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Long-term agricultural management reduces abundance and alters community structure of ground beetles (Coleoptera: Carabidae)

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ABSTRACT

Carabid beetles (Coleoptera: Carabidae) are beneficial predators and bioindicators of ground-dwelling arthropod diversity in agricultural landscapes. We studied changes in community composition, activity density, and diversity of carabids in a long-term agroecosystem study spanning 30 years in the US Midwest. We contrasted carabid community metrics measured by pitfall trap sampling in two conservation-oriented treatments in a corn-soybean-wheat rotation. One treatment uses conventional practices but with reduced agrochemical inputs (Reduced Input), while the other has no synthetic inputs (Biologically Based). Since a 1994–95 study on the same site, in 2019 overall carabid activity density had declined a minimum of 58–76 % with the four previously dominant species (all predators) declining 94–98 % and becoming uncommon to rare. In addition, carabid species richness, activity density, and community structure have diverged significantly under the two management regimes. In 2019 sampling, activity density decline in the Biologically Based treatment was mitigated by large increases in the abundance of two granivorous species (*Harpalus compar* (LeConte) and *Harpalus pensylvanicus* (DeGeer)). In contrast, carabid activity density in the Reduced Input treatment remained low. After decades of management, the Biologically Based treatment supported greater diversity and activity density of carabids compared to Reduced Input, and community structure shifted from predatory toward granivorous species. This long-term study contributes to the growing literature on insect decline in agricultural landscapes and demonstrates that changes in abundance and species turnover of the carabid communities can occur even under conservation-oriented management regimes.

1. Introduction

Insects are primary providers of ecosystem services in agroecosystems via contributions to decomposition, pollination, and suppression of crop pests. However, current research on long-term insect population trends indicates a global decline (Wagner et al., 2021; Rumohr et al., 2023; Mancini et al., 2023); for example, with a 75 % decline in flying insect biomass in some agriculturally dominated landscapes (Hallmann et al., 2017). Agriculture currently occupies 40 % of the global terrestrial land base (Sustainable Food and Agriculture, 2020). To meet the demand of a growing human population, agricultural production has become increasingly efficient through advancements in farming equipment, pest management, and high yielding commodity crops. However, land use change resulting from the intensification and expansion of agriculture have led to landscapes dominated by high-input row crop monocultures, contributing to the loss of biodiversity (Tscharntke et al., 2012) and reductions in ecosystem services that maintain air, water, soil health, and crop productivity over the long-term (Chee, 2004; Daily, 1997). Of particular concern are beneficial arthropods within agriculture, such as pollinators or predators; a meta-analysis in the United Kingdom found trends for the decline of service-providing invertebrates in croplands between 1990 – 2019 with an emphasis on areas of higher cropland intensification (Mancini et al., 2023). Climate change, habitat loss or isolation of semi-natural lands in agroecosystems, and widespread use of agrochemicals are all likely contributors to the decline in beneficial insect biodiversity and provision of services (Hallmann et al., 2017; Bianchi et al., 2006; Tscharntke et al., 2012; Rischen et al., 2021; Wagner et al., 2020).

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Ground beetles or carabids (Coleoptera: Carabidae) are common beneficial predators in agricultural landscapes and can be indicators of ecosystem change. However, carabids are also facing global declines. A meta-analysis on European carabids found the primary drivers of decline were the indirect effects of "anthropogenic activity" (pollution, land use, etc.), intensive agriculture, and climate change (Rumohr et al., 2023). Carabids consume agricultural pests such as aphids, slugs, the adults and larvae of Lepidoptera, as well as spiders or other non-insect arthropods (Lovei and Sunderland, 1996; Kirk, 1973; Lindroth 1961–1969). Although most carabids are polyphagous predators, some species primarily consume seeds (granivores) or plant material (herbivores) (Lovei and Sunderland, 1996; Lindroth 1961–1969). Carabid populations are sensitive to changes in environmental conditions, the most important of which are humidity and light at the soil surface (Thiele, 1979). In row crop agriculture, carabid species assemblages and activity density are indicative of agronomic management practices (Cárcamo et al., 1995; Clark et al., 1997) and thus serve as bioindicators for diversity of other ground-dwelling arthropods (Rainio and Niemela, 2002; Lovei and Sunderland, 1996). Studies of ground beetles in agroecosystems have previously examined how crop type (Cárcamo and Spence, 1994; Rivard, 1966), management (Cárcamo et al., 1995; Clark et al., 1997; Clark, 1999; Allen, 1979; Thomas et al., 2002; Holland et al., 1999; Cox et al., 2014), or conservation practices (Rischen et al., 2021; Knapp et al., 2022; Middleton and MacRae, 2021) impact their overall activity density, diversity, community composition and predation potential.

Production of corn (*Zea mays*, L.), soybean (*Zea mays* L. – *Glycine max* L.), and to a lesser extent wheat (*Triticum aestivum* L.) dominate agricultural landscapes of the Midwest, US. How these annual cropping systems are managed can influence carabid biodiversity and community structure. Although crop type may influence the microclimate of a field, multiple studies have demonstrated that the crop present in a given year does not strongly influence long-term carabid community composition or activity density, and instead management practices have the greatest impact (Cárcamo and Spence, 1994; Clark et al., 1997; Clark, 1999; Eyre et al., 2012; O'Rourke et al., 2008). For instance, tillage practices redistribute topsoil which could disrupt overwintering ground beetles (Kirk, 1973; Knapp et al., 2022) and within annual cropping systems, might filter for a community of carabids with high tolerance to soil disturbance (Macleod et al., 2004). Weed density, which is shaped by tillage practices and herbicide use, also influences carabids that feed on weed seeds (granivores) and may be more important for some species assemblages than the impacts of tillage alone (Anderson, 2003). Agricultural pesticides, including the use of Bt transgenic corn, neonicotinoid-coated seeds, and fungicides, have been found to influence the overall activity density of ground dwelling arthropods (Mullin, 2005; Douglas et al., 2015; Douglas and Tooker, 2016; Goulson, 2013), and subsequently their ability to suppress pests (Douglas et al., 2015). These and other factors may be key in understanding the effects of long-term management on community composition of carabids in annual cropping systems.

Long-term studies in agriculture, defined as more than 20 years in duration (Rasmussen et al., 1998) can provide unique insights into ecosystem change (Bahlai et al., 2021). The Long-Term Ecological Research (LTER) Main Cropping Systems Experiment (MCSE) at Kellogg Biological Station (KBS), Hickory Corners, Michigan was established in 1989 and compares crop management practices across a gradient of low to high management intensity (Robertson and Hamilton, 2015). Given the importance of carabids in agroecosystems, and their potential as indicators of agricultural disturbance, carabid communities were first studied in 1994–95, five to six years after the experiment was initiated (Clark et al., 1997), and again in 2019 after 30 years of continuous management. Here we focus on two annual row crop treatments within the MCSE, one representing conventional agriculture with reduced pesticide and fertilizer inputs (Reduced Input) and a second treatment (Biologically Based) with no synthetic inputs and minimal fertilizer application (Robertson and Hamilton, 2015). Our objectives were to first characterize any changes in overall carabid abundance (as measured by activity density) during the 25 years between the studies, and secondly to contrast carabid activity density, community structure, and feeding guilds resulting from the long-term application of the management regimes. We did not have *a-priori* predictions on how carabid communities may change over the 25-year period, in large part because such studies are rare, but predicted that long-term management under conservation-oriented management practices would result in distinct communities of carabids that differ in terms of diversity, activity density, and community composition.

2. Materials and methods

2.1. Study system

This study was conducted in 2019 at the Kellogg Biological Station, Long-Term Ecological Research site (KBS LTER) in Hickory Corners, Michigan (42.411078, −85.377195). The KBS LTER Main Cropping Systems Experiment (MCSE) was initiated in 1989 and includes continuously managed treatments representing a gradient of management intensity from conventional to minimal input in an annual corn-soybean-wheat rotation. Here, the term "management" concerns differences in chemical application, soil amendments, tillage, and cover crops. Each treatment is replicated n=6 times in 0.88 ha plots (87 m x 105 m) in a randomized complete block design (Fig. 1). Corn and soybean are planted in the spring while wheat is planted in the fall following soybean harvest and harvested mid-July of the following year (Robertson and Hamilton, 2015).

In 2019, the MCSE had been in place for 30 years allowing us to investigate the long-term effects of two conservation-oriented management regimes on carabid communities. The Reduced Input treatment receives approximately one-third the rate of synthetic chemical inputs (fertilizers and pesticides) as conventional management practices, whereas the Biologically Based treatment does not receive any synthetic pesticides with minimal fertilizer input to periodically adjust for crop removal. Following corn and wheat harvest, both treatments are chisel-plowed, and soil finished before seeding winter cover crops. Cereal rye (*Secale cereale L.*) is planted following corn, and medium red clover (*Trifolium pratense* L.) following wheat. Because wheat is fall-planted after soybean harvest, no additional cover crop is planted. In corn and soybean years, the Reduced Input treatment receives pre-emergence herbicides and is rotary-hoed and cultivated as necessary to further control weeds. The Biologically Based treatment receives no herbicides and relies exclusively on cover crops, rotary-hoeing, and cultivation for weed control. While the overall management goals for each treatment have remained in place since inception, the products applied (rates and application dates) have shifted to reflect current local practices and to address nutrient deficiencies and pest outbreaks. Details of the fertilizer and chemical applications in 2018–2019 are found in Supplemental Information (Table S2.1) with the full agronomic catalog available at the KBS LTER website (*kbs.lter.msu.edu*).

A new USDA-sanctioned conservation practice CP-43 Prairie Strips (USDA FSA 2019, USDA NRCS 2020) was implemented in the Reduced Input and Biologically Based treatments in 2019. Prairie Strips have previously been documented to increase biodiversity and to reduce soil and nutrient runoff in annual cropping systems (Schulte et al., 2017). Specifically, a mixture of native, warm season grasses and forbs (4 grass species, 18 forb species; see Kemmerling et al. 2022 SI Table 1) were seeded in 5 ×105 m areas in the middle of each plot, dividing the cropped area into two halves lengthwise. Plots were seeded on 25 April 2019, with an oat (*Avena sativa* L.) nurse crop and mowed in late July. Because the seeded native perennials are slow to establish, the nascent prairie strips consisted primarily of agricultural weeds and oats, with some prairie species in seedling stages. A multi-year study of ground dwelling arthropod communities (initially focused on Formicidae) was initiated in 2019 to examine the potential effects of prairie strip

Fig. 1. Experimental design for the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI (Robertson and Hamilton, 2015).

establishment and maturation (Helms et al., 2021). For this study we utilized data from the first year of this long-term effort, immediately after the strips were seeded. Like Helms (2021), we anticipated that the newly establishing strips would have little impact on carabid communities in the first year, which are largely determined by the previously established overwintering forms (Raderschall et al., 2022) and tested for such effects as described below.

2.2. *Sampling carabid activity density and diversity*

The study by Clark et al. (1997) sampled carabids in all seven MCSE cropping system treatments for a total of 42 plots and collected a total of 23,181 individuals (Clark et al., 1997; Fig. 1). Their study utilized five pitfall traps per replicate (7 cm diameter with funnel) which were collected weekly. In 1994 (a soybean year), samples were collected from

Table 1
Minimum estimated percent decline in carabid activity density from 1994 to 95–2019 in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. Due to the way data were reported in Clark et al. (1997), this table contrasts the daily catch rate for the four numerically dominant species in 1994–95 to all species captured in 2019. Thus, this is a conservative estimate of the actual community wide decline in activity density.

Treatment	1994–95 Daily Catch Rate per Trap	2019 Total Catch	1994–95 Total Catch	2019 Daily Catch Rate per Trap	Minimum % Decline
1994 Reduced Input	1.53	71	267	0.37	−75.82
1994 Biologically Based	1.65	133	289	0.69	−58.18
1995 Reduced Input	0.98	79	349	0.24	−75.51
1995 Biologically Based	0.96	129	340	0.38	−60.42

5 July – 8August; in 1995 (a wheat year), samples were collected from 22 May – 31 July. Due to the addition of the prairie strips, the sampling design in 2019 differed in several respects. In each plot, three transects were created running perpendicular from the prairie strip into the row crop. Transects were placed no closer than 10 m apart and terminated no closer than 20 m from a crop edge to control for edge effects. Along each transect, four sampling stations were established at distances of 0 (center of the prairie strip), 1, 5, and 20 m into the cropped area (Figure S1.1). As a result, there were four active pitfall traps during each week of sampling. Sampling periods occurred five times throughout the growing season, roughly every month (May – September). To avoid over-sampling any specific area of a plot, the sampled transects were rotated weekly, i.e., a different transect was selected to be sampled each week with no sampling occurring during the fourth week of each sampling period. In 2019, there were 15 sampling weeks over the growing season from 13 May – 19 September. To reduce disturbance in the plots, permanent sampling stations were established. At each station a 10 cm long by 5.8 cm (inside diameter) PVC pipe was buried into the soil and capped flush with the soil level. When utilized, the cap was removed, and a 5.8 cm diameter pitfall trap cup was placed into each PVC socket. Cups were filled with 60 ml of 95 % ethanol and a drop of unscented dish soap to break surface tension. Pitfall traps were placed in the ground even with the surface and clear plastic covers were placed above each pitfall trap to protect from rainfall. Cups were collected after 48 h; on particularly hot, dry days, the ethanol was replenished after 24 h. All samples were sorted removing the Formicidae, and the remaining catch was placed in vials with 95 % ethanol for storage (Helms et al., 2021). We subsequently sorted the samples, removing the carabids which were pinned and then identified to species using Lindroth (1961–1969), and verified by Dr. Gary Parsons, a Coleoptera specialist at Michigan State University.

2.3. Calculations for comparison to Clark et al. (1997)

Carabid beetle captures were notably reduced in 2019 compared to 1994–95 and we wished to determine the extent of change in activity density. We contacted the authors of Clark et al. (1997) for the original data, but it was not available, so our comparison is limited to data from figures and tables in the published paper. CMF and DAL independently extracted carabid activity density metrics from the published figures using the on-line tool *PlotDigitizer.com* and compared the counts for accuracy. To adjust for differences in sampling design and duration between the two studies, we standardized comparisons by calculating the number of beetles caught per trap per day (Saska et al., 2022) over the same sampling period each year (Table S2.5). The daily catch rate was calculated by dividing the total catch by the total sampling effort (number of traps per replicate x number of replicates x number of treatments x number of days each trap was deployed).

Clark et al. (1997) only reported the activity density of the four numerically dominant species, i.e. the most abundant species collected during both years which made up 87 % of all individuals captured. Other less abundant species were reported as a percentage of the overall two-year catch across all treatments but were not specified at the treatment level, and thus could not be directly contrasted to the 2019 data which focuses only on the Reduced Input and Biologically Based treatments. Therefore, we estimated changes in overall activity density by assuming that the four dominant species in 1994–95 represented the entire community (i.e. as if no other species were captured) and compared the daily catch rates for those four species to the same time periods in 2019 with all species included. This provides the most conservative estimate of the reduction in total abundance over 25 years, with recognition that if the (unknown) number of additional beetles were added to the 1994–95 counts the magnitude of change would be larger. Next, to assess potential turnover in dominant species, we compared the catch rates of the four dominant species in 1994–95 to those for the same species in 2019. Since the sampling dates for 1994–95 in Clark et al. (1997) vary in crop type and emergence times for carabids, we also compared the daily catch rates in 2019 to each year individually (i.e., within the corresponding sampling dates for 1994 and 1995 separately) (see Supplemental Information Figure S2.4).

We did not adjust daily catch rates to account for differences in trap diameter (5.8 cm in 2019 vs. 7 cm in 1994–95) because while increased pitfall trap diameter can influence community composition of carabid catches by slightly favoring larger species it does not strongly impact estimates of activity-density (Luff, 1975). To determine if observed changes in species turnover were potentially due to sampling bias, we measured the percent coverage (C) of the 2019 species diversity (Chao and Jost, 2012).

2.4. Statistical analysis for 2019 community comparisons

The 2019 dataset encompassed 720 48-hour trapping events (2 treatments x 6 replicates x 5 months x 3 transects x 4 distances from newly-establishing prairie strips). Since prairie strips were seeded just before data collection and not of primary interest for this study, we first tested whether distance from nascent strips (0, 1, 5, or 20 m) impacted carabid communities and found no evidence that this was the case (see Supplemental Information, Table S2.2). Next, we tested for differences in activity density between treatments and across months, pooling the catch from the 12 trapping events that occurred per replicate each month within each treatment. Using the R package *lme4* (Bates et al., 2015), we used Generalized Linear Mixed Models (GLMMs) with a Poisson distribution to test whether carabid activity density differed by treatment (Reduced Input vs. Biologically Based), month (May - September), or their interaction (Table S2.3). We compared this model to its subsets based on QAICc. We then tested whether diversity differed between treatments. Diversity was quantified three ways: as species richness, Hill-Shannon diversity (Jost, 2006; see also Roswell et al., 2021), and Chao1 richness estimator (Chao and Chiu, 2016). In all cases we summed the community across months to produce a single diversity estimate per replicate per treatment (n = 6), as diversity during any given month was low and considering months individually could hide effects of temporal turnover in composition. We used Linear Mixed models to test if diversity differed between treatments, with replicate as a random effect since the MCSE uses a randomized complete block design. Models for Hill-Shannon and Chao1 produced singular fits, so they were re-run as linear models with the random effect dropped. Post-hoc pairwise tests were performed using the “emmeans'' function in the R package *emmeans* (Lenth, 2024) to determine significant pairwise differences within the best fit model. Finally, we used Permutational Multivariate Analysis of Variance (PERMANOVA) to test if community composition differed by treatment and/or month (Bray-Curtis dissimilarity, 999 permutations), using the adonis2 function in the R package *vegan* (Oksanen et al., 2022). We used Non-metric Multidimensional Scaling (NMDS) to visualize these community differences (Bray-Curtis dissimilarity, $k = 3$, stress $= 0.08$). As in the previous analyses, for both the PERMANOVA and NMDS we pooled observations across months to compare the season-long communities per replicate field within each treatment.

3. Results

3.1. Comparison to Clark et al. (1997)

In 1994–95, the numerically dominant species were *Cyclotrachelus sodalis (LeConte), Poecilus lucublandus (Say), Pterostichus melanarius (Illiger),* and *Agonum placidum (Say)*; which made up 87 % of the total capture across all seven treatments (Clark et al., 1997). In total, 7470 individuals of these species were collected in the Reduced Input and Biologically Based treatments in 1994–95. In contrast, only 412 individuals of all carabid species were captured in the same treatments in the same time periods in 2019 (Table 1). After adjusting for sampling effort, the daily catch rates for all species captured in both treatments in 2019 were 58–76 % lower than the same time periods in 1994 and 1995. By treatment, daily catch rates in Reduced input were 75–76 % lower, whereas in Biologically Based rates were 58–60 % lower, which is likely a result of the increased population of *Harpalus* spp. by 2019. Reduced catch rates in 2019 were similar across both treatments and for all four of the 1994–95 numerically dominant species (Fig. 2). Overall, the activity density of these four species declined between 94 –98 % over the 25-year period. Additional comparisons by individual species, treatment, and year can be found in Table S2.4.

We also observed a shift in the trophic position of the dominant species between the two studies. The most abundant species in Clark's study were predators, whereas in 2019 we found granivorous and omnivorous species were dominant, specifically within the Biologically Based treatment. For example, predaceous *C. sodalis* and *P. lucublandus* were the two most abundant species in 1994–95 but both were rare in 2019 and replaced by the predators *Poecilus chalcites* (Say) and *Cicindelidia punctulata* (Olivier) (Table 2). In contrast, the granivorous *Harpalus compar* (LeConte) and *Harpalus pensylvanicus* (DeGeer) were the most abundant species in 2019, comprising nearly 45 % of the total capture; but were rare in 1994–95 with *H. pensylvanicus* making up 3 % of all captures (across all treatments in the array) and *H. compar* being either absent or making up such a small percent of the catch that it was not reported (Clark et al., 1997; Table 2).

3.2. Carabid activity density and diversity

During the 2019 study, we collected 456 individual carabids, representing 34 species, during 720 total trapping events between 18 May – 17 September 2019 (Table 2). We captured more than twice as many individuals in the Biologically Based treatment than in Reduced Input (321 vs. 135; Tables 2,3). Differences in activity density were due primarily to a few numerically dominant species in the Biologically Based treatment (Figure S3), particularly *H. compar* and *H. pensylvanicus.* Activity density peaked in July and August and was significantly different compared to both early and late season across both treatments ($p < 0.001$) (Fig. 3).

Community structure also differed between the treatments. While species richness was comparable between treatments, the Biologically Based community was less even, resulting in lower Hill-Shannon diversity (Table 3, Fig. 4). We calculated Chao1 estimators for both treatments and found a greater expected species richness in Biologically Based. The Reduced Input treatment had 23 species and five singletons while the Biologically Based treatment had 29 species including 11 singletons (Table 3). Coverage estimates suggest we sampled 98 % of the expected species richness across the two treatments; by treatment, we sampled 94 % in Reduced Input and 97 % in Biologically Based (Table 3). Finally, we compared the overall community composition of both treatments visually using a NMDS (Fig. 5) coupled with a PERMANOVA test and determined the communities were significantly different ($F_{0,1} = 5.1141$, $p < 0.005$).

4. Discussion

We found a shift in the activity density and community composition of carabids at the KBS LTER between 1994 and 95 and 2019. Specifically, we found evidence for a decline in the overall activity density of carabids of 58–76 % at a minimum and a 94–98 % decline in the daily catch rate of the previously dominant species. Moreover, we found that community structural differences between treatments increased, resulting from loss of predatory species and increased dominance of granivores in 2019 compared to 1994–95.

4.1. Comparison to Clark et al. (1997)

The first objective of this study was to compare our findings for carabid community composition and activity density to a 1994–95 study at the same site (Clark et al., 1997). We found that the overall activity density of all carabids, and that of the formerly numerically dominant carabid species had declined precipitously (Table 1, Fig. 2). Most notably, we found a severe decline in the activity density of *C. sodalis* and *P. lucublandus*, which decreased from 31 % and 25 % of the total catch respectively in 1994–95 to less than 2 % each in the combined treatments for 2019. An autumn breeder that overwinters in the larval form, *C. sodalis* is often cited in the literature as sensitive to disturbance and favors semi-natural grasslands (Larsen et al., 2003). The loss of *C. sodalis* in both cropping system treatments suggests the species is sensitive to long-term disturbance regimes caused by tillage, seeding, or harvesting of the row crop. Although Clark et al. (1997) found that *A. placidum* and *P. lucublandus* favored tilled croplands in the MCSE in 1994–95, they were largely absent by 2019 at which time the dominant predator was *P. chalcites*, which is known to be better adapted to managed landscapes (Gardiner et al., 2010; Larsen et al., 2003; Pisani Gareau et al., 2020). Surprisingly, the invasive predator *P. melanarius* was not common in either of the treatments in 2019, despite a higher activity density in 1994–95 and documented reports of high abundance across agroecosystems in the Midwest, US and Ontario, Canada (Lindroth 1961–1969; Larsen et al., 2003; Neame and Galpern, 2025).

4.2. Carabid activity density and community composition in 2019

After 25 years of consistent crop management, the carabid communities at KBS LTER were dominated by either generalist predators or granivores depending on cropping treatment. The Reduced Input treatment, which receives agrochemical (herbicide and insecticide) applications and less tillage, is dominated by predaceous carabids. In comparison, the Biologically Based treatment, which receives zero input of agrochemicals but increased soil disturbance to control weeds, is dominated by granivorous carabids, such as *H. compar* and *H. pensylvanicus*. We suspect some of these changes are the result of changes in food availability. Without herbicides, Foxtail species (*Setaria spp)*, are difficult to control in the Biologically Based treatment (KBS LTER Agronomy Data, field observations) and could be supporting the populations of the granivorous species *H. compar* and *H. pensylvanicus*. Kirk (1973) reported increased activity density of *H. pensylvanicus* where foxtail was abundant. Granivores have also been found to benefit from the legacy effects of previous years' plant or crop diversity, leading to increased individual fitness and higher reproduction the following year

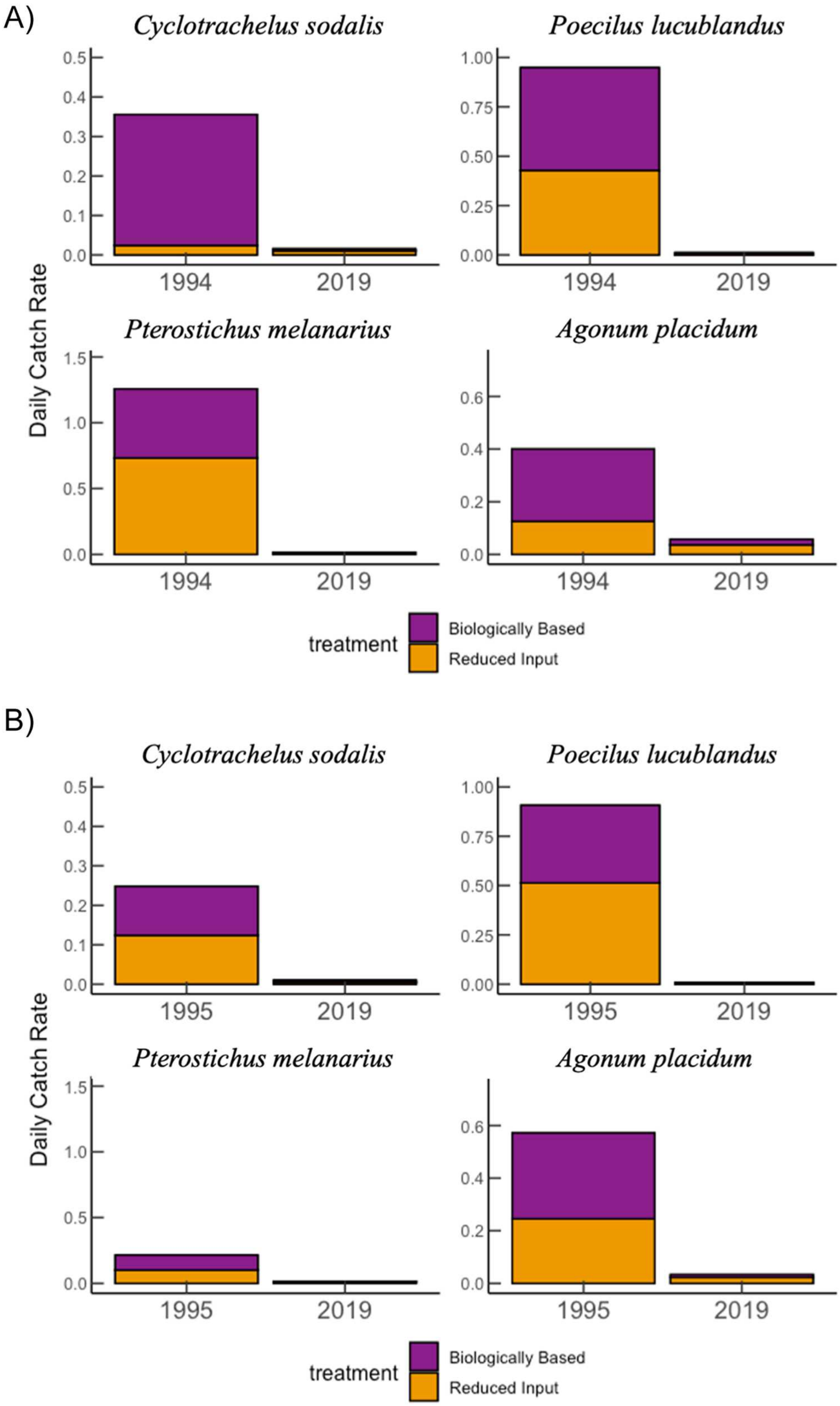

Fig. 2. Daily catch rates for the dominant carabid species in A)1994 and B)1995 as compared to 2019. The four numerically-dominant carabid species in 1994–95 (22 May – 8 August; Clark et al. 1997) had higher daily catch rates compared to 2019 (21 May – 7 August) for both the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Table 2
Summary of 2019 carabids by total count, percent, and rarity (<1 % of total) by treatment (Reduced Input and Biologically Based) and overall, at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Species		**Reduced Input**			**Biologically Based**			**Total (all treatments)**		
	Function	Count	%	Rare <1 %	Count	%	Rare <1 %	Count	%	Rare <1 %
Agonoleptus conjunctus (Say)	Predator	2	1.48		3	0.93	R	5	1.10	
Agonum cupripenne (Say)	Predator	2	1.48		1	0.31	R	3	0.66	R
Agonum octopunctatum (Fabricius)	Predator	0	0		1	0.31	R	1	0.22	R
Agonum placidum (Say)	Predator/Omnivore	9	6.67		5	1.56		14	3.07	
Amara familiaris (Duftschmid)	Omnivore	2	1.48		15	4.67		17	3.73	
Amara littoralis (Mannerheim)	Omnivore	4	2.96		10	3.12		14	3.07	
Amara pensylvanicus (DeGeer)	Granivore/Omnivore	0	0		1	0.31	R	1	0.22	R
Anisodactylus rusticus (Say)	Omnivore	0	0		5	1.56		5	1.10	
Anisodactylus sanctaecrucis (Fabricius)	Omnivore	3	2.22		0	0.00		3	0.66	R
Bembidion quadrimaculatum (Linnaeus)	Predator	4	2.96		5	1.56		9	1.97	
Bembidion rapidum (LeConte)	Predator	0	0.00		2	0.62	R	2	0.44	R
Bembidion versicolor (LeConte)	Predator	10	7.41		5	1.56		15	3.29	
Bradycellus rupestris (Say)	Predator	2	1.48		0	0		2	0.44	R
Chlaenius tricolor (Dejean)	Predator	6	4.44		0	0		6	1.32	
Cicindela punctulata (Olivier)	Predator	16	11.85		23	7.17		39	8.55	
Clivina impressifrons (LeConte)	Predator/Omnivore	0	0		1	0.31	R	1	0.22	R
Colliuris pensylvanicus (Linnaeus)	Predator	0	0		1	0.31	R	1	0.22	R
Cyclotrachelus sodalis (LeConte)	Predator/Omnivore	2	1.48		2	0.62	R	4	0.88	R
Dyschirius truncatus (LeConte)	Predator	0	0.00		1	0.31	R	1	0.22	R
Elaphropus anceps (LeConte)	Predator/Omnivore	4	2.96		5	1.56		9	1.97	
Harpalus affinis (Schrank)	Granivore/Omnivore	1	0.74	R	1	0.31	R	2	0.44	R
Harpalus caliginosus (Fabricius)	Granivore/Omnivore	0	0		2	0.62	R	2	0.44	R
Harpalus compar (LeConte)	Granivore/Omnivore	4	2.96		117	36.45		121	26.54	
Harpalus herbivagus (Say)	Granivore/Omnivore	1	0.74	R	1	0.31	R	2	0.44	R
Harpalus pensylvanicus (DeGeer)	Granivore/Omnivore	8	5.93		75	23.36		83	18.20	
Harpalus rubripes (Duftschmid)	Omnivore	0	0		3	0.93	R	3	0.66	R
Loricera pilicornis (Fabricius)	Predator	2	1.48		3	0.93	R	5	1.10	
Poecilus chalcites (Say)	Predator/Omnivore	24	17.78		26	8.10		50	10.96	
Poecilus lucublandus (Say)	Predator/Omnivore	3	2.22		0	0		3	0.66	R
Pterostichus melanarius (Illiger)	Predator	12	8.89		1	0.31	R	13	2.85	
Pterostichus permundus (Say)	Predator/Omnivore	0	0		1	0.31	R	1	0.22	R
Scarites vicinus (Chaudoir)	Predator	0	0		3	0.93	R	3	0.66	R
Stenolophus ochropezus (Say)	Predator/Omnivore	12	8.89		2	0.62	R	14	3.07	
Stenolophus plebejus (Dejean)	Predator	2	1.48		0	0		2	0.44	R
Total		**135**			**321**			**456**		

Table 3
Summary table for 2019 carabid diversity metrics by treatment (Reduced Input and Biologically Based) at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Diversity Metrics	Reduced Input	Biologically Based	All Treatments
Total Count	135	321	456
Genus	15	17	19
Species	23	29	34
Singletons	5	11	6
Doubletons	7	10	6
Shannon Diversity (H')	2.77	2.16	2.56
Shannon Evenness (E)	0.88	0.64	0.73
Coverage % (C)	93.63	97.23	98.25

(Raderschall et al., 2022; Pisani Gareau et al., 2020). In the Biologically Based treatment, *H. compar* and *H. pensylvanicus* accounted for 60 % of the total catch, whereas in the Reduced Input treatment these species were rarer, and the most common species was the predaceous beetle *P. chalcites* (which was relatively common across both treatments). The dominant species in 2019 are generalists with greater tolerance for disturbed environments.

Carabids are capable of dispersal, either by flight or ground movement, and could potentially move between treatments at the LTER. Due to the experimental design of the study site, the Reduced Input and Biologically Based treatments are sometimes directly next to one another; thus, the data suggests that the significant differences in carabid communities between the two treatments are due to local management factors, and not limited by dispersal ability. The results of our study further support that long-term, consistent crop management has led to distinct communities by treatment, despite crop rotation or variations in annual conditions.

Overall, we found a noticeable decline in the activity density of carabids in 2019 relative to 1994–95 across both treatments. The change we documented is of a similar magnitude to declines in insect biomass found in long-term datasets in Europe, such as the 75 % decline in flying insect biomass observed by Hallman et al. (2017). A long-term study on carabids within a preserved woodland in Germany did not find declines in biomass, but did report overall declines in species diversity of carabids; in particular, the authors found a decline in spring-breeding species likely due to early application of pesticides in the surrounding environment (Homburg et al., 2019). A 44-year comparison experiment by Harris et al. (2019) at the Hubbard Brook Experimental Forest found dramatic reductions in carabid capture rates. Like Harris, we argue that our observed change in carabid abundance is outside the natural range of variation in insect populations and indicative of larger population decline. As indicator species for ground-dwelling arthropods in managed landscapes, our findings on the impacts to carabids are relevant for future study and conservation of other service-providing arthropods within agricultural settings. However, it should be noted that unlike other long-term studies, we do not have continuous data from 1994 to 95–2019 and cannot assess trends beyond comparing the two time points.

4.3. Factors affecting carabid community composition

Multiple factors may be contributing to the species turnover and a decline in overall activity density within the carabid community at the

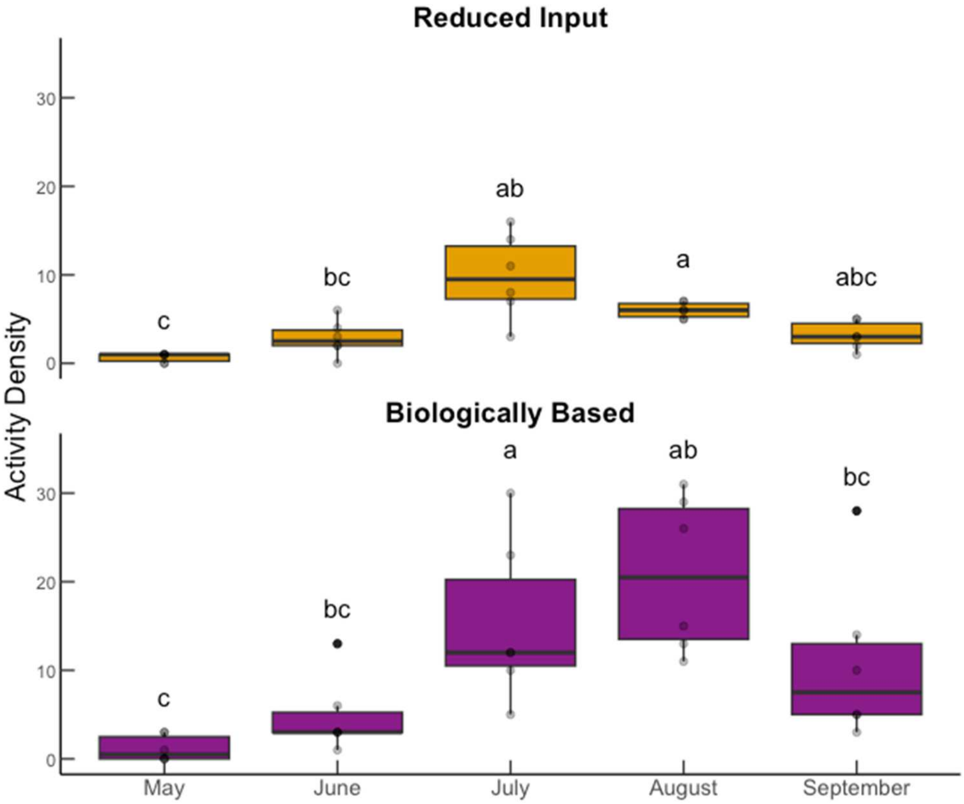

Fig. 3. Comparison of activity density (abundance) for 2019 by month and treatment. Activity density per plot in 2019 was higher in the Biologically Based treatment than Reduced Input and peaked during July and August, respectively. By treatment, early and late season were significant compared to mid-season activity density. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

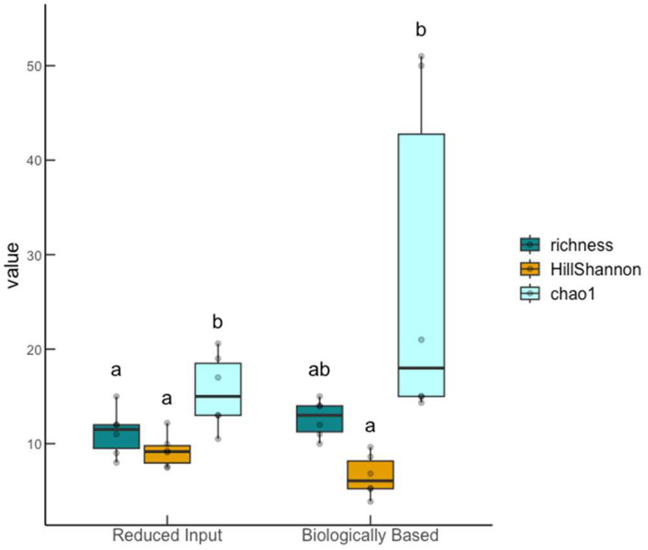

Fig. 4. Comparison of diversity metrics (richness, HillShannon, and chao1) for 2019 by treatment. Diversity metrics for 2019 carabid species was similar for both richness and Hill-Shannon adjusted richness, but varied for chao1 diversity estimate in the Biologically Based treatment compared to Reduced Input, within the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

KBS LTER site, including changes in abiotic factors, prey availability, and pesticide use that directly or indirectly influence carabids and their food sources.

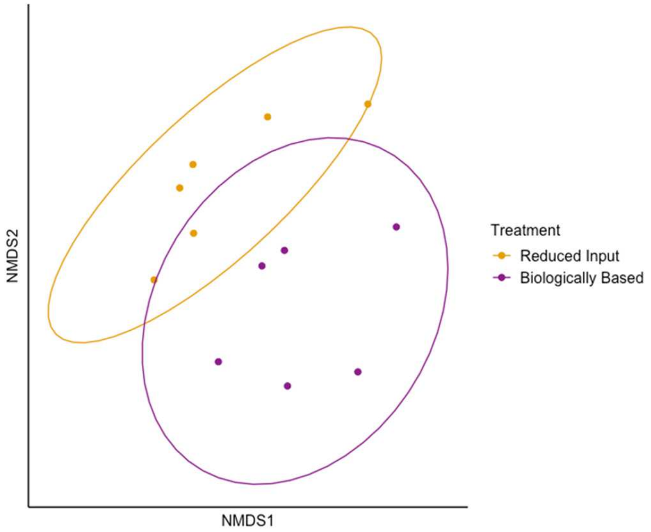

Fig. 5. Non-metric Multidimensional Scaling (NMDS) graphical comparison of 2019 carabid community composition by treatment. The NMDS plot (Bray-Curtis dissimilarity, k = 3, stress = 0.08) illustrates that community composition differs between Reduced Input and Biologically Based treatments within the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

4.3.1. *Abiotic conditions*

Weather data for KBS LTER suggests an increase in annual temperature and precipitation events since 1989 (https://lter.kbs.msu.edu/datatables/12). Although emergence times and overall fitness for carabids may potentially be impacted by climate change (Pozsgai and

Littlewood, 2014), we did not find phenological changes in the dominant community over 25 years at the MCSE that could contribute to species turnover. The shift in community composition from 1994 to 95–2019 is more likely due to the long-term agricultural management strategies that either directly or indirectly impact carabids through reduced food availability or application of agrochemicals for pest and weed seed suppression.

However, it should be noted that Pozsgai and Littlewood (2014) suggest that carabid foraging, reproduction, and dispersal are vulnerable to variable spring weather and shortened summer seasons due to high temperatures and reduced soil moisture. According to the National Climate Assessment, precipitation in the Midwest is expected to increase 8–20 % (although the consistency of precipitation events like flood or drought are difficult to predict) and temperature extremes will include 10 more days above 95 degrees Fahrenheit annually (USGCRP, 2023).

4.3.2. *Reduction in prey availability*

Predatory ground beetles consume many agricultural pests (Lindroth 1961–1969; Douglas et al., 2015), and introduction of new insecticides and weed control methods could contribute to a loss of available prey. For example, the formerly abundant pest European corn borer (*Ostrinia nubilalis* (Huber)) (Hurley et al., 2002) and Western corn rootworm (*Diabrotica virgifera virgifera* (LeConte)) (Gassmann, 2021) are now nearly completely controlled by Bt crop traits. Similarly, the soybean aphid (*Aphis glycines* (Matsumura)) is now suppressed by the widespread use of neonicotinoid seed treatments, although the effectiveness of seed treatment is debated (Gaspar, 2014).

A long-term study on ladybeetles at KBS LTER, the same cropping system used in our study, found declines in the populations of both native and exotic species, associated with the loss of their preferred prey, the soybean aphid; however, native ladybeetle populations tended to thrive in patches of refuge habitat with alternative prey (Bahlai et al., 2015). This ongoing long-term study also found that coexistence between two exotic ladybeetle species, *Harmonia axyridis* and *Coccinella septempunctata* both introduced for pest suppression, was highly dependent on local environmental conditions, leading to temporal niches (Arnold et al., 2023). Those data suggest that community dynamics of beneficial predators are strongly impacted by prey availability or prey response to local management practices.

For carabids and other ground-dwelling arthropods, reduction in prey availability within the crop may encourage intraguild predation and competition for limited resources. Not only will this influence overall carabid population activity density and diversity, but also their pest suppression potential in crops.

4.3.3. *Direct or indirect effects of pesticides*

Pesticides commonly used in Midwestern row crops could have both direct and indirect effects on carabids. Studies on the non-target impact of neonicotinoid seed treatments and other synthetic insecticides have shown that ground dwelling arthropods, as natural predators and scavengers, are vulnerable to direct exposure and indirect loss of prey. A laboratory study of neonicotinoid treated seed by Mullin (2005), resulted in near 100 % mortality in 17 of the 18 species of carabids tested. Of those, *P. chalcites* and *H. pensylvanicus,* two of the numerically dominant species in our study, were noted as the most tolerant of both fungicide and neonicotinoid exposure and may have come to dominate the 2019 community in part for this reason.

Indirect exposure to insecticides, either through ingestion of exposed prey or prey that has fallen after a foliar application, is a likely pathway for non-target effects on carabids. In a study by Douglas et al. (2015) on the grey garden slug (*Deroceras reticulatum* (Müller)), an agricultural pest in soybean crops, the slugs were not affected by ingestion of neonicotinoid coated seeds; however, over 80 % of the carabids that consumed the exposed slugs experienced some adverse effect. However, the chronic, non-target impacts of neonicotinoids on carabids are understudied. In our study, we found a prevalence of granivorous *Harpalus spp.* and the predator *P. chalcites* in both treatments at higher activity density than either year of Clark et al. (1997). It may be possible that these species are more tolerant to insecticide use as compared to the numerically dominant species of 1994–95. In general, the literature suggests that long-term pesticide use and consistent disturbance from agricultural management practices are the primary cause of carabid declines in agroecosystems (Mullin, 2005; Douglas et al., 2015).

5. Conclusion

Impacts of long-term cropping system management are important in defining the community composition and activity density of carabids in agroecosystems. When compared to a similar study on carabids 25 years prior at the KBS LTER, we found a decline in overall activity density and strong turnover in which species dominated the community. Our study found a distinct granivore-dominated community of carabids in the Biologically Based treatment that differed strongly from the Reduced Input treatment. This change could have been a result of multiple factors, including direct or indirect toxicity due to insecticide use, reduction in prey availability from the widespread use of seed treatments and Bt traits, competition, impacts of weed management, or changes in rainfall and temperature patterns due to climate change. This study demonstrates that even conservation-oriented practices can fail to halt insect decline and species turnover in agriculture. Future work must focus on functional implications of turnover in carabid species composition in annual cropping systems, and on understanding the specific mechanisms that lead to these types of changes.

CRediT authorship contribution statement

Douglas A Landis: Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Nathan L Haan**: Writing – review & editing, Validation, Formal analysis. **Cynthia M Fiser**: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109337.

Data availability

Data will be made available on request.

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