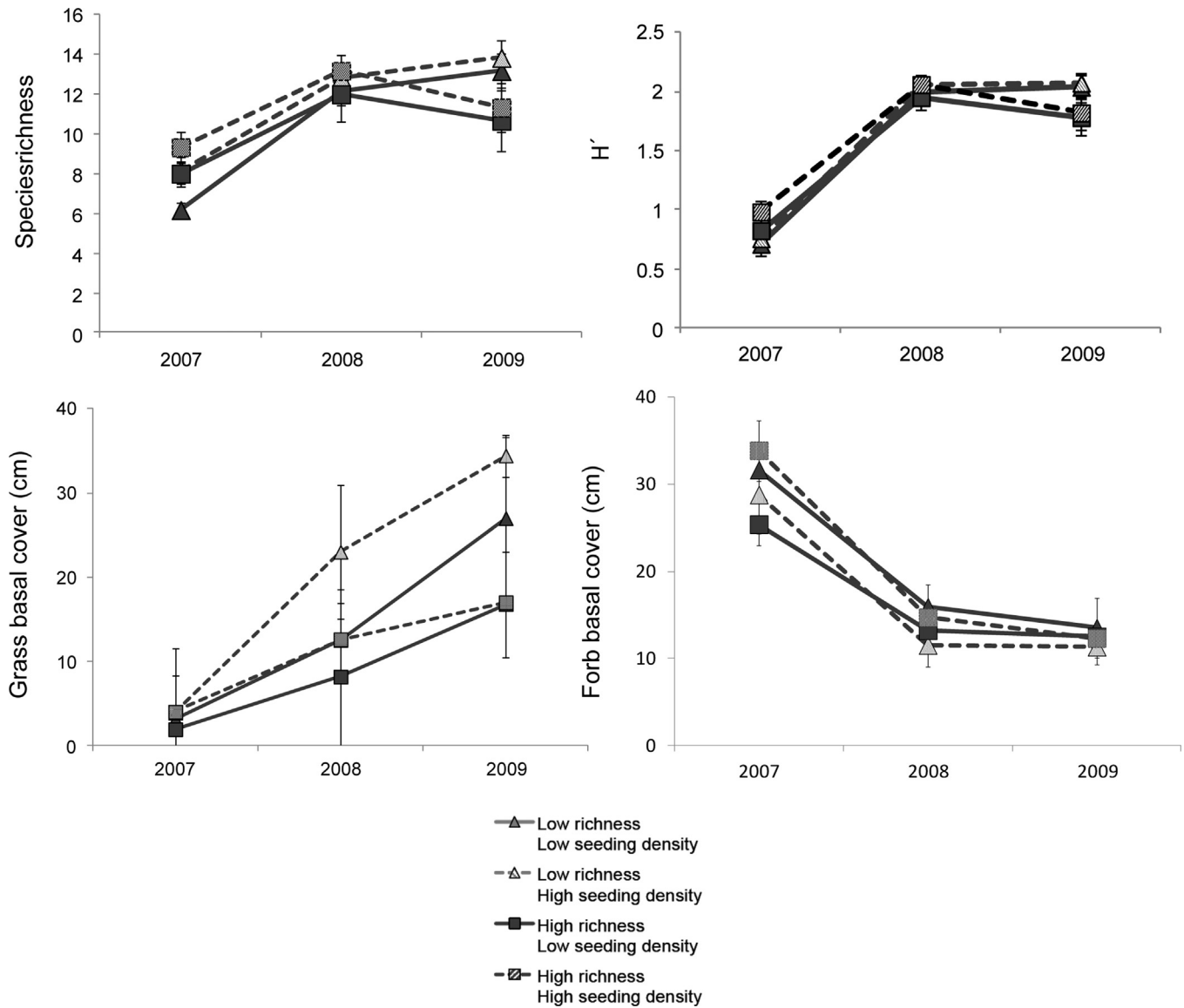


Fig. 5. Species richness, Shannon–Weaver diversity index ( $H'$ ), grass basal cover, and forb basal cover of plant species assessed during 2007–2009. Values are least-square means ( $\pm$ SE) from mixed-model analysis.  $N = 6$  plots per treatment.

and richness of surface-dwelling predatory invertebrates in our study should be interpreted as showing no response to differences in grass basal cover or plant species composition rather than differences in plant richness per se. In addition, the abundance and richness of some invertebrates with large ranges such as spiders and ground beetles may be influenced more by factors that operate at larger spatial scales (e.g., land use and presence of corridors) rather than within plot factors (e.g., local habitat characteristics), and several studies have found spider and ground beetle communities to respond strongly to variables at landscape scales in the order of 200–500 m (Aviron et al., 2005; Dauber et al., 2005; Hendrickx et al., 2007; Gardiner et al., 2010; Maisonhaute et al., 2010). Ants have been found to respond more strongly to local microclimatic and soil characteristics (e.g., insolation and soil humidity) (Dauber et al., 2005). Because soil structure in tallgrass prairie restorations changes slowly, taking many years to approach the structure of soil in native prairie (Jastrow, 1987), differences in soil characteristics had likely not emerged among the treatments at the time the study was conducted. Other characteristics that may affect invertebrate density and diversity but were beyond the scope of this study

include prey availability and presence of competitors or enemies (Kromp, 1999; Landis et al., 2000).

We did not detect large differences in the response of feeding guilds to the plant community. This result is expected with omnivores because they have a larger resource base and can feed on plant materials when prey are scarce, whereas carnivores have a more restricted resource base and may be more closely associated with the availability of prey, which is in turn determined by the composition of the plant community in the treatments. However, the proportion of insect species that were carnivores was small, making the detection of any treatment differences difficult for this feeding guild. Harvey et al. (2008) found that the proportion of carnivorous ground beetles in the community declined with time, herbivores increased, and proportion of omnivores peaked in the second year. We found that the populations of both omnivorous and carnivorous ground beetles declined with time.

In conclusion, the responses of the invertebrate communities in these experimental tallgrass restoration plots reflect the relatively low richness of plant species found in both low and high richness treatments in young (second–fourth growing season) restorations

that still had a large proportion of unsown, weedy plant species. In addition, the species composition of the plant community, vegetation structure, and vegetation density, varied significantly from year to year during the study. These changes in the plant community as the restorations mature in turn affect the invertebrate community. Our study indicates that prairie managers and agricultural producers interested in increasing the richness and diversity of spiders and ground beetles early in restoration should use higher seeding densities. However, high plant community richness and density does not appear to ensure a corresponding high abundance or richness of most predatory invertebrates early in prairie restorations. Over time the high richness treatments should become more diverse as conservative plant species that were seeded appear, which may result in greater differences in the invertebrate communities. If a land manager is managing for the long-term (>5 years), it may be advisable to plant the greatest number of plant species that can be afforded to increase the availability of resources and microhabitats available to a range of predatory invertebrates as the restoration develops.

Because at the local scale, the composition of invertebrate communities may be best predicted by the species composition of the plant community, future research could use techniques such as co-correspondence analysis or habitat affinity indices to relate differences in plant species composition to invertebrate abundance and richness in tallgrass prairie restorations (Schaffers et al., 2008; Déri et al., 2011). In addition, while natural habitats provide valuable sources of predatory invertebrates for pest control in adjacent cropland, the spillover of predatory invertebrates from managed to natural systems has been the subject of far less research than the spillover of predatory invertebrates from natural to managed systems (Blitzer et al., 2012). Future research should focus on the movement of predatory invertebrates between tallgrass prairie restorations and adjacent cropland to determine whether these restorations serve as sources or sinks for different groups of invertebrates, including pest insects. Finally, because a variety of habitats are needed to provide resources for all stages of the life cycles of some invertebrates (Landis et al., 2005), future research could be conducted at larger scales to study the effect of differing richness levels and configurations of tallgrass prairie and other habitats such as hedgerows on invertebrate assemblages within the tallgrass prairie region.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.10.024>.

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