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Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa

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Summary

Ground beetle assemblages were monitored in six different habitats (tallgrass prairie, oats, corn, soybean, old-field, woods) at four sites in northeastern Iowa from 1994 to 1998. The objective of this study was to quantify the influence of habitat type on the activity and distribution of ground beetles. Over five years, 13,654 ground beetles representing 107 different species were captured. Of these, 14 species represented 85 % of the captured beetles. Based on habitat use, we categorized 24 as generalist species, 14 as agricultural species, 12 as grassland species, 39 as prairie specialists, and 19 as woodland species. Tallgrass prairie hosted a significantly more ($P < 0.05$) diverse assemblage of ground beetles than was found in the other habitats. Prairie also had a higher percentage of habitat specialists in its assemblage than did the less stable agricultural habitats which were dominated by generalists. NMS ordination and indicator species analysis revealed distinct ground beetle assemblages and identified indicator species in the various habitats, allowing species assemblages to be used as habitat indicators.

Key words: Coleoptera, Carabidae, ground beetles, pitfall traps, tallgrass prairie

Introduction

Ground beetles or carabids (Coleoptera: Carabidae) are one of the most common and abundant beetle families, comprised of about 40,000 known species (Lövei and Sunderland 1996). Of the epigaeic insects, ground beetles are among the most numerous and most important groups (Harris & Whitcomb 1974), primarily as polyphagous predators of other invertebrates (Whitcomb & Bell 1964; Larochelle 1990; Loreau 1990). As predators, carabids tend to patrol the soil surface and attack other epigaeic invertebrates (Whitcomb & Bell 1964). Although a large and ubiquitous group, many species of ground beetles are highly selective and restricted to a particular habitat (Thiele 1977; Evans 1983; Niemelä et al. 1992). This habitat selectivity makes carabids well suited to be used as ecological indicators of changes within terrestrial communities (Thiele 1977; Freitag 1979; Dufrêne et al. 1990; Maelfait & Desender 1990; Larsen et al. 1996), as they have been used as ecological indicators to assess grassland use in England (Eyre & Rushton 1989).

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Except for the agriculturally important species, ground beetles in Iowa have been relatively unstudied. This has been especially true of the ground beetles of the geologically distinct northeastern corner of Iowa. In this study, we examined the influence of habitat on the activity and distribution of northeastern Iowa ground beetles. Over a five-year period from 1994 to 1998, pitfall traps were used to monitor ground beetle assemblages in a variety of habitats at four sites in northeastern Iowa. One common characteristic among these sites was the presence of tallgrass prairie habitat. The primary objective of this research was to inventory the ground beetles found in a variety of habitats in NE Iowa to identify potential habitat specialists for use as possible ecological indicators. We then intend to use these indicator species to monitor the effects of management practices such as fire in tallgrass prairies on prairie-obligate invertebrates.

Materials and Methods

Study Sites

From 1994 through 1998, ground beetles were intensively sampled from a variety of habitats at four sites in northeastern Iowa (Fig. 1). Hayden Prairie, a 97.2-ha native remnant tallgrass prairie managed by the Iowa Department of Natural Resources, is located in Howard County (UTM zone 15, 550105E, 4809715N). Hayden Prairie is surrounded completely by fields of corn (*Zea mays* L.), and soybean (*Glycine max* (L.) Merr.). Anderson Prairie is a 9.4-ha reconstructed tallgrass prairie located on the Luther College campus in Decorah, Winneshiek County (UTM Zone 15, 597396E, 4796283N). Anderson Prairie is managed by Luther College, and is surrounded by a bur oak (*Quercus macrocarpa* Michx.) and shagbark hickory (*Carya ovata* (Mill.) Koch) forest known as Hickory Ridge Woods to the northeast and northwest, and was bounded on the southwest by continuous cropping of oats (*Avena sativa* L.). To the southeast is old-field habitat. Effigy Mounds National Monument, managed by the National Park Service, is located on bluffs overlooking the Mississippi River on the border of Allamakee and Clayton Counties (UTM Zone 15, 647536E, 4774137N). Effigy Mounds National Monument has 25-ha of primarily reconstructed prairie divided between a northern unit and southern unit, along with numerous hill prairie remnants of less than 0.25-ha each. These prairies are completely surrounded by oak/hickory forests, although nearby are several soybean, corn, and old-field habitats. Chipera Prairie is a 31.2-ha native remnant tallgrass prairie managed by the Win-

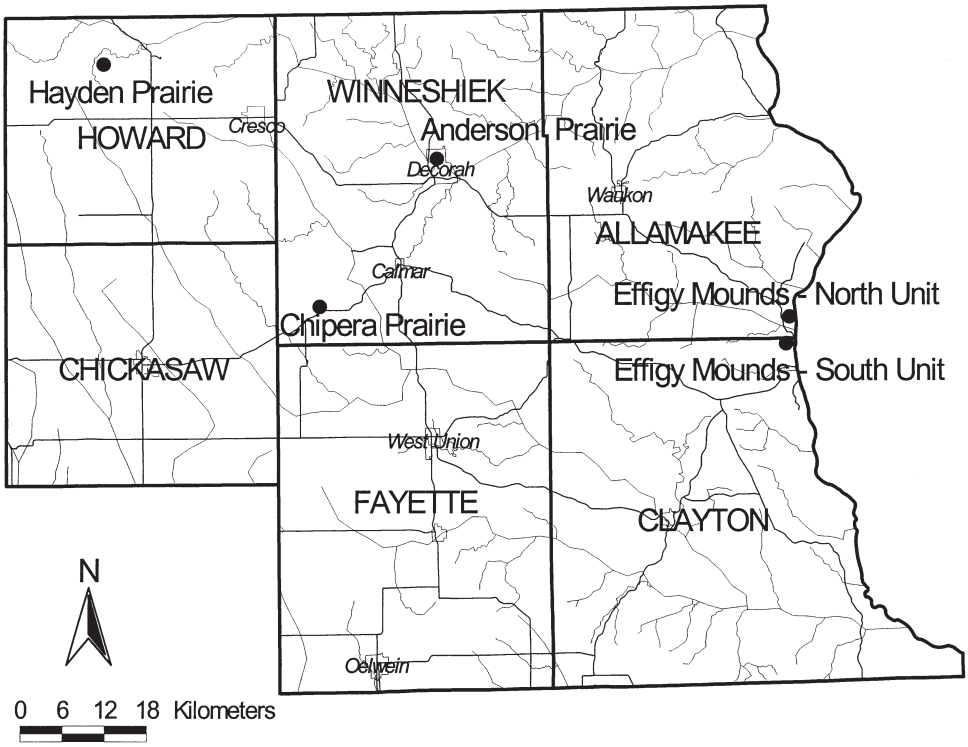

Fig. 1. Locations of four sites in Northeastern Iowa sampled from 1994 to 1998 for ground beetles from six different habitats (prairie, old-field, oats, corn, soybean, woods) with pitfall traps

neshiek County Conservation Board. Located in Winneshiek County (UTM Zone 15, 580825E, 4775593N), this site includes a 2-ha wooded area and is completely surrounded by corn and soybeans, with oats and old-field habitats also present.

Ground Beetle Sampling

Ground beetles were collected in pitfall traps exposed in the field for one-week-long periods in early-June, mid-July, and late August from 1994 through 1998. Each trap was constructed from one 473 mL plastic cup (9 cm dia) placed into the ground so the lip of the cup was at or slightly below the ground surface. Each cup was fitted with a funnel constructed from a 207 mL casual cup insert (Sweetheart® Cup Company, Chicago, Illinois) to prevent beetle escape. Approximately 50 mL of 50 % propylene glycol was then added as a preservative.

During each trapping period, 12 traps were placed in a single transect line at 10 m intervals in tallgrass prairie (n = 4), woods (n = 2), old-field (n = 1), and active agricultural habitats (corn, oats, or soybeans, n = 6) present at each site. After each trapping period, traps were removed and holes refilled. Damaged or disturbed traps were noted and excluded from the analysis. Samples were washed and stored in 70 % ethanol. Ground beetles were then identified to species using keys in Lindroth (1961–1969) and Noonan (1991), and names standardized using Bousquet and Larochelle (1993). Voucher specimens are housed in the reference insect collection in the Hoslett Museum of Natural History, Luther College, Decorah, Iowa.

Ground Beetle Faunal Analysis

The total abundance of ground beetles and species richness was determined for each habitat. Because of variation in the number of recovered traps and length of trap exposure in the field, abundance data were transformed to number of beetles captured per trap per day for some of the analyses. We calculated Shannon's diversity index (*H'*) using log base *e*, Pielou's evenness index (*J'*) (Krebs 1989), and French's (1994) hierarchical richness index (*HRI*) for the ground beetle fauna of each habitat type.

Differences in carabid community composition between tallgrass prairie sites, woodland sites, actively cropped agricultural sites (oats, corn, and soybeans), and the single old-field site were initially compared using non-metric multidimensional scaling (NMS) ordination. Non-metric scaling is a non-parametric ordination technique that performs well with datasets where the underlying species response patterns cannot be specified *a priori* (Clarke 1993). For this analysis, Sorenson's distance (also referred to as Bray-Curtis distance) was used and significance of ordination axis was evaluated by comparing the solution stress of the observed data to the stress observed in 50 randomizations of the observed data. Because the potential conservation value of tallgrass prairie habitat for rare species was of specific interest within this study, all species were included in this analysis.

Habitat preference of individual beetle species was evaluated using indicator species analysis (Dufrêne and Legendre 1997). Indicator species analysis is a randomization-based test that compares the relative abundance and the relative frequency of individual species across different sampling areas and expresses a species' affinity for a sampling area as % indication of a particular sampling area (Dufrêne and Legendre 1997).

Statistical comparisons of all samples combined among tallgrass prairie (n = 4), woodland (n = 2), and active agricultural habitats (n = 6) were performed for the total number of ground beetles, species richness, and activity density (average number of ground beetles caught per trap per day) using the nonparametric analysis of variance Kruskal-Wallis test (Zar 1999). Ecological indices were calculated both on raw count data and data transformed to number of beetles captured per trap per day. To test for significant differences among the Shannon diversity values, we used a pairwise comparison test by Hutcheson (1970) described by Zar (1999). Since the trends and results were the same, only raw count data analyses are reported.

Accumulation curves were generated using EstimateS software (Colwell 1997). Curves generated compare cumulative species number and sampling effort for all annual samples from each site and habitat type.

Five classifications regarding habitat specialization were used to categorize each ground beetle species as follows: *generalist* species are those well represented in all habitat types; *grassland* species are those found primarily in prairie and old-field habitats, with some occasionally occurring in agricultural but not wooded habitats; *agricultural* species are those with over 70 % of collected individuals in cropped agricultural habitats such as corn, oats, or soybeans; *prairie* specialists are those where over 90 % of collected individuals were found in tallgrass prairie habitat; and *woodland* specialists are those where over 90 % of collected individuals were found in wooded habitats.

Abundance classifications were arbitrarily defined as follows: *abundant* (A) species represented over 10 % of all the individuals collected; *common* (C) species represented 1–10 % of all individuals; *uncom-*

Table 1. Total number of ground beetles collected in pitfall traps from six habitats at four sites in northeastern Iowa from 1994–1998. Native or introduced status as indicated by Bousquet & Larochelle (1993), relative abundance, and habitat specialization indicated

Taxa	Agric.	Old Field	Prairie	Woods	Total	Status	Abundance	Habitat
Chlaenius platyderus Chaudoir	419	38	2014	179	2650	native	A	generalist
Cyclotrachelus sodalis (LeConte)	634	13	1405	208	2260	native	A	generalist
Pterostichus stygicus (Say)	29	39	465	992	1525	native	A	generalist
Poecilus lucublandus (Say)	340	12	834	97	1283	native	C	generalist
Pterostichus permundus (Say)	326	2	625	10	963	native	C	generalist
Calathus gregarius (Say)	3	7	816	127	953	native	C	generalist
Cyclotrachelus seximpressus (LeConte)	62	0	336	13	411	native	C	generalist
Agonum cupripenne (Say)	92	3	198	0	293	native	C	grassland
Harpalus pensylvanicus (DeGeer)	250	1	28	0	279	native	C	agricultural
Poecilus chalcites (Say)	210	0	32	0	242	native	C	agricultural
Bembidion quadrimaculatum oppositum Say	146	4	35	53	238	native	C	generalist
Pterostichus melanarius (Illiger)	*a* 104	0	41	46	191	introduced	C	generalist
Amara cupreolata Putzeys	0	34	114	1	149	native	C	grassland
Oxypselaphus pusillus (LeConte)	39	0	102	0	141	native	C	grassland
Pterostichus femoralis (Kirby)	2	3	124	2	131	native	U	prairie
Galerita janus (Fabricius)	23	0	86	18	127	native	U	generalist
Pterostichus mutus (Say)	0	0	5	113	118	native	U	woodland
Amara impuncticollis (Say)	1	1	101	1	104	native	U	prairie
Anisodactylus harrisii LeConte	4	2	95	2	103	native	U	prairie
Anisodactylus sanctaecrucis (Fabricius)	98	0	2	0	100	native	U	agricultural
Pterostichus commutabilis (Motschulsky)	1	0	99	0	100	native	U	prairie
Chlaenius emarginatus Say	0	0	29	53	82	native	U	generalist
Harpalus herbivagus Say	18	3	59	1	81	native	U	generalist
Anisodactylus rusticus (Say)	1	2	77	0	80	native	U	prairie
Agonum placidum (Say)	51	0	11	5	67	native	U	generalist
Agonum palustre Goulet	*a* 0	4	35	20	59	native	U	generalist
Pterostichus trinarius (Casey)	*b* 0	0	0	56	56	native	U	woodland
Amara rubrica Haldeman	0	2	49	1	52	native	U	prairie
Brachinus americanus (LeConte)	0	0	1	42	43	native	U	woodland
Brachinus ovipennis LeConte	0	0	1	40	41	native	U	woodland
Carabus goryi Dejean	0	0	1	39	40	native	U	woodland
Elaphropus anceps (LeConte)	31	0	9	0	40	native	U	agricultural
Bembidion versicolor (LeConte)	30	0	9	0	39	native	U	agricultural
Agonum fidele Casey	*a* 2	0	29	4	35	native	U	generalist
Bembidion rapidum (LeConte)	28	0	4	1	33	native	U	agricultural
Selenophorus opalinus (LeConte)	30	0	2	0	32	native	U	agricultural
Sphaeroderus stenostomus lecontei Dejean	1	0	7	22	30	native	U	generalist
Platynus decentis (Say)	0	0	2	27	29	native	U	woodland
Synuchus impunctatus (Say)	*a* 0	0	4	25	29	native	U	generalist
Dyschirius globulosus (Say)	5	1	19	1	26	native	U	grassland

Taxa	Agric.	Old Field	Prairie	Woods	Total	Status	Abundance	Habitat
Dicaelus elongatus Bonelli	0	0	25	0	25	native	U	prairie
Scarites quadriceps Chaudoir	22	0	3	0	25	native	U	grassland
Agonum gratiosum (Mannerheim)	0	0	21	0	21	native	U	prairie
Chlaenius tricolor Dejean	2	1	13	5	21	native	U	generalist
Agonum nutans (Say)	0	0	18	0	18	native	U	prairie
Notiophilus aeneus (Herbst)	0	0	5	13	18	native	U	generalist
Cymindis americanus Dejean	0	0	15	2	17	native	U	generalist
Bembidion praticola Lindroth	*b* 0	0	16	0	16	native	U	prairie
Amara aeneopolita Casey	0	0	13	0	13	native	U	prairie
Anisodactylus ovularis (Casey)	0	0	12	1	13	native	U	prairie
Trichotichnus vulpeculus (Say)	*b* 0	0	0	13	13	native	U	woodland
Syntomus americanus (Dejean)	0	0	10	0	10	native	R	prairie
Dicaelus politus Dejean	0	0	1	8	9	native	R	woodland
Amara angustata (Say)	0	0	8	0	8	native	R	prairie
Amphasia interstitialis (Say)	0	0	0	8	8	native	R	woodland
Badister notatus Haldeman	0	0	6	2	8	native	R	generalist
Clivina impressefrons LeConte	8	0	0	0	8	native	R	agricultural
Loricera pilicornis (Fabricius)	*a* 7	0	1	0	8	holarctic	R	agricultural
Carabus maeander Fischer von Waldheim	0	0	7	0	7	holarctic	R	prairie
Carabus sylvosus Say	0	0	0	6	6	native	R	woodland
Chlaenius purpuricollis Randall	0	0	6	0	6	native	R	prairie
Dicaelus sculptilus sculptilus Say	0	0	6	0	6	native	R	prairie
Harpalus caliginosus (Fabricius)	4	0	2	0	6	native	R	agricultural
Pterostichus adstrictus Eschscholtz	*a* 0	0	1	5	6	holarctic	R	woodland
Stenolophus conjunctus (Say)	5	0	1	0	6	native	R	grassland
Amara obesa (Say)	3	0	2	0	5	native	R	agricultural
Anisodactylus agricola (Say)	0	0	1	4	5	native	R	generalist
Bembidion graciliforme Hayward	1	0	4	0	5	native	R	grassland
Calleida punctata LeConte	1	0	4	0	5	native	R	prairie
Patrobus longicornis (Say)	3	1	1	0	5	native	R	generalist
Amphasia sericea (Harris)	0	0	4	0	4	native	R	prairie
Brachinus tenuicollis LeConte	0	0	0	4	4	native	R	woodland
Acupalpus partiarius (Say)	1	0	2	0	3	native	R	grassland
Apenes lucidulus (Dejean)	*b* 0	0	1	2	3	native	R	generalist
Chlaenius amoenus Dejean	*b* 0	0	3	0	3	native	R	prairie
Chlaenius pusillus Say	0	0	3	0	3	native	R	prairie
Dicaelus purpuratus splendidus Say	0	0	3	0	3	native	R	prairie
Elaphropus granarius (Dejean)	0	0	3	0	3	native	R	prairie
Harpalus somnulentus Dejean	0	1	2	0	3	native	R	grassland
Myas cyanescens Dejean	*a* 0	0	0	3	3	native	R	woodland
Pterostichus luctuosus (Dejean)	0	0	3	0	3	native	R	prairie
Stenolophus rotundicollis (Haldeman)	*a* 0	2	1	0	3	native	R	grassland

Taxa	Agric.	Old Field	Prairie	Woods	Total	Status	Abundance	Habitat
Calleida decora (Fabricius)	0	0	2	0	2	native	R	prairie
Chlaenius sericeus (Forster)	1	0	1	0	2	native	R	grassland
Chlaenius tomentosus (Say)	0	0	2	0	2	native	R	prairie
Cymindis neglectus Haldeman	0	0	2	0	2	native	R	prairie
Harpalus compar LeConte	0	0	2	0	2	native	R	prairie
Hartonymus hoodi Casey	0	0	2	0	2	native	R	prairie
Panagaeus fasciatus Say	0	0	2	0	2	native	R	prairie
Stenolophus lecontei (Chaudoir)	2	0	0	0	2	native	R	agricultural
Stenolophus ochropezus (Say)	0	0	2	0	2	native	R	prairie
Acupalpus carus (LeConte)	0	0	1	0	1	native	R	prairie
Bembidion postremum Say *a*	0	0	0	1	1	native	R	woodland
Bradycellus rupestris (Say)	1	0	0	0	1	native	R	agricultural
Bradycellus semipubescens Lindroth *b*	0	0	1	0	1	native	R	prairie
Calosoma calidum (Fabricius)	0	0	1	0	1	native	R	prairie
Chlaenius impunctifrons Say	0	0	0	1	1	native	R	woodland
Diplocheila obtusa (LeConte)	0	0	1	0	1	native	R	prairie
Discoderus parallelus (Haldeman)	0	0	1	0	1	native	R	prairie
Harpalus affinis (Schrank) *b*	1	0	0	0	1	introduced	R	agricultural
Harpalus eraticus Say	0	1	0	0	1	native	R	grassland
Harpalus erythropus Dejean	0	0	1	0	1	native	R	prairie
Nebria lacustris Casey	0	0	0	1	1	native	R	woodland
Notiobia terminata (Say)	0	0	1	0	1	native	R	prairie
Pterostichus corvinus (Dejean) *a*	0	0	1	0	1	native	R	prairie
Scaphinotus bilobus (Say) *b*	0	0	0	1	1	native	R	woodland
Trichotichnus autumnalis (Say) *b*	0	0	0	1	1	native	R	woodland
Totals:	3042	177	8155	2280	13654			
Number of Species:	44	23	91	49	107			
Shannon's Diversity Index (H'):	2.617 a	2.319 b	2.622 a	2.342 b				
Pielou's Evenness Index (J'):	0.692	0.740	0.581	0.599				
Hierarchical Richness Index:	5.618	4.525	6.184	5.275				
Trap Days:	1,581	88	10,163	1,439				
Beetles/Trap/Day:	1.924	2.011	0.802	1.584				

Diversity indices followed by the same letter are not significantly different ($P = 0.05$) as determined by a paired *t*-test (Hutcheson 1970).
a State record documented in Purrington & Larsen (1997)
b State record documented in Purrington et al. (2000)

mon (U) species represented 0.1–1 % of all individuals; while *rare* (R) species were represented by less than 0.1 % of all ground beetles collected.

Results

Overall, 13,654 ground beetles were collected from six habitat types at four sites, representing 107 different species (Table 1). Fourteen species dominated the samples, representing 85 % of the total capture. Nine of these 14 species were generalists, well represented in agricultural, grassland, and wooded habitats, three of these being abundant and six common. Three grassland species were common in both old-field and prairie habitats. Two additional common species were collected from agricultural areas. None of the woodland (n = 19) or prairie (n = 39) specialists were encountered often enough to categorize as abundant or common.

Significantly more beetles were collected from tallgrass prairie habitats than either woodland or active agricultural habitats (H = 6.28; df = 2; P = 0.043). However, no significant differences among habitats in activity density, the numbers of beetles captured per trap per day (H = 3.00; df = 2; P = 0.223) were observed.

There were significant differences in the number of species found in the various habitats (H = 8.95; df = 2; P = 0.011). Tallgrass prairie, by far the most diverse habitat sampled in terms of number of plant species, contained the richest assemblage of ground beetles with a total of 91 species. Wooded habitats contained the second richest assemblage with a total of 49 species. On average, active agricultural habitats had lower species richness than either tallgrass prairie or woodland habitats; although when corn, oats, and soybean habitats were combined they contained a total of 44 species. In tallgrass prairie, we categorized 45 % of all species as prairie specialists and only 25 % of species as generalists. This was a much higher percentage of habitat specialists than any of the other habitats sampled. In contrast, typically over 40 % of the species in habitats other than tallgrass prairie were generalists.

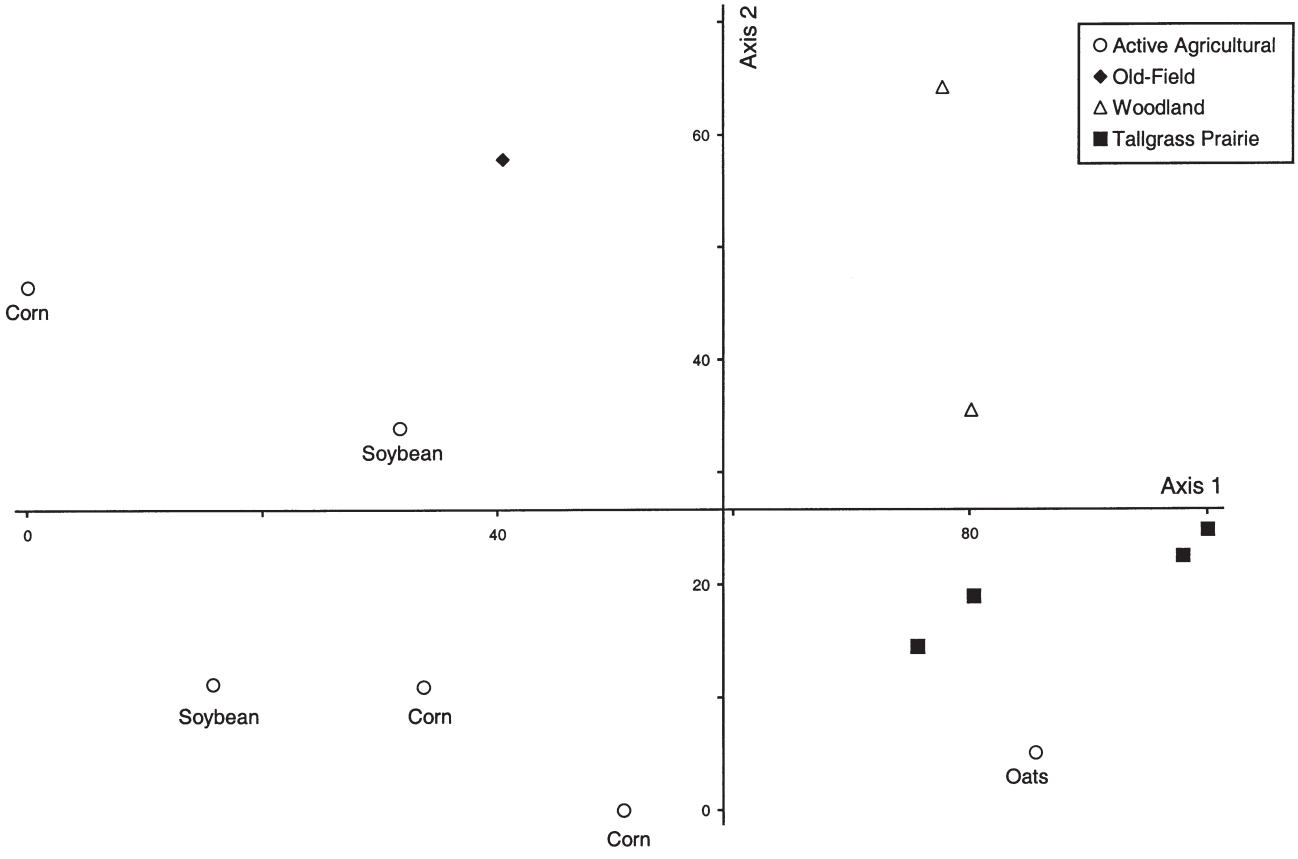

Fig. 2. NMS ordination of 13 locations in northeastern Iowa, based on 107 carabid species depicting differences in carabid assemblage among four habitat types; actively agricultural sites, an abandoned old-field site, woodland sites, and tallgrass prairie sites. Differences in crop type among active agricultural areas are labeled accordingly. Axis 1 and 2 of this ordination explain 76.9 % of the variance

Table 2. Randomization tests of significance and variance explained by NMS ordination of 107 carabid beetle species collected over 5 years from 13 sites in Northeastern Iowa

	Stress in observed data			Stress in randomized data, monte-carlo test of significance				
Axis	Min	Mean	Max	Min	Mean	Max	p	Variance Explained
1	21.87	39.031	53.063	26.187	45.410	53.039	0.0196	0.549
2	8.022	14.036	35.143	13.52	21.208	32.739	0.0196	0.220

When evaluating the number of beetles in each habitat type, generalist species dominated all habitats. Despite the dominance in number of species of prairie specialists in the prairie habitat, prairie specialists were either uncommon or rare, and in total represent less than 9 % of all the ground beetles captured in the prairie habitat. Of these, *Pterostichus femoralis* (Kirby) was the most often-encountered prairie specialist, yet this species was uncommon in tallgrass prairie. In addition to hosting many generalist species, soybean also hosted the largest percentage of beetles categorized as agricultural.

Tallgrass prairie habitat contained the most diverse ground beetle community in terms of species richness, abundance, and the highest *H'* and *HRI* diversity values (Table 1). Wooded habitat had the second greatest number of species and abundance. The combined agricultural habitats (corn, oats, and soybeans) were fairly diverse with the second highest *H'* and *HRI* diversity values, although individually these habitats were much less diverse.

Non-metric scaling ordination shows clear differences, along ordination axis 1, between the beetle assemblage observed in woodland and tallgrass prairie habitats and the assemblage observed in active agricultural habitats (Fig. 2, Table 2). However, the specific crop grown in agricultural habitats influenced beetle compositions within agricultural habitats. The beetle assemblage of the area cropped with oats was similar (percent similarity = 63 %) to tallgrass prairie habitats. This similarity was largely driven by two common species *Agonum cupripenne* (Say) and *Pterostichus permundus* (Say) that were collected in relatively large abundance in both the oat field and prairie habitats. Differences in beetle assemblages between woodland and tallgrass prairie habitats were apparent along ordination axis 2 (Fig. 2, Table 2). Beetle composition of the single old-field site was between agricultural habitats and woodland habitats.

Species accumulation curves (Fig. 3) based on trapping effort show few additional species are likely to be found with additional sampling efforts. The curves concur with other data that tallgrass prairie has the greatest species richness of the habitats we sampled. Woodland habitats are intermediate, and agricultural habitats posses the fewest species of ground beetles.

Twenty species with strong habitat affinities were identified using indicator species analysis (Table 3). Thirteen of these species showed strong affinity for woodland habitats, while seven species showed strong affinities for tallgrass prairie habitats. No habitat specific patterns for agricultural areas using indicator

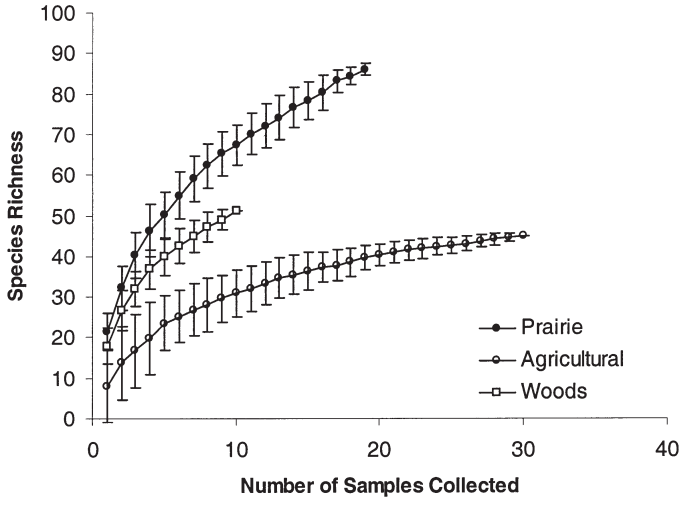

Fig. 3. Species accumulation curves for ground beetles in tallgrass prairie, agricultural, and woodland habitats in Northeastern Iowa based on annual pitfall trap samples collected over 5 years from each site and habitat

Table 3. Indicator values, randomization tests of significance and habitat affinities for 20 carabid beetles collected from woodland and tallgrass prairie habitats in northeastern Iowa

Carabid Species	Abundance Class	Indicator Value (IV)	Randomization test of significance (*P*)	Habitat Affinities		
				Agricultural (n = 6)	Tallgrass Prairie (n = 4)	Woodland (n = 2)
Woodland Species:						
Amphasia interstitialis	R	100.0	0.013	–	–	100
Carabus sylvosus	R	100.0	0.013	–	–	100
Myas cyanescens	R	100.0	0.013	–	–	100
Trichotichnus vulpeculus	R	100.0	0.013	–	–	100
Carabus goryi	U	98.7	0.013	–	–	99
Pterostichus mutus	U	97.8	0.013	–	1	98
Platynus decentis	U	96.4	0.013	–	1	96
Synuchus impunctatus	U	92.6	0.013	–	2	93
Pterostichus adstrictus	R	90.9	0.013	–	2	91
Anisodactylus agricola	R	88.9	0.026	–	3	89
Sphaeroderus stenostomus lecontei	U	85.2	0.035	–	7	85
Notiophilus aeneus	U	83.9	0.046	–	8	84
Chlaenius emarginatus	U	78.5	0.048	–	16	79
Prairie Species:						
Amara cupreolata	C	98.3	0.002	–	98	1
Amara impuncticollis	U	97.4	0.003	–	97	1
Anisodactylus harrisii	U	93.4	0.011	1	93	2
Agonum cupripenne	C	76.3	0.028	8	76	–
Agonum nutans	U	75	0.048	–	75	–
Pterostichus permundus	C	72.5	0.049	25	72	1
Pterostichus femoralis	U	71.9	0.14	–	72	2

analysis. Of the woodland species identified by indicator species analysis, five were classified as rare, while the remaining seven were classified as uncommon. Of the tallgrass prairie species identified by indicator species analysis, three were identified as common; the remaining four were identified as uncommon.

Discussion

Ground beetles are known to have clear associations with broad habitat types (Niemelä et al. 1992). The characteristics of different habitats can strongly influence the abundance of individual ground beetle species, and therefore affect community structure (Clark et al. 1997). Although not significant, there was a trend for decreased activity density (number of beetles captured per trap per day) in tallgrass prairie habitats as compared to other habitats. This suggests that physical structure of the habitat may affect the utilization of that habitat by ground beetles. One aspect of physical structure that may impede ground beetle activity is plant stem density. Greenslade (1964), Honěk (1988), and Rivard (1966) all found ground beetle activity greater in crops at sparser densities than in crops grown at greater density. The lowest activity density occurred in tallgrass prairie, which had the highest observed stem density of the six habitats.

In northeastern Iowa, some ground beetle species are restricted to certain habitat types as apparent specialists, while other species can be categorized as generalists, found in a wide variety of habitats. Variability in preference for one type of habitat over another in ground beetles is fairly common (Esau & Peters 1975; Best et al. 1981; Wallin 1986). Despite the relatively few sites sampled, we believe this five-year study is robust in its results yet conservative in our categorization of habitat specialization.

Tallgrass prairie clearly contained the greatest overall ground beetle diversity of any of the habitats in terms of abundance, species richness, and the various *H'* and *HRI* diversity indices calculated despite the relatively low activity density (beetles per trap per day). Some studies have shown carabid activity and abundance is greater in more diverse habitats (Carcamo & Spence 1994; Perfecto et al. 1986). However, the more diverse habitats in those studies rarely involved more than two or three plant species intercropped in polyculture. In contrast, tallgrass prairie often contains well over 200 species of grasses and forbs, and forms a dense and complex vegetational physical structure. The diverse floristic and physical complexity of this habitat likely creates a preferable microclimate for ground beetles, and offers more niches than are found in less diverse habitats. The natural enemies hypothesis by Root (1973) predicts an increase in abundance of natural enemies in more vegetationally complex systems. Our results show ground beetle species richness was greater in the more complex prairie and wooded habitats, habitats dominated by perennial plants. Perennial-dominated habitats are preferred by at least one species of carabid, *Cyclotrachelus sodalis* (LeConte) (Clark et al. 1997). This species was abundant in both prairie and wooded habitats, and was identified as a generalist in our study.

In a comparison between annual wheat and perennial grasslands, French & Elliott (1999) found distinct differences between the ground beetle assemblages in those habitats. NMS ordination revealed differences in the assemblages of ground beetles among the different habitats here in northeastern Iowa as well. In particular, the corn/soybean and prairie/oats combinations were most similar. Once identified, the species comprising these assemblages can potentially be used as indicators of habitat type and possible environmental change within those habitats.

Tallgrass prairie possesses the most diverse ground beetle assemblage, and also contains the highest percentage (43 %) of specialists in comparison with the other habitats. Prairie specialists are here defined as organisms narrowly adapted to tallgrass prairie habitat, and not typically found in surrounding non-prairie habitats. These specialists are apparently either directly or indirectly dependent on the tallgrass prairie for survival. Among the other habitats, oats, corn, and soybean habitats were all highly disturbed on an annual basis and lack vegetational diversity.

Pitfall traps provide an efficient method of investigating the activity of adult carabids and have been used in a multitude of studies (Greenslade 1964). However, it is acknowledged that pitfall trap data should be interpreted cautiously because insect activity (Thiele 1977; Adis 1979), population density, and weather (Mitchell 1963; Epstein & Kulman 1990) all influence trap catches. In addition, our limited methods and discrete sampling periods may have missed a few species, especially those active in early spring and late fall. Additional sampling at those times may have resulted in a greater leveling-off of the species accumulation curves (Fig. 3).

Before the 1850s, tallgrass prairie in Iowa covered well over 80 % of the state, but today, tallgrass prairie habitat has been reduced to less than one hundredth of one percent (Smith 1998). As a result, prairie-dependent species of ground beetles and other organisms have been severely impacted and in many cases have been extirpated from the landscape. Panzer (1988) documented that in Illinois prairies, prairie specialist insects are very uncommon or rare. Our results concur

with his conclusion, as all beetle species we classified as prairie specialists (those represented by 90% of their total abundance in prairie habitats) were either uncommon or rare when compared to the rest of the fauna. Interestingly, of the prairie specialist species identified using indicator species analysis, three species were classified as common when compared to the rest of the fauna. These species were also represented in relatively large abundance in the old-field habitat and oats field. While not statistically conclusive, the presence of these prairie specialist species in abandoned old-field habitat and perennial wild oats, suggest that only a few prairie specialist species may be capable of existing outside of tallgrass prairie habitat. These results highlight the importance of conserving and properly managing our few remaining fragments of native remnant tallgrass prairie habitat for the preservation of insect biodiversity.

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