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Carabid beetles (Coleoptera: Carabidae) of the Midwestern United States: a review and synthesis of recent research

Kenneth W. McCravy[1,*] and Jonathan G. Lundgren[2]

[1]Department of Biological Sciences, Western Illinois University,
1 University Circle, Macomb, Illinois 61455
[2]USDA-ARS, North Central Agricultural Research Laboratory,
Brookings, South Dakota 57006
*Corresponding author; e-mail: KW-McCravy@wiu.edu
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Summary
Carabid beetles comprise a diverse and ubiquitous family of insects. Carabids are important in conservation biology and often have close associations with particular habitat types, making them useful biomonitoring organisms. Many carabids are also important biological control agents due to their predatory habits, but feeding habits within the family are quite diverse, and seed-eating or granivorous carabids can play an important role in shaping plant diversity and distributions. These qualities have particular relevance in the highly cultivated and fragmented landscape of the Midwestern U.S., and this region has become a very active one for carabid research in a variety of areas. In this paper, we review the state of carabid research in the Midwestern U.S., focusing on work published since the mid-1990s in carabid biogeography, conservation biology, biological control/pest management, feeding ecology and parasitism/health. Potentially productive directions for future research are discussed.

Keywords
Carabidae; biological control; geographic distributions; conservation biology; feeding ecology; habitat associations; seed predation; parasites

Introduction

The Carabidae, or ground beetles, is a large and diverse family of coleopterans, with approximately 40,000 described species worldwide (Lövei and Sunderland, 1996) and over 2600 species and subspecies in Nearctic North America (Ball and Bousquet, 2001). Carabids are found throughout the world between 78°56’ N and 55° S latitude (Ball and Bousquet, 2001), and range from below sea level to 5300 m altitude (Mani, 1968). Most adult carabids are uniformly dark in color, but some species are variously marked. In general, a margined pronotum, large head and mandibles, and striate elytra

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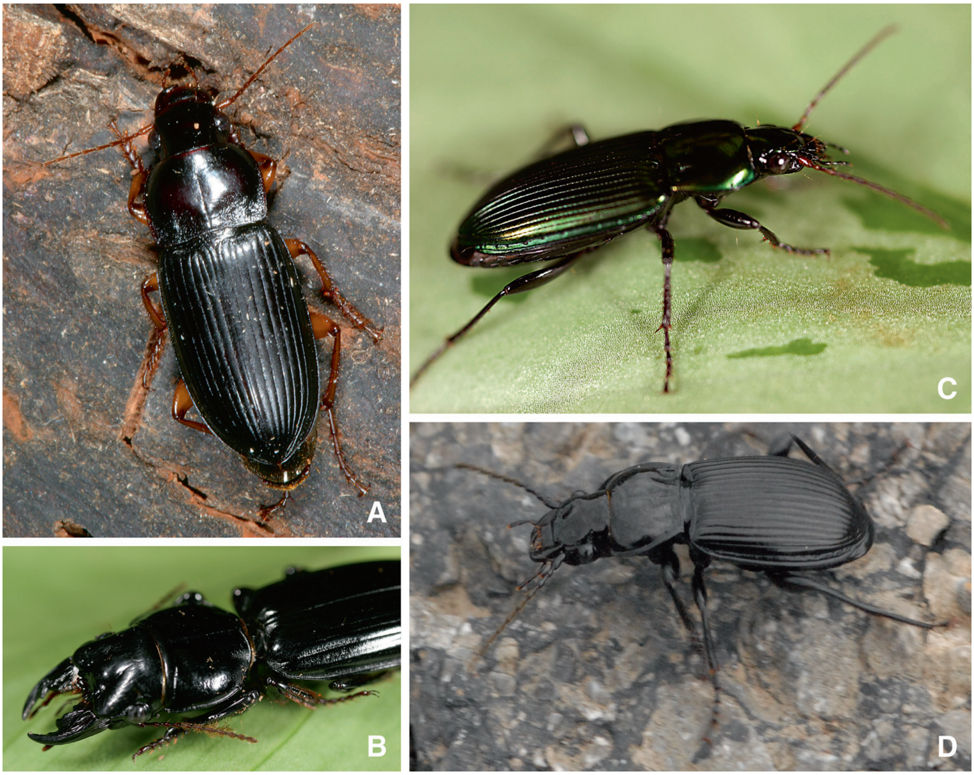


Figure 1. Common carabids of the Midwestern U.S.: (A) *Harpalus pensylvanicus*, (B) *Scarites quadriceps*, (C) *Poecilus chalcites*, (D) *Pterostichus melanarius*. (Photo (D) courtesy of James Lindsey at Ecology of Commanster).

are present, but substantial variation exists (Figure 1). Larvae are campodeiform and subcylindrical or slightly flattened, with a prognathous to hyperprognathous head (Ball and Bousquet, 2001). Most carabids are polyphagous olfactory-tactile or day-active optical predators (Brandmayr and Zetto Brandmayr, 1980), but other feeding habits, such as phytophagy and parasitoidism, are represented as well (Ball and Bousquet, 2001).

Carabids are ecologically important insects. As predators, they may play an important role in suppressing populations of other invertebrate species (Lövei and Sunderland, 1996). Carabids are also an important food source for many vertebrate species (Larochelle, 1975a, b; 1980). Many species of carabids favor specific habitats, and their distributions are often affected by soil type, vegetative cover, and microclimate. These characteristics make carabids useful indicators of habitat conditions and ecological change (Thiele, 1977; Niemelä et al., 1992; Beaundry et al., 1997; Ings and Hartley, 1999; Villa-Castillo and Wagner, 2002; Rainio and Niemelä, 2003; McCravy and Willand, 2005; Pearce and Venier, 2006; Willand and McCravy, 2006; Fuller et al., 2008).

In the Midwestern United States much of the original forest and prairie has been converted to agriculture (Iverson, 1988; Herkert, 1994; Rosenblatt et al., 1999). In Illinois, for instance, over 80% of the land has been converted to row crops or pasture over the past 160 years (Iverson, 1988; Getz and Hofmann, 1999; Rosenblatt et al., 1999). This transformation of much of the Midwest to a landscape composed of habitat fragments within a matrix of cultivated land has generated increasing interest in the conservation biology of arthropod groups such as the carabids. At the same time, carabids are also the focus of interest as biological control agents of invertebrate pests associated with these agricultural crops. Consequently, the Midwestern U.S. has become a region of very active research on carabids in a variety of areas. In this paper, we review recent research on carabids in the Midwestern U.S. and identify areas in need of future research. The 12 states considered in this paper include Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, Ohio, South Dakota, and Wisconsin. While this review focuses on carabid research in the Midwestern U.S., important research on most of the topics discussed in this paper is also being carried out in other regions of the world. The papers cited in this review should serve as a gateway to the broader carabid literature.

Geographic distributions

Bousquet and Larochelle (1993) is the most up-to-date source for geographic distributions of carabids in America north of Mexico. However, many new records for Midwestern states have been published more recently, including some substantial range extensions. An example of the latter involves the tiger beetle *Cicindela trifasciata* F., a highly vagile species generally associated with saline or alkaline mud flats (Graves and Pearson, 1973). This species is primarily found in coastal regions from Texas to Virginia, with records also from Maryland, New Jersey, and Massachusetts, and isolated inland records from Oklahoma, Arkansas and Tennessee (Charlton and Kopper, 2000, and references therein). A small population of this species was found in the Flint Hills region of Kansas, roughly 90 km south of the Nebraska border, a location roughly 1200 km inland from the Gulf Coast, representing the most northwesterly published record for the species (Charlton and Kopper, 2000). It should be noted that there is some disagreement among systematists regarding classification of the tiger beetles. Some authorities place the tiger beetles in the subfamily Cicindelinae within the family Carabidae. Others place the tiger beetles in a separate family, the Cicindelidae. We include the tiger beetles in the Carabidae for the purposes of this review.

Among 39 carabid species new to five upper Midwestern states (19 for Illinois, 11 for Iowa, three for South Dakota, eight for Wisconsin and two for Michigan, with three species being new to more than one state), Purrington et al. (2000) reported unusually disjunct collections of *Helluomorphoides nigripennis* (Dejean) from western Illinois and *Chlaenius amoenus* Dejean from northeast Iowa. The former is a myrmecophilous species previously known only from the Atlantic and Gulf coastal plain and piedmont, whereas the latter species had previously only been reported from the southeastern states (Purrington et al., 2000). Another substantial range extension was established for the "beautiful tiger beetle," *Cicindela pulchra* Say, by Larsen and Willis (2008). This species was collected in western South Dakota, ca. 400 km north of its previously established northernmost limit in southern Nebraska.

Many new carabid records have been established for the state of Minnesota during the past decade. Tinerella (2000), Tinerella and Rider (2000), and Tinerella and Rider (2001) reported eight new state species records for carabids (including one tiger beetle) collected in tallgrass prairies in western Minnesota. Demonstrating how little is known of upper Midwestern carabid distributions, Gandhi et al. (2005) reported new Minnesota records for 13 genera and 100 species of carabids, representing 21% and 31% increases over previous published records, respectively. In addition to new material, examination of numerous private and museum collections contributed to these new records, demonstrating the importance of these holdings for biodiversity research. This intensive survey notwithstanding, a single individual of *Harpalus ochropus* Kirby was later found in Superior National Forest, four miles west of Gunflint, Cook County, Minnesota, representing the first record of this species in Minnesota and the lower 48 contiguous states (Purrington and Maxey, 2006).

Diversity and distributions of North Dakota carabids are likewise poorly understood, but Tinerella (2003) added substantially to this knowledge base, reporting 43 new state records based on new material as well as examination of state and university collections. Despite this impressive addition, the faunal list for North Dakota is still relatively small at 275 species, suggesting that further collection would be fruitful in a state that has a variety of habitats and transitional life zones (Tinerella, 2003).

In addition to new state records and range extensions, new carabid taxa have been established in the Midwest. Spomer (2004) described a new subspecies of *Cicindela nevadica* LeConte, *Cicindela nevadica makosika* Spomer, from the Badlands of South Dakota. This species is associated with wet, saline, or alkaline soils in western North America. The population of *C. n. makosika* appears to be isolated from other conspecifics by at least 160 km, and is phenotypically most similar to *C. n. tubensis* Cazier from northeast Arizona (Spomer, 2004). Habitat destruction by cattle may be a threat to the *C. n. makosika* population (Spomer, 2004).

A new species of carabid, *Anillinus aleyae* Sokolov and Watrous, has recently been described from the Ozark region of southern Missouri (Sokolov and Watrous, 2008). This represents a northward range extension of ca. 170 km from the closest known congeners in the Ouachita Mountains (Figure 2). The genus *Anillinus*, containing 30 species, is widely distributed in the U.S. The center of *Anillinus* diversity is the southern Appalachians, and its geographic range covers a large area east of the Mississippi River, with a small disjunct distribution, including five species, in the Ouachita Mountains of Arkansas and Oklahoma (Sokolov and Watrous, 2008). The discovery of *A. aleyae* in the Missouri Ozarks is important biogeographically since it partially fills the gap between eastern and western *Anillinus*. Further studies of *A. aleyae* biogeography and affinities could shed light on potential distributional tracks of *Anillinus* ancestors between the Appalachian and Ozark/Ouachita lineages, as well as the possibility of a trans-Arkansas River track between the Ozark and Ouachita Mountains (Sokolov and Watrous, 2008).

Figure 2. Schematic distribution of the *Anillinus* species. 1-range of eastern species; 2-range of western species; solid circles-sampling sites of *A. aleyae*, new species. (From Sokolov and Watrous, 2008, The Coleopterists' Bulletin by Coleopterists Society. Copyright 2008 Reproduced with permission of Coleopterists Society - BIOONE in the format Journal via Copyright Clearance Center).

To summarize, scores of new state records and at least two new taxonomic descriptions of carabid species have been established in the Midwestern U.S. over the past decade. These discoveries underscore the need for ongoing faunistic studies of carabids in the region. Furthermore, carabid distributional changes could provide important information on the effects of climate change on terrestrial arthropods. Fundamental knowledge of carabid diversity, distributions, and abundance is essential for effective applications in these areas.

Phylogeographic studies of Midwestern carabid species also hold much promise. Phylogeography can be used to identify evolutionary significant units below species level that may have high value for conservation efforts. Much of the Midwestern landscape has been highly altered by human activities. Phylogeographic analyses also have the potential to clarify the relative roles of historical vs. human-induced effects on carabid diversity at as well as below the species level. Geographic information systems (GIS) also offer great potential for investigating biogeographic patterns in relation to climate, landforms, and human activities. An excellent example of the application of GIS to these types of problems is provided by Noonan's (1999) large-scale biogeographic study of the carabid subgenus *Anisodactylus*.

Carabid habitat associations and activity patterns

Carabids are important as biological indicators because of their often close associations with specific habitat types. Recent research in the Midwestern U.S. has revealed details of carabid associations with particular habitats. It should be kept in mind that most studies of carabid diversity and habitat associations rely heavily on pitfall trapping.

As with virtually any insect trapping technique, pitfall traps have inherent biases, some of which may be species- or habitat-dependent. Because they target only certain members of the surface-active community, pitfall traps are a poor metric for describing species abundance or community diversity. Studies comparing results of pitfall trapping with other carabid sampling techniques in a variety of habitats are needed to evaluate these potential biases (Lundgren et al., 2006). Studies comparing different pitfall trapping methods would also be useful, since variation in pitfall trapping methodology may result in differing abundances and species composition of carabids collected. For instance, McCravy and Willand (2007) found significant differences in total numbers collected, as well as species-specific effects, in a study comparing carabid collections using six different pitfall trap preservatives in a west-central Illinois deciduous forest. Pitfall trap collections of carabids are best described in terms of 'activity-density' since these collections are a function of the activity levels of the carabids as well as their abundance (Greenslade, 1964).

In the heavily forested state of Michigan, Petrillo and Witter (2009) examined habitat associations and species richness of carabids inhabiting northern hardwood forests. They compared carabid communities of northern red oak (*Quercus rubra* L.)-American beech (*Fagus grandifolia* Ehrh.) (both in the Fagaceae) stands of the Michigan Lower Peninsula (OBLP), sugar maple (*Acer saccharum* Marsh., Aceraceae)-American beech stands of the Lower Peninsula (MBLP), and sugar maple-American beech stands of the Upper Peninsula (MBUP). Significant habitat associations were found for five of 19 species captured, including *Carabus goryi* Dejean (MBLP), *Calathus gregarius* Say (OBLP), *Pterostichus adstrictus* Eschscholtz (MBUP), *Pterostichus coracinus* (Newman) (MBUP), and *Pterostichus melanarius* Illiger (MBUP). Significant differences were found among carabid assemblages of these different stand types within the broadly-defined northern hardwood forest community, with relatively low richness and activity-density in the OBLP. The OBLP stands had relatively open canopies and dry soils, suggesting that microclimatic conditions play an important role in shaping carabid communities in these habitats.

Werner and Raffa (2000, 2003) and Latty et al. (2006) conducted 2-yr studies of the diversity, seasonal activity and response to logging history of ground-occurring beetles (including carabids) in Wisconsin and Michigan forests, Werner and Raffa (2000) focused on effects of management practices in even-aged, uneven-aged, or old growth northern hardwood or eastern hemlock-dominated sites. Carabid diversity was highest in old growth hemlock hardwoods and lowest in old growth northern hardwoods. Five carabid species (*Calosoma frigidum* Kirby, *Harpalus fulvilabris* Mannerheim, *Platynus decentis* (Say), *P. coracinus*, and *Pterostichus mutus* (Say) had significant associations among management regimes. Species distributions among management regimes were consistent between years, and species composition was more closely associated with presence of management than with a particular management regime, tree species dominance, or canopy structure. These results suggest that a variety of forest types is needed to maintain regional carabid diversity.

Werner and Raffa (2003) found that carabid abundance and species richness were highest in the early portion and middle of the season, and suggested that this may be a reflection of the relatively high abundance of lepidopteran and hymenopteran larvae that serve as food sources. These results indicate that an entire season of trapping is probably needed to adequately assess species richness. Temporal patterns in trap catches of the most common species were similar between years, suggesting that a single year of sampling may be sufficient for a general overview of seasonal activity in abundant species. The invasive carabid *P. melanarius* was the fourth most common ground beetle collected in this study. The authors observed that temporal niche partitioning may be an important factor in reducing interspecific competition, and that an introduced species such as *P. melanarius* could affect seasonal activity and stability of native species through competition for scarce resources. Studies addressing the potential of this invasive species to disrupt ecological communities are needed.

Carabid community structure in relation to logging history and forest cover changes was examined by Latty et al. (2006). Their results suggest that carabid community structure is strongly dependent on habitat heterogeneity and is associated with such forest characteristics as coarse woody debris, snags, gap area, understory vegetation and forest floor depth. The authors suggest that, since old-growth forest has declined precipitously in the region since European settlement, abundance of carabid species that prefer old-growth forests has undergone a general decline as well.

Larsen et al. (2003) examined carabid assemblages in six northeastern Iowa habitats (tallgrass prairie, old field, woods, and three agricultural habitats – corn, soybean and oats) during a 5-yr study. Of 107 species collected, 24 were classified as generalists, 14 as agricultural species, 12 as grassland species (found in non-wooded habitats, primarily prairie and old field), 39 as prairie species, and 18 as woodland species. Nonmetric multidimensional scaling revealed distinct carabid assemblages among the six habitats examined, with the oat habitat having 63% similarity with the tallgrass prairie and the old field habitat sharing similarities with both agricultural and woodland habitats. Although many of the species classified as habitat specialists were based on small sample sizes, 20 indicator species were identified, 13 for woodland habitats and seven for tallgrass prairie (Table 1). If natural prairie and forest areas in the Midwestern U.S. continue to succumb to pressure from human encroachment and associated development and cultivation, these habitat specialists will be at particular risk for local extirpation.

Focusing on the habitats of a single species, Brust et al. (2005) examined the biology of the flightless tiger beetle *Cicindela cursitans* LeConte in south-central Nebraska. This species was most strongly associated with areas having moist clay soils, particularly low moist clay ditches, preferring grassy locations with some exposed soil or sites with sparse vegetation. Few individuals were associated with heavy vegetation. Oviposition only occurred in moist, fine particle (< 0.105 mm) soils. Larval burrows were most abundant in moist clay ditches near the bases of plants. Despite its inability to fly, *C. cursitans* can evidently colonize suitable habitat relatively quickly, and may have potential as a biological indicator of success in wet meadow restoration projects (Brust et al., 2005).

In developing a rearing protocol for the carabid *Poecilus chalcites* (Say), Lundgren et al. (2005) obtained information on habitat requirements for this species. They found

Table 1. Indicator values, randomization tests of significance and habitat affinities for 20 carabid beetles collected from woodland and tallgrass prairie habitats in northeastern Iowa. C: common; U: uncommon; R: rare. (This table was published in Pediobiologia, Vol. 47, K. J. Larsen, T. T. Work and F. F. Purrington, Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa, pp. 288-299, Copyright Urban & Fischer Verlag, 2003).

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	0.048	_	75	_
Pterostichus permundus	C	72.5	0.049	25	72	1
Pterostichus femoralis	U	71.9	0.14	_	72	2

that, in addition to diet, factors such as substrate type and moisture content affect larval size, development, and pupation rates. In particular, larval development times and pupation rates varied significantly with substrate type. Larval development rates were lowest (i.e., larval duration greatest) in soil composed of 35% coarse sand, 35% fine sand, 20% kaolin clay and 10% peat moss, and pupation rate was significantly greater for larvae reared in unsteamed Fer-Til® potting soil (which had very high organic matter content) than the other soil types tested, including steamed potting soil. The authors suggested that the unsteamed soil may have provided endosymbionts that were lost due to antibiotics provided to the beetles in the diet (Lehman et al., 2009). Larvae reared in vermiculate with 66.7% water weighed significantly more than those in vermiculate containing 50% or 33.3% water, indicating that *P. chalcites* larvae are sensitive to substrate moisture conditions. These results suggest that agricultural practices which help maintain soil moisture and high organic matter could play a major role in maintaining this potentially important biological control agent.

Habitat disturbance also has important implications for carabid diversity and community composition. Studies by Larsen and Williams (1999), Larsen and Work (2003) and Cook and Holt (2006) have addressed the effects of fire on tallgrass prairie carabid assemblages. In their study of Iowa tallgrass prairie carabids, Larsen and Williams (1999) examined variation in carabid assemblages from two years post-burn to same year burn. They found that species richness decreased with time since burning, but species diversity (based on Shannon's diversity index) and evenness increased. Carabid assemblages were least similar (56.6% similarity) between the two year interval and same year burn plots, with the one year interval and same year burn plots being most similar (80.3%) and the two year interval and one year interval plots having 70.7% similarity. In a larger study of Iowa tallgrass prairie carabids, Larsen and Work (2003) also found greatest diversity several years after a fire. As the authors note in both studies, effects of fire vary depending on the carabid species in question. Carabid species can vary dramatically in their immediate and longer-term responses to fire, and prairie specialist species tended to become less diverse with increasing time since burning. Larsen and Williams (1999) and Larsen and Work (2003) also point out that carabid activity levels are probably greater in more recently burned prairie because of less vegetation to hinder their movements. Cook and Holt (2006) found that, overall, the carabid community of Konza Prairie in Kansas was relatively stable in relation to fire frequency, with the most dramatic effects occurring among the most common carabid species. However, despite large overall sample sizes, sample sizes for many species were too small for statistical analysis and firm conclusions regarding effects of fire.

Another important type of habitat disturbance of increasing importance in the Midwestern U.S. is colonization by invasive species. Kleintjes et al. (2002) examined the carabids associated with reed canary grass (Poaceae), *Phalaris arundinacea* L., an invasive species of lowland and riparian areas that has had a negative impact on native plant species in Wisconsin (Barnes, 1999). Seventeen species of carabids were collected, which is in the lower range of species richness for carabid assemblages in the upper Midwest. All species had been previously documented in Wisconsin, and most are considered habitat generalists (Kleintjes et al., 2002).

Gandhi et al. (2008) investigated the short-term effects of a catastrophic windstorm and subsequent salvage logging/prescribed fire fuel reduction treatments on carabids in a northeastern Minnesota sub-boreal forest consisting of aspen/birch/conifer and jack pine cover types. They found that windstorm effects reduced the activity-abundance of carabids, but prescribed burning increased it. A 6-fold greater number of carabids were collected in burned than in unburned forest, and both burned and salvaged forest plots had greater species richness, diversity and uniqueness. Analyses of percentage similarity of carabid species assemblages among habitats suggested that carabid faunas of the two cover types were distinct in undisturbed habitats, but that disturbance tended to remove these differences (Figure 3). The invasive carabid *Pterostichus melanarius* was the most abundant species collected in this study, accounting for 35% of the almost 30,000 individuals collected. This species was present in all habitats, and is apparently becoming quite common in the northern regions of the Midwestern U.S. When *P. melanarius* was excluded from the analyses, carabid assemblages of undisturbed and wind-disturbed aspen/birch/conifer sites were quite similar (Figure 4). The authors suggest that the abundance of this invasive species in disturbed habitats could potentially alter carabid successional pathways (Gandhi et al., 2008).

Anthropogenic habitat disturbances have had a dramatic impact on the Midwestern U.S. landscape, and this has undoubtedly affected carabid assemblages.

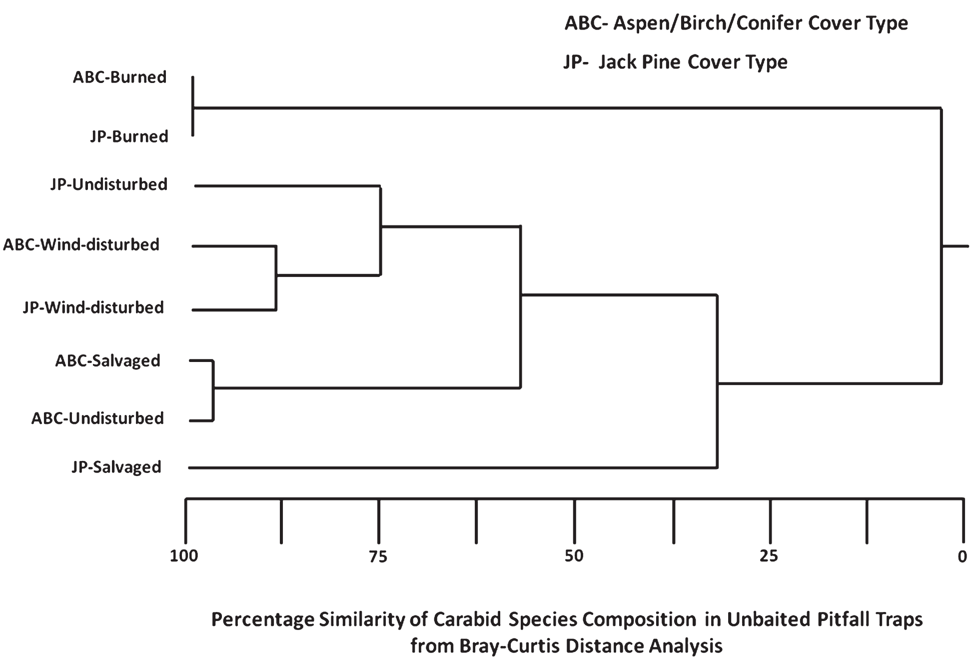


Figure 3. Dendrogram of the percentage similarity of the ground beetle species trapped in unbaited pitfall traps in 2000-2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types. (From Gandhi et al., 2008, Forest Ecology and Management by Elsevier BV. Reproduced with permission of Elsevier BV in the format Journal via Copyright Clearance Center).

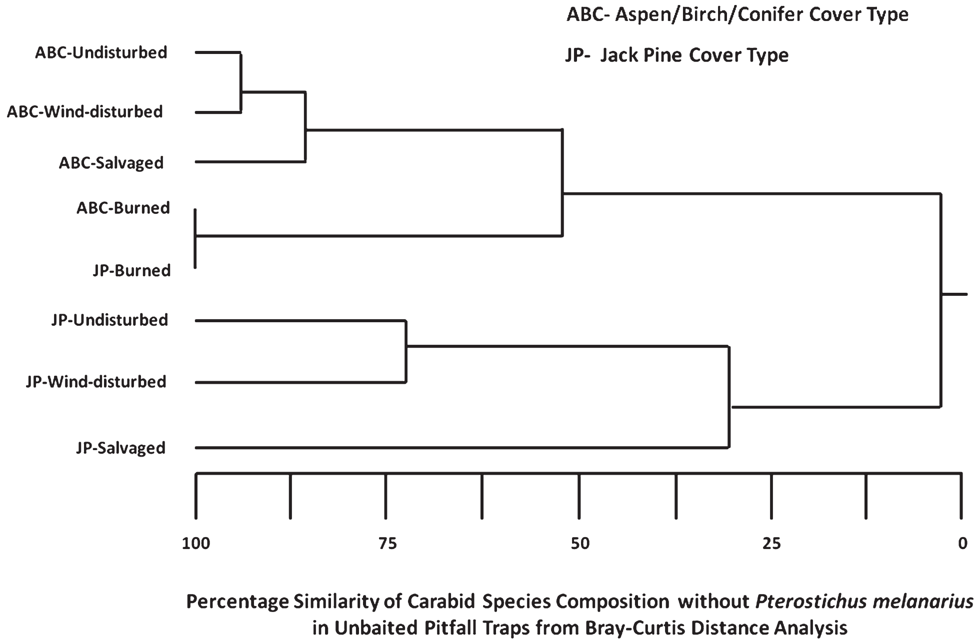


Figure 4. Dendrogram of the percentage similarity of the ground beetle species trapped in unbaited pitfall traps in 2000-2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types without *P. melanarius*. (From Gandhi et al., 2008, Forest Ecology and Management by Elsevier BV. Reproduced with permission of Elsevier BV in the format Journal via Copyright Clearance Center).

Larsen et al. (1996) examined the effects of nutrient enrichment with fertilizer and heavy metal-contaminated sewage sludge on carabid communities of old field habitats in southwestern Ohio. Carabid abundance, diversity, and species richness were significantly higher in the nutrient enriched and sludge treatments, but no evidence of bioconcentration of heavy metals was found, suggesting that carabids are useful indicators of environmental disturbance but not useful as indicators of heavy metal contamination in old fields.

Silverman et al. (2008) focused on the effects of a 17 m wide, ~1.3 km long oil pipeline corridor constructed through a forested private reserve area in the Hocking Hills region of southeastern Ohio. Nonmetric multidimensional scaling showed that the corridor carabid assemblage was distinct from that of the forest interior and from the forest/corridor ecotone assemblage (Figure 5). Presence of the corridor led to colonization by early successional species. Open-habitat species were rare in the forest, and forest species were absent from the corridor, suggesting that habitat fragmentation had taken place. For instance, *Pterostichus trinarius* (Casey), a common forest species, was absent from the corridor and populations on either side of the corridor were likely isolated. Furthermore, oil pipeline installation and regular mowing of the corridor now means permanent habitat change and fragmentation (Silverman et al., 2008).

There is growing evidence that such forest fragmentation can have substantial impacts on carabid communities. In the highly fragmented landscape of northwestern

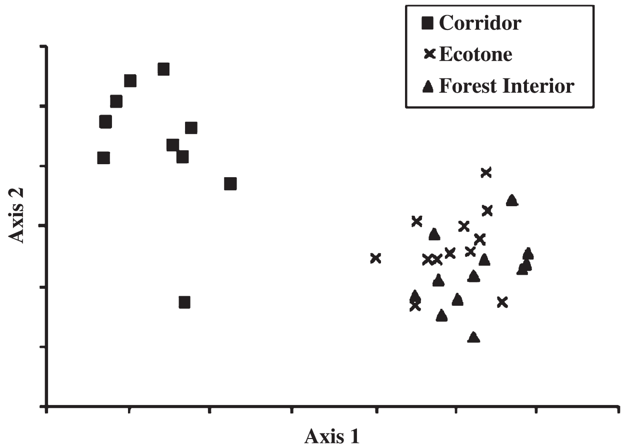


Figure 5. A nonmetric multidimensional scaling plot showing arrangement of pitfall traps in forest-dividing corridor, ecotone, and forest interior habitats as based on the similarities in carabid species assemblages along hypothetical environmental gradients. The R^2 value for axis 1 is 85.1%, and for axis 2 is 6%. The correlation value (*r*) for the two axes is -0.73. (From Silverman et al., 2008, Environmental Entomology by Entomological Society of America. Copyright 2008 Reproduced with permission of Entomological Society of America in the format Journal via Copyright Clearance Center).

Ohio, Oates et al. (2005) examined the activity/density, species richness, diversity, and similarity of carabid assemblages associated with forest fragments of different sizes – small (9 to 10 ha) and large (20 to 40 ha). Although preliminary, their results suggested a trend of greater species richness and diversity in larger fragments, and relatively low similarity among forest fragments regardless of fragment size.

Agricultural land dominates much of the Midwestern U.S., and cultivation has led to reduction of forests into small fragments throughout much of the region. In west-central Illinois, corn and soybean fields dominate much of the landscape, but surface coal mining has also been important economically in this area. Many of these mines were abandoned decades ago and filled with soil and refuse. Plant succession then led to small habitat islands of herbaceous and woody vegetation within agricultural fields. McCravy and Willand (2005) examined the carabid communities associated with four of these coal mine remnants, ranging from 0.10 to 0.25 ha, and surrounding soybean fields. The remnants harbored a carabid assemblage distinct from the surrounding fields, but the assemblages of the remnant interiors were not different from the edge and perimeter (5 m interior to the edge) assemblages, suggesting that the remnants were not large enough (or sufficiently mature) to harbor an authentic primeval carabid fauna. Several indicator species were found which were significantly associated with the field or edge habitats.

Habitat disturbance also affects the diel activity patterns of carabid species. An accompanying study of the diel activity patterns of these carabid species revealed significant variation in the activity patterns of three species in relation to habitat (Willand and McCravy, 2006). Remnant and edge *P. chalcites* showed significantly greater diurnal activity than did those associated with the soybean field (Figure 6).

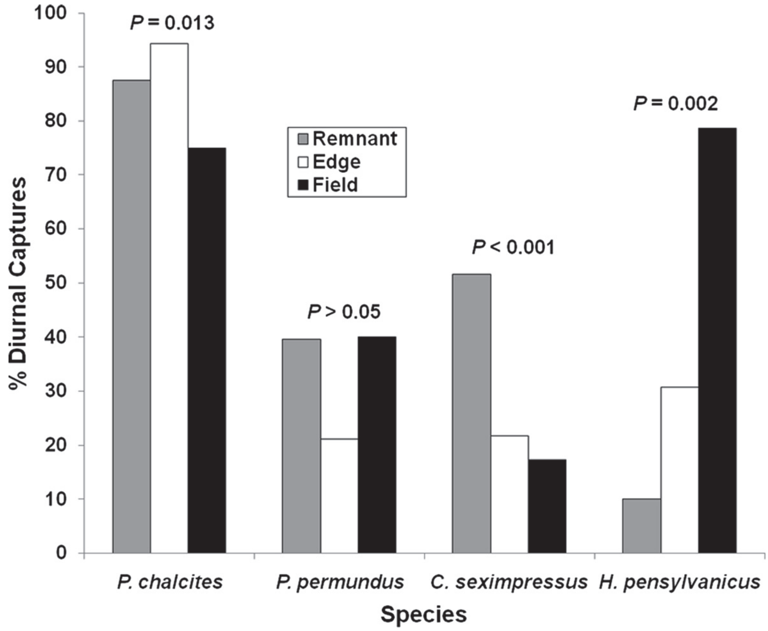


Figure 6. Diurnal activity (i.e., collected during dawn to dusk) of four species of carabid beetles by habitat (coal mine remnant, field edge, and soybean field) in west-central Illinois in 2002 based on captures in pitfall traps: *Poecilus chalcites* (*N* = 844 individuals), *Pterostichus permundus* (*N* = 194), *Cyclotrachelus seximpressus* (*N* = 160), and *Harpalus pensylvanicus* (*N* = 37). (This figure has been reproduced with permission from The Great Lakes Entomologist. For full citation, please see References section of this paper, under Willand and McCravy, 2006).

Cyclotrachelus seximpressus (LeConte) was also more active diurnally in the remnant. *Harpalus pensylvanicus* (DeGeer), on the other hand, showed greatest nocturnal activity in the remnant and edge. Lundgren et al. (2006) also found evidence for habitat-related variation in diel activity among ground-dwelling arthropod predators (including carabids), with relatively greater predation occurring at night in high intensity organic farming transition systems. The authors suggested that these results could be due to different arthropod assemblages in the lower intensity systems, or differences in predator behavior. The findings of Willand and McCravy (2006) for *P. chalcites* suggest that predator behavior can vary substantially over time, perhaps due to habitat changes. This species showed roughly equal nocturnal and diurnal activity in soybean fields early in the season (June) when soybeans provided little cover, but were almost totally diurnal in later months when cover was much denser. Using time-sorting pitfall traps, Lundgren et al. (2009b) examined the diel activity patterns of generalist predators associated with the western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Chrysomelidae), in a South Dakota cornfield. The western corn rootworm is a primarily subterranean herbivore that feeds on corn roots and is a major pest species. Predators generally fell clearly into diurnally- or nocturnally-active guilds. The carabid *Scarites quadriceps* Chaudoir, for instance, was captured during the night, whereas *P. chalcites* was captured primarily during the day. Results for both species agree with those found in Illinois by Willand and McCravy (2006).

Crist and Ahern (1999), in a study of carabid distribution and abundance in habitat patches and mowed areas in an old field in southwestern Ohio, found a seasonal pattern to carabid use of habitat patches. They found that *H. pensylvanicus* and *Calathus opaculus* LeConte tended to shift to smaller patches or mowed areas late in the season, behaviors which were consistent with their preferred temperatures. Substantial year-to-year variation in carabid diel activity patterns has also been documented. Snider and Snider (1997), in a long-term study of C. *frigidum* activity patterns in northern Michigan forests, found that percentage of diurnal captures of this species in pitfall traps ranged from 53% to 95%, with the lower number occurring during a year of low rainfall and perhaps being associated with drought conditions and low prey availability.

Many carabid species are closely associated with specific habitats, and genetic diversity and population structure may be altered in a fragmented landscape (Keller et al., 2004). As noted previously, an oil pipeline corridor only 17 m in width may have interrupted gene flow in a population of *P. trinarius* (Silverman et al., 2008) in Ohio. Fragmentation of Swiss forests by road construction has led to reduced gene flow and genetic variation in the flightless carabid *Carabus violaceus* L. (Keller and Largiadèr, 2003, Keller et al., 2004), showing that such disturbances can alter carabid genetic structure. Studies of the effects of habitat fragmentation on the genetics of carabid populations in the Midwest are needed, particularly for habitat specialists such as the forest species *P. trinarius*. Genetic analyses could also shed light on dispersal patterns and gene flow among potentially isolated carabid populations.

Detailed studies of variation in carabid habitat quality are also needed. For instance, prairie habitats can vary greatly in plant species composition and presence of native prairie vs. invasive species. Small habitat fragments in particular may be subject to colonization by invasive plants. Invasive plant species, such as garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara and Grande (Brassicaceae), and tree of heaven, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), can dramatically alter herbaceous cover and species composition through aggressive growth and production of allelochemicals (Heisey, 1990; Roberts and Anderson, 2001).

Frequency of burning and other management protocols can also affect plant species composition and structure, with resulting microclimatic effects that may influence carabid species assemblages. Of course, to evaluate the potential effects of microclimatic changes on carabid communities, an understanding of carabid microclimatic requirements is needed. Detailed, species-specific studies of habitat and microclimatic requirements of carabids could contribute much valuable information. There is also evidence that habitat changes can influence carabid behavior, such as diel and seasonal activity patterns. Further studies of the potentially interacting effects, both short- and long-term, of habitat disturbance and fragmentation, invasive species, and habitat management on carabids are needed.

Manipulating roadside habitats to conserve carabid species within the landscape represents another fruitful area of research. There is evidence that roadside habitat restoration can benefit pollinating insects such as butterflies and native bees (Ries et al., 2001, Hopwood, 2008), and roadside habitat may also serve as dispersal corridors for carabids (Vermeulen, 1993). In a study of roadside arthropods in the Netherlands, 40% of the total number of Dutch carabid species were collected in roadside habitats, even though only a very small fraction of the country's total roadside habitat was sampled (Noordijk et al., 2009). In the highly fragmented landscapes that constitute much of the Midwestern U.S., roadside habitat management practices that encourage diverse vegetation could be important in providing suitable habitat for carabids, or for allowing carabid dispersal among suitable habitats.

Conservation of carabids associated with cultivated habitats

Effects of agricultural practices on carabids

In the Midwestern U.S., agriculture is of great importance economically, and carabids are abundant and important components of agricultural environments. The insectivorous habits of many carabids make them potentially important biological control agents of pest insect species. But feeding habits vary within the Carabidae, and some carabid species are seed predators that can provide effective biological control of weed species as well. However, agricultural landscapes are highly disturbed and simplified habitats that can be hostile environments to many biological control agents (Landis et al., 2000). Effects of agricultural practices on carabid assemblages have been a major focus of research in the Midwestern U.S.

Lundgren (2005) and Lundgren et al. (2006) investigated the potential effects of organic transition systems on beneficial ground dwelling arthropods, including carabids. They examined three organic transition systems, including pasture/ley (low intensity management and input), cash grain (intermediate intensity) and vegetable (high intensity) systems. Activity levels of ground-dwelling arthropods, as measured by pitfall sampling, were reduced in the low intensity habitat, perhaps because the more stable environment resulted in less arthropod movement. However, quadrat sampling yielded the greatest density of beneficial arthropods in the low intensity system. Greatest predation rates on restrained wax moth (*Galleria mellonella* L.) (Pyralidae) caterpillars were found in the low intensity system, and seed removal was greatest in this habitat as well, suggesting that low intensity cropping systems are advantageous to these beneficial arthropods. O'Rourke et al. (2008) also investigated the effects of crop management intensity on carabid assemblages. They examined carabid activity-density and species richness in a conventional 2-yr corn/soybean rotation system and a low input 4-yr corn/soybean/tricale underseeded with alfalfa/alfalfa rotation system. The 2-yr system received greater chemical inputs in the form of nitrogen fertilizer and herbicides, whereas the 4-yr system received greater mechanical weed control. Carabid species richness and activity-density levels were greatest in the low input 4-yr rotation system (Table 2), supporting the hypothesis that low chemical input agricultural practices provide more favorable environments for carabids.

Table 2. Activity-density, species richness, Simpson's evenness index, and Simpson's diversity index estimates for adult carabid beetles in each cropping treatment and crop rotation in 2003 and 2004, Boone Co., IA. Values are pitfall trap per year ± SE. Cropping treatment or crop rotation means followed by the same letter within columns are not significantly different ($P > 0.05$); Tukey pairwise comparison test. Activity-density and species richness comparisons performed on ln (x + 1)-transformed data. (From O'Rourke et al., 2008, Environmental Entomology by Entomological Society of America. Copyright 2008. Reproduced with permission of Entomological Society of America in the format Journal via Copyright Clearance Center).

	Activity-density	Species richness	Simpson's evenness	Simpson's diversity
Cropping treatment				
Corn, 2-yr	16.79 ± 1.94a	8.13 ± 0.61a	0.37 ± 0.04b	0.62 ± 0.05c
Corn, 4-yr	28.34 ± 2.08ab	9.88 ± 0.91ab	0.24 ± 0.03ab	0.53 ± 0.04bc
Soybean, 2-yr	37.22 ± 4.47b	8.38 ± 0.68a	0.20 ± 0.05a	0.29 ± 0.05a
Soybean, 4-yr	44.31 ± 8.15b	9.25 ± 0.59ab	0.18 ± 0.02a	0.35 ± 0.05ab
Triticale-alfalfa, 4-yr	36.97 ± 7.64ab	13.63 ± 1.72b	0.26 ± 0.04ab	0.61 ± 0.07c
Alfalfa, 4-yr	47.69 ± 9.39b	11.63 ± 0.65ab	0.18 ± 0.02a	0.46 ± 0.07abc
Crop rotation				
2-yr	27.01 ± 2.90A	8.25 ± 0.53A	0.28 ± 0.03B	0.46 ± 0.04A
4-yr	39.33 ± 3.65B	11.09 ± 0.72B	0.21 ± 0.01A	0.49 ± 0.02A

Ellsbury et al. (1998) examined carabid assemblages in four crop rotation systems under high (fertilizer, herbicide, and insecticide treatments), managed (fertilizer and herbicide treatments), and low (postemergence herbicide treatment only) chemical input levels in eastern South Dakota. They found that dominant carabid species varied by crop, with *Cyclotrachelus alternans* (Casey) dominant in corn and alfalfa, *Poecilus lucublandus* (Say) dominant in wheat, and *C. alternans* and *P. lucublandus* equally abundant in soybean plots. *Harpalus pensylvanicus* had the greatest relative abundance in the low-input plots. Relatively high hierarchical richness index values were found in the managed plots (Table 3). These results occurred without the yield losses found in the low input plots, indicating that a moderate level of management intensity can maintain carabid assemblages without significant loss of yield (Ellsbury et al., 1998). Studies such as these are important in addressing the need for less environmentally damaging agricultural practices that still maintain crop yield levels and conserve potentially important biological control agents.

Non-target effects on carabids

Insecticides are commonly used against agricultural pests in the Midwestern U.S., and are often important and effective pest management tools. But broad-spectrum insecticides such as many organophosphates and carbamates are coming under increased scrutiny by regulatory agencies, and use of these insecticides may be restricted in favor of reduced-risk insecticides, including insect growth regulators, neonicotinoids and botanicals, that may have lower impacts on non-target organisms (O'Neal et al., 2005).

Table 3. Number of species collected (*N*), Shannon-Weaver diversity index (*H'*), evenness (*J'*), and hierarchical richness index (HRI) for carabid species collected in 1993 and 1994 near Brookings, South Dakota. Data are grouped by crop, rotational sequence, and level of chemical and cultural input. Rotations: C-C, continuous corn; C-S, corn-soybean rotation; C-Cr, corn-soybean rotation ridge-tilled; C-S-W-A, corn-soybean-wheat underseeded to alfalfa-alfalfa in 4 yr rotation. (From Ellsbury et al., 1998)

Source of trap data	Treatment	*N*		*H'*		*J'*		HRI	
		1993	1994	1993	1994	1993	1994	1993	1994
Crop	Corn	23	29	0.865	0.845	0.635	0.577	4384	3870
	Soybean	19	22	0.875	0.750	0.684	0.578	2487	3580
	Wheat	15	20	0.856	0.947	0.728	0.728	1705	892
	Alfalfa	14	20	0.735	0.778	0.678	0.565	1010	931
Rotation	C-C	20	23	0.862	0.897	0.687	0.659	1135	1175
	C-S	19	21	0.913	0.804	0.714	0.608	1961	2003
	C-Cr	21	23	0.846	0.782	0.640	0.575	2324	2275
	C-S-W-A	21	28	0.862	0.847	0.652	0.585	3359	4716
Input level	High	19	27	0.864	0.842	0.528	0.588	2708	3120
	Managed	21	26	0.830	0.785	0.628	0.555	3008	3500
	Low	23	29	0.906	0.868	0.666	0.594	3120	3896

O'Neal et al. (2005) compared the effects of reduced-risk vs. broad-spectrum insecticides on carabid assemblages in highbush blueberry farms in southwestern Michigan. Pitfall trap captures of only one carabid species, *Harpalus eraticus* Say, were affected by different insecticide programs, with an eight-fold greater number of captures in the reduced-risk fields. This was probably the result of high broad-spectrum insecticide use by growers during the months of June and July when *H. eraticus* are in the larval and pupal stages in the soil. However, in one blueberry farm with no ground cover between blueberry rows, there was no effect of insecticide program on *H. eraticus* captures, suggesting an interaction of habitat type with effects of insecticide type on these carabids.

Genetically modified (GM) crops with genes that produce insecticidal proteins are increasing in importance in the Midwest and throughout the United States. For instance, transgenic "Bt corn," containing genes from the soil bacterium *Bacillus thuringiensis* (Berliner) (Bt) that express crystalline proteins toxic to pest insects, accounted for 63% of all corn planted in the United States in 2010 (National Agricultural Statistics Service, 2010). The diverse feeding habits of carabids suggests that they may be exposed to Bt toxins via several avenues, including consumption of plant material and feeding on other invertebrates exposed to the toxin. Several studies in the Midwestern U.S. have addressed this issue.

Much of this research has focused on toxic effects of Bt toxins on *P. chalcites*. Duan et al. (2005) examined the potential for using *P. chalcites* larvae in assessing nontarget impacts of GM crops that express plant-incorporated protectants (PIPs). They evaluated the effects of the protease inhibitor E-64 on growth, development and survival of immature *P. chalcites* over a 28-d exposure period, with three levels of E-64 in the larval diet (60 µg/g, 150 µg/g, and 600 µg/g of diet). The highest (600 µg/g) dose adversely affected larval growth and development after two, three, and four weeks of exposure, but no affect on survival was found. Duan et al. (2006) exposed *P. chalcites* larvae to 28 d of continuous exposure to Cry3Bb1 protein at a dose of 930 µg/g of diet, which was 10 times the maximum concentration expressed in the Monsanto Company genetically modified corn MON 863. This dose had no adverse effect on survival, growth or development of *P. chalcites* larvae. Ellsbury et al. (2005) also examined potential nontarget effects of MON 863 and Cry3Bb1 corn on carabid communities in the northern Midwest corn belt, and found no significant effect on carabid abundance.

Lopez et al. (2005) evaluated the usefulness of carabids for testing nontarget effects of transgenic (Bt) corn in Iowa cornfields. No significant negative effects of transgenic corn or insecticidal (permethrin) treatments were found. They concluded that *H. pensylvanicus* may be the most useful species for testing nontarget effects in Iowa cornfields because of its abundance, ubiquitous distribution, and generalist feeding habitats. However, there was substantial temporal and spatial variation in population levels and community composition. In general a small number of carabid species dominated a particular community, suggesting that the most abundant 2-4 species could be used as indicator species in a given locality. Based on statistical power analyses, the authors concluded that only very large treatment differences are likely to be detected by standard experimental designs and analyses.

Bhatti et al. (2005) and Wolfenbarger et al. (2008) investigated potential effects of Bt crops on nontarget invertebrates, including carabids. The former study found no consistent adverse effects of MON 863 Bt corn expressing the Cry3Bb1protein on any nontarget ground-dwelling invertebrates in comparison with a non-Bt isoline. However, foliar (permethrin) and soil (tefluthrin) insecticide applications decreased carabid and spider abundances. In a meta-analysis of Bt crop (cotton, maize, and potato) effects on nontarget arthropods, Wolfenbarger et al. (2008) likewise found no uniform effects of Bt crops on nontarget arthropod functional guilds, whereas conventional insecticidal treatments produced relatively large effects. Based on the above studies, there appears to be little evidence for adverse effects of Bt crops on carabids or nontarget invertebrates in the Midwestern U.S. On the contrary, these results suggest that replacement of conventional insecticides with Bt crops may conserve natural enemies and thus enhance the effectiveness of these nontarget biological control agents.

Alternative habitats for carabid conservation

Agricultural landscapes are generally subjected to intensive management and heavy disturbance which can significantly alter carabid assemblages. Providing alternative habitats in the form of refugia or cover crops could benefit carabids and increase their biological control services. Carmona and Landis (1999) investigated the effects of habitat refuge strips (perennial flowering plants, grasses, and clovers) and cover crops (red clover) on activity-density of carabids in a soybean/oats/corn rotation in south-central Michigan. Although refugia had greater carabid activity-density, this did not result in increased populations in the field crop habitats. As noted by the authors, one explanation for these results may have been the relatively high dispersal abilities of carabids, particularly larger-sized species. This could have allowed those beetles to move readily between habitat refugia, decreasing detectable refugia effects on crop fields. Field crop habitats with a cover crop, on the other hand, had significantly higher carabid activity-density than did those without a cover crop. Likewise, Lundgren and Fergen (2011) found that corn fields that had a preceding winter cover crop had more of some carabid species than cornfields preceded by bare soil (especially *Polyderis* sp.), and that this increase in predator abundance was associated with fewer western corn rootworm immatures (*Diabrotica virgifera*). In further studies of the effects of agroecosystem habitat diversity, Lee et al. (2001) examined the potential for habitat refugia, consisting of grasses, legumes, and flowering plants, to provide a buffer for carabid assemblages against the effects of insecticide applications in a Michigan cornfield. In this study, barriers were used to prevent movement of carabids among plots. An early season treatment with the soil insecticide terbufos, which is commonly used against corn rootworm in the Midwestern U.S., reduced carabid activity-density and altered species composition. As insecticide toxicity declined during summer, insecticide-treated plots adjacent to habitat refugia had significantly higher carabid activity-density than did treated plots not associated with refugia. Carabid community composition within plots was also affected by presence or absence of refugia. Results of these studies suggest that agroecosystem diversification may help maintain carabid populations and potentially provide pest control benefits, but that more research on the problem of translating the benefits of habitat refugia into increased biological control in the crop environment is needed.

Werling and Gratton (2008) and Gaines and Gratton (2010) examined carabid diversity and seed predation in Wisconsin potato fields and nearby non-crop habitats associated with agri-environmental schemes (AES) that provide incentives for farm practices that preserve non-crop habitat, increase habitat heterogeneity, or enhance biodiversity. They found that seed predation and carabid diversity were positively associated in crop and non-crop habitats, and that AES practices increase overall carabid diversity and seed predation at the landscape level. However, the benefits mostly occurred in the non-crop rather than the crop habitats. They suggested that approaches that spatially integrate crop and non-crop habitats, and reduction of ground-level disturbances within the crop habitat, may increase the benefits of AES.

Biotic interference

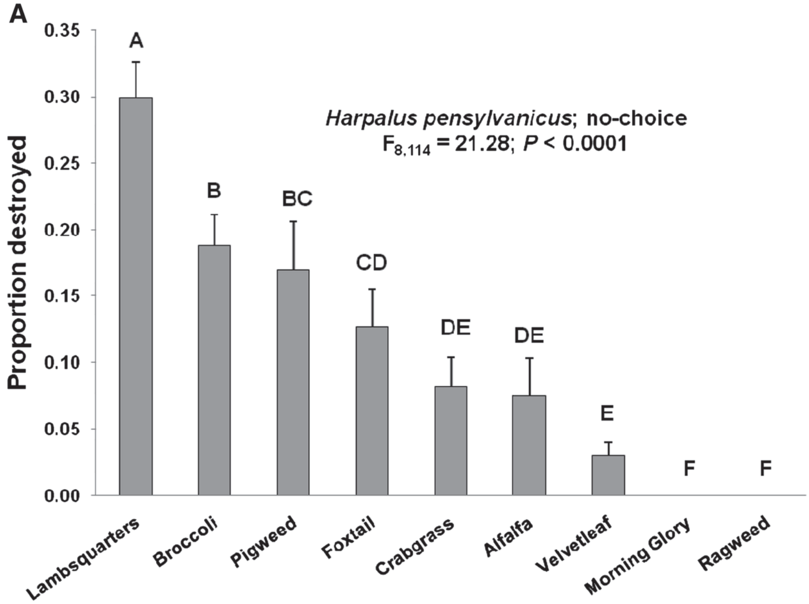
Biological control programs using beneficial arthropods are components of a larger biological system composed of many complex biotic and abiotic interactions. Carabids are a part of this system, and under certain conditions their feeding habits may actually interfere with effective biological control of economic pests. Evidence for such biotic interference has been found in association with biological control efforts using arthropod natural enemies of purple loosestrife (*Lythrum salicaria* L.) (Lythraceae).

Purple loosestrife is an invasive plant that has become widespread in wetland habitats of North America, including the Midwestern U.S. (Thompson et al., 1987). Establishment of this plant can alter wetland decomposition rates, reduce pollination, seed output, and diversity of native plants, and reduce habitat suitability for some wetland bird species (Blossey et al., 2001). The herbivorous chrysomelid beetles *Galerucella calmariensis* L. and *Galerucella pusilla* Duftschmidt have been widely released as part of a biological control program targeting purple loosestrife (Hight et al., 1995). Work by Sebolt and Landis (2004) in Michigan showed that the exotic *P. melanarius* was abundant at the study sites and was one of several arthropod predators that readily consumed immature stages of *G. calmariensis* in no-choice feeding trials. Field experiments utilizing predator exclusion cages resulted in *G. calmariensis* adult emergence rates up to three times greater in caged than in open treatments. The authors concluded that, while not limiting the establishment of *G. calmariensis* populations, the activities of arthropod predators may slow growth of *G. calmariensis* populations and delay effective biological control of purple loosestrife. Wiebe and Obrycki (2004) also examined potential biotic interference of the purple loosestrife biological control agent *G. pusilla* in Iowa wetlands, where *Galerucella* populations have shown less growth than in other Midwestern states. Carabids were the most abundant insect ground-dwelling predators, and could cause substantial *G. calmariensis* pupal mortality since pupation occurs in leaf litter. These studies demonstrate a downside to predation from carabids, and also illustrate the adverse ecological impacts of exotic carabids.

Omnivory in Carabidae – implications for weed management

Although they are best appreciated for their ability to consume insect prey, research in the Midwestern U.S. is helping to show that most carabids are best described as omnivores, and many will readily consume seeds and thereby shape plant diversity and dispersion within a habitat. Lundgren (2009) reviewed the taxa that consume weed seeds, and identified the seeds consumed by 171 carabid species. Many of the most conspicuously granivorous taxa reside within the Zabrini and Harpalini, and a better understanding of the full extent of the dietary breadth of other more "predatory" taxonomic groups (e.g., Pterostichini, Chlaeniini, etc.) will undoubtedly reveal at least a partial reliance on seeds.

Granivorous carabids often possess physiological and morphological adaptations that underscore their dietary breadth, and research suggests that dietary breadth may vary within a species as much as among species. Carabids often display distinct preferences for specific seeds (Marino et al., 1997; Harrison et al., 2003; Heggenstaller et al., 2006; O'Rourke et al., 2006; White et al., 2007), which is driven in part by the seed's nutritional content and defenses. In one laboratory study, Lundgren and Rosentrater (2007) found that two carabids, *H. pensylvanicus* and *Anisodactylus sanctaecrucis* F., displayed preferences for seeds that were based on the relative strengths of the seed coats and internal densities of the seeds (Figure 7). Studies from Europe have documented a range of other seed characteristics that influence seed preference in carabids,



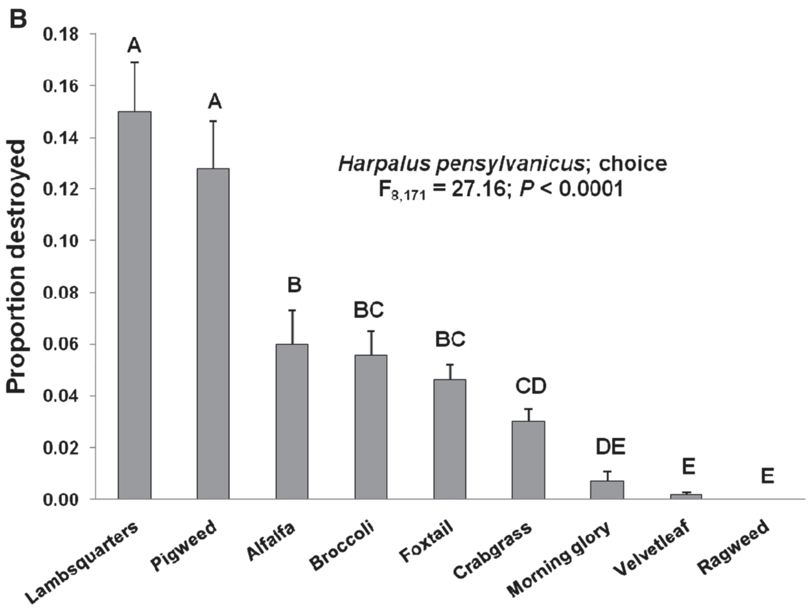


Figure 7. The proportion of seed destroyed by *Harpalus pensylvanicus* under no-choice (A) and choice (B) conditions. (From Lundgren and Rosentrater, 2007).

especially seed size (Honěk et al., 2007; Honěk et al., 2011). Lundgren (2009) concluded that carabid seed preferences are first influenced by seed size (seeds that are too large are avoided), and then by a myriad of other characteristics of those seeds that fall within an acceptable size range.

Dietary breadth of carabids is also influenced by the bacterial residents in their guts. The simple bacterial communities that reside within carabid guts are influenced by diet, and antibiotics can be used to reduce the diversity and abundance of specific bacterial taxa (Lundgren et al., 2007; Lehman et al., 2009). Lundgren and Lehman (2010) found that antibiotics also reduced seed consumption by *Harpalus pensylvanicus* (and *A. sanctaecrucis* and the cricket *Acheta domesticus* L.; J.G.L., unpublished data). A multivariate analysis showed that seed consumption was strongly correlated with the presence of a strain of the bacterium *Enterococcus faecalis*, and when this bacterium was removed from the guts of *H. pensylvanicus*, seed consumption was reduced dramatically. This bacterium is a common gut resident in many herbivorous insects, and the closest genetic match to this strain of *E. faecalis* was isolated from fermenting plant material. The authors suggest that these facultative symbioses between bacteria and host insects could have very important implications for their diet.

The sheer abundance of carabids in Midwestern cropland, particularly many granivorous taxa, has prompted extensive research on how manipulating carabid populations can influence cropland weeds. Several studies in the Midwest have shown statistical correlations between seed predator abundance/diversity and increased seed predation rates in a habitat. Seed removal rates can range up to 32% per day, but these numbers fluctuate widely among the habitats, seed predator species, seed species, and time period in question (Marino et al., 1997; Menalled et al., 2000; Davis and Liebman, 2003; Harrison et al., 2003; Lundgren et al., 2006; O'Rourke et al., 2006; White et al., 2007; Westerman et al., 2008; Westerman et al., 2009; Williams et al., 2009). Also, it is important to note that carabids are not always the dominant seed predator in a system, and sometimes crickets, ants, and rodents are more important contributors to seed removal than carabid populations (Marino et al., 1997; Harrison et al., 2003; O'Rourke et al., 2006; White et al., 2007; Westerman et al., 2008; Gaines and Gratton 2010). Although the predictability of seed predation rates still hinders farmers from relying solely on seed predation to manage weed populations, work has shown that seed predator conservation efforts may help to improve the reliability of seed predation by carabids in cropland.

Carabids can be important granivores of weed communities, and their impact on weed seeds is enhanced when disturbance to cropland is reduced, ground cover is increased, and more diversity (within a habitat and in the landscape) is incorporated into farmland. Within an agroecosystem, weed seed predation rates and granivorous carabid populations are often greater in perennial field margins than they are within fields (Carmona and Landis, 1999; Menalled et al., 2001; Gaines and Gratton, 2010). Yet seed predation likely shapes the plant communities within crop fields as well, and granivore populations can be conserved and promoted through directed farm management practices. Specifically, reducing tillage and optimizing the timing of tillage are often cited as important ways to increase seed predator populations within cropland, as is increasing vegetation cover (Cromar et al., 1999; Davis and Liebman, 2003; Heggenstaller et al., 2006; O'Rourke et al. 2008). For example, Westerman et al. (2008) found that it took several weeks for insect seed predators (carabids and crickets) to respond to increasing seed densities in Iowa maize fields, and tillage likely narrowed the window of opportunity for predation to occur. Although reducing tillage seems to conserve seed predators, it does not always result in greater seed predation (Heggenstaller et al., 2006; Williams et al., 2009). Also, reducing pesticide inputs, especially insecticides, is crucial to preserving natural enemies of weed seeds (Bhatti et al., 2005; O'Rourke et al., 2006; O'Rourke et al., 2008). Finally, diversifying cropland through the use of smaller fields of more crop species, and deploying diversified crop rotations (especially that rely in part on perennial crops) can help encourage seed predator diversity and abundance (Menalled et al., 2000; Davis and Liebman, 2003; Heggenstaller et al., 2006; O'Rourke et al., 2008). As we learn more about the diet of carabid beetles and seed predator communities, as well as the factors that affect the impact that these communities have on weed seed populations, seed predation will likely serve a critical role within integrated weed management strategies (Westerman et al., 2005; Westerman et al., 2006).

Prey defense against carabid predation

Many herbivorous pest insects possess effective defenses against attack by natural enemies, and these defenses can influence the effectiveness of biological control efforts (Pasteels et al., 1983; Dettner, 1987; Bowers, 1992). For instance, predators of the western corn rootworm feed on this pest with widely varying degrees of success (Lundgren et al., 2009c). Western corn rootworm larvae possess predator-repellent hemolymph defense based on rapid coagulation on predator mouthparts (Lundgren et al., 2009a). This hemolymph defense is especially repellent to the carabids *H. pensylvanicus* and *Harpalus rufipes* (DeGeer). Mouthpart cleaning after attack also varied among carabid species. *Harpalus pensylvanicus* and *H. rufipes* discontinued their attack after repulsion, whereas *P. melanarius*, *Pterostichus anthracinus* (Panzer) and *Poecilus cupreus* (L.) returned to eat the rootworm larvae after initial repulsion (Lundgren et al., 2010). In general, sucking predators such as wolf spiders appear to be better adapted for preying on western corn rootworm than are chewing predators (Lundgren et al., 2009c). Studies such as these that examine the details of pest insect defenses against predators are important, since a greater knowledge base on pest defensive mechanisms could lead to novel approaches to "tipping the balance" in favor of their natural enemies.

Carabid parasites and morphological anomalies

Research in the Midwestern U.S. has revealed a number of ecto- and endoparasites and pathogens of carabids. Robert W. Husband and his colleague David O. Husband have described numerous species of mites associated with carabids, primarily from Michigan. Many of these are new species of *Eutarsopolipus*, a genus of mites restricted to the Carabidae. These include *Eutarsopolipus elzingai* Husband from the carabid *Stenolophus* (formerly *Agonoderus*) *comma* (F.) in Kansas (Husband, 1998a), *Eutarsopolipus fischeri* Husband from *H. pensylvanicus* in Michigan (Husband, 1998b), *Eutarsopolipus davidsoni* Husband from *Chlaenius sericeus* Forster in Michigan (Husband, 2000), *Eutarsopolipus brevichelus* Husband and Husband from *Stenolophus lecontei* (Chaudoir) in Missouri (Husband and Husband, 2003), *Eutarsopolipus shpeleyi* Husband from *Pterostichus luctuosus* Dejean in Michigan (Husband, 2007), and *Dorsipes mackenzyae* Husband and Husband from *P. luctuosus* in Michigan (Husband and Husband, 2007). In addition, Husband and Husband (2004) discuss the distribution of three species of mites that are subelytral parasites of *Stenolophus comma* (Fabricius) and *S. lecontei* in Michigan, including *Crotalomorpha camini* Lindquist and Krantz, representing the first record of the mite family Crotalomorphidae in Michigan. Further information on *Stenolophus* species parasitized by subelytral mites, and occurrence of these mites in the U.S.A. and southern Canada, is given in Husband and Husband (2005).

Carabids also harbor a variety of endoparasites. Clopton (1998) and Clopton and Nolte (2002) have investigated the gregarine intestinal parasites of carabids. Gregarine protists are common parasites of invertebrates. They are in the Phylum Apicomplexa and are closely related to *Plasmodium* and *Toxoplasma*, the genera that include the causative agents of malaria and toxoplasmosis. Clopton (1998) described a new species of gregarine, *Torogregarina sphinx* Clopton, from *Bembidion laevigatum* Say collected from the bank of the Missouri River in southeastern Nebraska. Clopton and Nolte (2002) reported a newly-described genus and species of gregarine, *Clitellocephalus americanus* Clopton, isolated from the carabid *Cratacanthus dubius* (Beauvois) collected in the sandhills of western Nebraska.

Nematomorphs, or horsehair worms, are widely distributed but little-studied aquatic worms that are free-living in the adult stage, but as juveniles are internal parasites, primarily in insect hosts (Pechenik, 2010). Hanelt and Janovy (2000) collected the nematomorph *Gordius difficilis* (Montgomery) from a creek in a juniper forest in western Nebraska. This represented the first report of this species from the Midwestern U.S., and a range extension of over 2,500 km from previously reported localities in Massachusetts and western North Carolina. Pitfall trapping along the creek revealed the carabid *Chlaenius prasinus* Dejean as the definitive host of this parasite, representing the first report of *C. prasinus* as a host of nematomorphs.

As mentioned previously, carabids are considered useful bioindicators of habitat disturbance, and large-scale health issues associated with carabid populations are cause for concern. Gandhi and Herms (2008) reported a large occurrence of morphological anomalies in carabids in ash-dominated forest stands in southeastern Michigan. About 10% of trapped individuals and 32% of species possessed morphological anomalies that included tumors, cysts, fossae, misplaced setae, missing and fused elytral striae, and incomplete pronotum. Within species, these anomalies were most prevalent in the introduced carabid *P. melanarius*. Possible factors considered by the authors included water pollution, acid rain, atmospheric nitrogen deposition, genetic inbreeding due to habitat fragmentation, and parasites. The high prevalence of anomalies in *P. melanarius* in this study, combined with anomalies found in this species in previous studies, led the authors to suggest that non-native carabids may be particularly susceptible to factors that cause these anomalies.

The number of new carabid parasite records established in recent years is an indication of how little is known about carabid parasitism and other factors that may affect carabid health. Further documentation of carabid parasites and pathogens is needed, especially considering the role of many carabid species as important bioindicators and biological control agents. Studies addressing the complex interactions between infection levels and habitat factors also represent a potentially important area of research. For instance, there is growing evidence that low genetic diversity in vertebrates is associated with decreased ability to cope with parasites (Lively et al., 1990; Coltman et al., 1999). If habitat fragmentation is leading to decreased genetic diversity in carabid populations, this could lead to increased susceptibility of these populations to parasitism or other adverse environmental effects, which could in turn contribute to a downward spiral in population size and decreased population viability.

Conclusion

Carabids represent an abundant and speciose component of many terrestrial ecosystems. In the highly modified and fragmented habitats that comprise much of the Midwestern U.S., carabids are playing increasingly important roles in conservation biology and biological control of agricultural pests, and may even have potential for biological control of pests in other intensively managed habitats, such as golf courses (Smitley et al., 1998; Jo and Smitley, 2003). However, carabids can also have adverse ecological effects, and the invasive *P. melanarius* is a species of increasing concern in much of the Midwestern U.S. Knowledge of their biogeography, habitat requirements, feeding ecology, and factors that affect carabid health is needed to more fully understand their roles in conservation biology and pest management. In addition, their ecological and behavioral diversity make them compelling model organisms in studies of a more fundamental nature. Much of this research is being conducted in the Midwestern U.S.A.

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