Ant communities and ecosystem services in organic versus conventional agriculture in the U.S. Corn Belt

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Abstract

Reducing the use of synthetic fertilizers and pesticides can limit negative impacts of agriculture on insects and is a crucial step towards sustainable agriculture. In the U.S., organic agriculture has the potential to reduce greenhouse gas emissions, pollutant runoff, and biodiversity loss in the Midwestern Corn Belt—an area extending over 500,000 km^2 devoted to intensive production of corn *Zea mays*, often in rotation with soy *Glycine max* or wheat *Triticum aestivum*. Working in 30-year-long landscape experiments in this region, we tested for impacts of conventional versus organic agriculture on ant communities (Hymenoptera: Formicidae) and potential ecosystem services they provide. Organic fields supported higher ant diversity and a slightly more species-rich ant assemblage than conventionally managed fields but did not otherwise differ in community composition. Despite similar community composition, organic and conventional fields differed in seasonal patterns of ant foraging activity and potential for natural pest suppression. Conventional plots experienced higher overall ant foraging activity, but with the timing skewed towards late in the growing season such that 75% of ant foraging occurred after crop harvest in a wheat year and was therefore unavailable for pest suppression. Organic fields, in contrast, experienced moderate levels of ant foraging activity throughout the growing season, with most foraging occurring during crop growth. Organic fields thus supported twice as much pest suppression potential as conventional fields. Our results highlight the importance of timing in mediating ecosystem services in croplands and emphasize the value of managing landscapes for multiple services rather than yield alone.

Key words: Fertilizers, Formicidae, pesticides, pest suppression

Introduction

Organic agriculture—farming without inputs of synthetic fertilizers or pesticides—is a key component of global efforts to sustainably manage agricultural ecosystems to meet the needs of humans for food, fiber, and fuel while also supporting biodiversity and ecosystem services (Badgley et al. 2007; Reganold & Wachter 2016; Schulz et al. 2021). Despite making up only a small percentage of total crops (~1% both globally and within the U.S.), the production of certified organic crops is rapidly increasing around the world (Reganold & Wachter 2016; USDA 2019). By avoiding industrial fertilizer and pesticide inputs, organic agriculture promises to avoid or reduce some of the harmful impacts of intensive agriculture (Tilman 1999; Foley et al. 2005). Organic crops, for example, tend to emit fewer greenhouse gases, improve water and soil quality, support greater biodiversity, and deliver additional ecosystem services compared to conventional agriculture, often at the expense of reduced yields (Badgley et al. 2007; Syswerda & Robinson 2014; Reganold & Wachter 2016; Kravchenko et al. 2017). But for many agricultural systems we lack an understanding of how organic methods impact biological communities and the ecosystem services they mediate (de Ponti et al. 2012; Reganold & Wachter

2016). We address this issue by testing the impacts of organic versus conventional agriculture on a bioindicator taxon that is a predominant component of cropland biodiversity—the ants (Hymenoptera: Formicidae)—in one of North America's largest and most productive agricultural systems.

The environmental costs associated with conventional agriculture, and their possible mitigation through organic agricultural practices, are highlighted in the U.S. Corn Belt. The Corn Belt is a large region in the Midwestern U.S.A.—over half a million square kilometers—in which landscapes are overwhelmingly devoted to the production of corn *Zea mays* monocultures (Hudson 1994; Green et al. 2018). The corn is used primarily for animal feed and ethanol and is often grown in annual rotations with soy *Glycine max* or wheat *Triticum aestivum* (Hudson 1994; USEPA 2018). The intensive corn production in this region comes at the cost of extensive habitat loss (Fargione et al. 2009; Lark et al. 2015), greenhouse gas emissions that contribute to climate change (Robertson et al. 2017), soil and nutrient runoff that pollutes waterways and leads to the formation of hypoxic dead zones downstream (USEPA 2018), lower biodiversity (Syswerda & Robertson 2014; Helms et al. 2020), and reduced delivery of additional ecosystem services like natural pest suppression (Jackson 2008; Landis et al. 2008; Dosskey et al. 2012; Zhang et al. 2020). To mitigate or reduce the impacts of conventional agriculture, organic methods are increasingly practiced in the region but still make up only a minuscule fraction of crops (≤ ~0.5 % of all corn, soy, and wheat crops nationally in 2011, USDA 2019). Given the large size of the Corn Belt, the adoption of alternative methods over even a small portion of the area can have ramifications for entire landscapes. Understanding the biological impacts and potential tradeoffs associated with this growing agricultural sector is thus key for optimizing the conservation of biodiversity and the delivery of ecosystem services across the region.

To test for impacts of organic agriculture on biological communities and ecosystem services in the Corn Belt, we leverage long-term landscape experiments that compare varying agricultural regimes. We do so by characterizing the ant communities that have developed in crop fields over the past thirty years of continuous organic or conventional management of corn-soy-wheat rotations. Soil organisms, including ants, constitute most biodiversity in agricultural ecosystems and mediate many of their ecosystem services (Brussaard et al. 1997; Giller et al. 1997). Ants in particular are ideal organisms for answering questions about the long-term impacts of land use on ecosystem services (Agosti et al. 2000) because they are among the most abundant and functionally diverse groups of soil organisms (Hölldobler & Wilson 1990), their richness and diversity are correlated with environmental conditions, including the presence or abundance of other organisms (Peck et al. 1998; Andersen & Majer 2004; Wodika et al. 2014; Peters et al. 2016; Dilworth et al. 2021), they are involved in many ecosystem services (Del Toro et al. 2012; Wills and Landis 2018) including being the major mediators of natural pest suppression on farms in the Corn Belt (Grieshop et al. 2012, Wills et al. 2019, Helms et al. 2020), and they are long-lived perennial species that respond to environmental conditions at multiple time scales. By developing through years of differential survival, reproduction, and dispersal of colonies, ant community composition reflects climate and land use conditions over long time scales (years to decades, Underwood & Fisher 2006). Ant colonies also respond rapidly to their environment by altering patterns of foraging activity (over minutes to weeks) to take advantage of optimal foraging temperatures or sudden availability of resources (Albrecht & Gotelli 2001; Bujan et al. 2016). In these ways ant communities not only reflect the environmental conditions and biodiversity value of different management regimes, but also contribute to the function of agricultural landscapes and the ecosystem services they provide.

We explore how ant community composition and ecosystem service potential differ under organic versus conventional management by continuously comparing ant communities and foraging activity throughout the growing season among replicate plots varying in synthetic chemical use and associated agricultural practices. To do so we test whether conventional agriculture 1) reduces ant species richness and diversity, 2) reduces functional richness and diversity, 3) increases the prevalence of disturbance-tolerant exotic species at the expense of native ants, or 4) reduces ant foraging activity and thereby 5) lowers the potential for pest suppression services by ants. Our results uncover novel mechanisms mediating the delivery of ecosystem services in croplands.

Materials and Methods

Study location

We tested the effects of agricultural practices on ant biodiversity and ecosystem services in a long-term experiment managed by the Kellogg Biological Station Long-Term Ecological Research site in southwest Michigan, USA (42˚24′18″ N, 85˚24′02″ W, 275 m a.s.l.). The Main Cropping System Experiment was established in 1989 and consists of replicate 1-hectare plots maintained under several management regimes representative of the U.S. Corn Belt. We compared ant communities that had developed over 30 years in two of the treatments—one which experiences no inputs of industrial fertilizers or pesticides (USDA certified organic treatment), and one which receives chemical inputs (industrial fertilizers, herbicides, and fungicides) at one third the typical regional rates (conventional treatment). Both treatments are managed as corn-soy-wheat rotations (*Zea mays*-*Glycine max*-*Triticum aestivum*) on the same rotation schedule, are tilled annually, and are regularly planted with leguminous cover crops (various clovers *Trifolium sp.* or hairy vetch *Vicia villosa*, depending on year; detailed agronomic logs available online, KBS LTER 2020).

We compared the organic and conventional treatments of this experiment in 2019 during a wheat year of the rotation. Plots were tilled and planted with the same variety of soft red winter wheat at the end of the previous growing season (October 2018), after the harvest of that year's soy crop. Wheat seeds planted in conventional plots were treated with a mix of several fungicides and one neonicotinoid insecticide (thiamethoxam), while wheat seeds in organic plots were not treated with pesticides. Organic plots received no additional weed management beyond tilling prior to planting wheat the previous autumn. For additional nutrient inputs, in late March organic plots were seeded with a leguminous cover crop of red clover (*Trifolium pratense*). Interseeding low-growing legumes into wheat or other crops is a common practice in organic agriculture, as the legumes increase available soil nitrogen through fixation by symbiotic rhizobia bacteria without competing with the crop for light (Badgley et al. 2007; Regan et al. 2020). Conventional plots, in contrast, were sprayed twice with herbicides (a glyphosate-based herbicide in October after planting wheat and a pyroxsulam-based herbicide in April), and instead of spring cover crops received a mix of industrial fertilizers (nitrogen, potassium, and sulfur) in March, April, and May. Conventional plots were also sprayed with fungicides twice in June. Wheat from both treatments was harvested on 25 July. After harvest the organic treatments were mowed once for weed control at the end of August and experienced no further management for the rest of the season. Conventional plots, however, were sprayed with another dose of glyphosate-based herbicide in mid-August, mowed in late August, and then planted with a fall cover crop of red clover.

Our work within these organic and conventional treatments was also partly oriented in regard to a future study on the influence of restored native vegetation on agricultural insect communities. In the year of our study in both treatments a 5-m wide strip embedded through the center of each plot was left clear of wheat. The strips were seeded with a native prairie seed mix on 25 April, mowed in late July, and throughout the study period were dominated by a mix of short agricultural weeds and cover crops (common ragweed *Ambrosia artemisiifolia*, stinking chamomile *Anthemis cotula*, oat *Avena sp.*, lamb's quarters *Chenopodium album*, ryegrass *Lolium* sp., and red clover *Trifolium pratense*), with native prairie vegetation expected to develop in subsequent years. Strip management and planted species composition were identical across plots and treatments.

Ant sampling

To characterize the composition and seasonal activity of the ant communities that had developed in organic and conventional fields, we captured foraging workers by repeatedly sampling grids of pitfall traps throughout the growing season. Grids consisted of 12 pitfall sampling stations in each plot (6 replicate plots per each of 2 treatments, for a total of 144 sampling stations), arranged into three east-west transects spaced 15 to 30 meters apart. Each transect contained 4 sampling stations—located 1, 5, and 20 meters from the edge of the wheat-free strip down the field center, and one in the center of the strip, allowing us to test or control for potential impacts of the strip. To avoid edge effects all sampling stations were located at least 20 meters from the outside edge of the plot.

To avoid digging-in effects from continually excavating pitfall traps, and to facilitate repeated sampling, at the beginning of the growing season we installed a semi-permanent pitfall tube at each sampling station, into which pitfall traps could be placed at will. Pitfall tubes consisted of vertical PVC pipes (5.08 cm diameter, ~15 cm deep) buried with their top ends slightly below the level of the soil surface. Pitfall tubes were stoppered when not in use, forming a nondescript surface continuous with the surrounding soil. We waited at least 72 hours after first installing pitfall tubes before sampling ants. To capture foraging ants at a station, we opened the pitfall tube and placed a plastic container (5.08 cm diameter, 120 mL) inside it such that the cup's rim was flush with the soil surface. Containers were partially filled with 95% ethanol mixed with a few drops of unscented detergent to break surface tension. To protect traps from flooding, we mounted a clear plexiglass rain cover (15.24 x 15.24 cm squares) about 10 cm above the ground over each trap. Traps were collected after 48 hours and stored in ethanol at -20 ˚C. Captured ants were then sorted, counted, and identified using regional guides (covering ants of Ohio, Coovert 2005; New England, Ellison et al. 2012) and a global taxonomic database (AntWeb 2020), with representative voucher specimens for each species from each trap pinned and stored in the senior author's reference collection.

We trapped ants on a repeating four-week sampling schedule. In week one we placed and collected traps (48 hours for each trap) at all four sampling stations (located 1, 5, and 20 meters from the wheat-free strip, and one in the strip) in one east-west transect from each plot (4 sampling stations x 1 transect x 6 replicate plots x 2 treatments = 48 pitfall traps per week). We repeated the process during weeks two and three for the other two east-west transects in each plot, such that after three weeks all 144 sampling stations (72 in each treatment) had each been sampled for one 48-hour period. We did not trap ants during the fourth week for this experiment, although ants were occasionally collected for other projects from the same sampling stations during that week. We repeated this four-week routine five times during the growing season from 13 May to 19 September 2019, for a total of 720 pitfall traps (5 repeated samplings from each of 144 sampling stations). This routine allowed for representative coverage of growing conditions throughout the season (ants were collected in 15 calendar weeks spread over a 19-week sampling period), helped preclude large sampling effects due to weather conditions in any particular week, and ensured that repeated samplings were not overly destructive on ant colonies (each station was trapped for 240 cumulative hours spread over five 48-hr periods separated by several weeks). It also prevents confounding temperature or weather effects on comparisons among treatments, since organic and conventional plots were sampled concurrently throughout the season. Samples from 10 traps were lost or damaged, leaving 710 pitfall traps for analyzing ant community composition.

Data analysis

We calculated the estimated species richness and species diversity for each replicate plot (6 plots per treatment, total of 12 plots) using the program EstimateS 9.1.0 (Colwell 2013) with Chao2 sample-based rarefaction and the inverse Simpson's diversity index. To do so we combined species occurrences from all repeated pitfall traps (maximum of 5 traps) from each sampling station. We conservatively treated the occurrence of workers from a given species in at least one pitfall trap at a station as indicating the presence of one colony of that species, regardless of how many or how frequently workers were captured (Ellison et al. 2007; Gotelli et al. 2011). In this way we derived a species list for each of the 144 sampling stations (12 per plot), with each species assumed to have a colony abundance of one (conservatively assuming all workers came from the same colony). This list of species detected at a station over five sampling periods was treated as one sample in our analyses of species richness and diversity (12 samples per plot). All further analysis was performed in the program R (R Core Team 2018). We compared ant community composition among treatments with non-metric multidimensional scaling based on

Bray-Curtis dissimilarity in the package *vegan* (Oksanen et al. 2018), using number of stations where a species occurred as the measure of abundance (maximum of 12 inferred colonies per species per plot).

To test treatment effects on functional variation among ant communities, we assigned ant species to one of five guilds—honeydew gatherer, omnivore, predator, thief ant, or seed disperser—using regional guides (Coovert 2005; Ellison et al. 2012). While these functional classifications are not stringent (even non-specialized ants may opportunistically feed on insect prey or honeydew), they nevertheless capture much ecological variation and are useful in interpreting the responses of ants to changes in land management (Helms et al. 2020). We measured functional richness per plot, and then calculated functional diversity for each plot using the inverse Simpson's diversity index, based on how many colonies from each guild were detected among all 12 sampling stations in the plot.

We compared the prevalence of exotic ants among treatments—an indicator of habitat disturbance (Holway et al. 2002)—by calculating the relative abundance in each plot of the only invasive species at the Kellogg Biological Station, the Eurasian pavement ant *Tetramorium immigrans* (Helms et al. 2019; 2020). We did this by calculating the proportion of sampling stations in each plot that contained pavement ant colonies.

Finally, to test for treatment effects on ant foraging activity throughout the growing season, and thereby the potential for ants to hunt or drive away crop pest insects (Wills et al. 2019), we counted the number of worker ants of each species captured in pitfall traps (activity = number of worker ants foraging in the trap catchment area per 48-hour period). We excluded from these analyses an additional 63 pitfall traps that had been partially or wholly flooded by rain when we collected them from the field, likely impacting the counts of worker ants contained in the trap (although they were still useful for detecting the presence of species, and therefore used in community composition analyses), leaving 637 pitfall samples for foraging activity analysis. We analyzed ant foraging activity both at the community level (all workers of all species) and within individual species for the three most common species. When examining foraging patterns of individual ant species, we avoided conflating the absence of a species with the absence of foraging activity by using activity data only from sampling stations at which a species was known to occur (at least one worker ant of that species detected at any time during the growing season).

We tested variables for normality with the Shapiro-Wilk test. Comparisons of ant communities between treatments use averages or medians per plot (n = 6 per treatment) with paired *t*-tests for normally distributed variables and Kruskal-Wallis tests for other data. We report means and standard deviations for normally distributed data, medians and interquartile ranges (IQR) for others. We compared foraging patterns among organic and conventional plots throughout the season using ANCOVAs of total ant activity across all sampling stations (maximum n = 24 per treatment per week) with sampling week as a covariate.

We expected no effects of the wheat-free strips in each plot (the nascent prairie strips), since identical strips occurred in all plots of both treatments, and all comparisons among treatments occurred at the level of plots (for community comparisons, n = 6 plots per treatment) or the entire experiment (ant activity, n = 72 per treatment). Further, the mating seasons of most regional ants, and thus the period when nascent colonies of new species may be recruited, occurs during the summer (Coovert et al. 2005), with mature colonies not expected until at least the following year, precluding drastic changes in ant community composition during our study period (Scharnhorst et al. 2021). We nonetheless tested for effects of the strips in two ways. First, we visually compared community composition of sampling stations within plots through community ordination at the sub-plot level, grouping sampling stations according to distance from strip. In this visualization, each plot consisted of 4 micro-communities of 3 sampling stations each (3 stations in the strip, and 3 each at 1, 5, and 20 meters distance from the strip). We found no obvious changes in community composition with distance from strip. This is to be expected because the strips had just been seeded concurrently with this study and its plant communities were still dominated by agricultural opportunists rather than native prairie species (see *Study location*). Our second test of the effects of wheat-free strips focused on ant foraging activity, however, which may respond rapidly to small-scale changes in resources or micro-climate. We tested whether ant activity varied with distance from the wheat-free strips, and did so differently in the two treatments, using a linear regression that included distance, sampling week, treatment, and plot effects and their interactions. We found no consistent effect on ant activity of distance from the wheat-free strip alone or in combination with any other variable (distance $P = 0.87$, distance by time interaction $P = 0.55$, distance by treatment interaction $P = 0.45$, distance by plot interaction P all > 0.15). Again, this is likely due to the vegetation of the wheat-free strips being mostly comprised of agricultural opportunists that also occurred in surrounding crops.

Results

Ant communities

We collected 710 pitfall traps over four months of the growing season, capturing 1,808 foraging ants of 15 species (Table 1). More ant species occurred in organic plots than in conventional plots over the entire experiment (12 versus 10 species), but there was not a consistent difference in estimated species richness between organic and conventional plots (*t*-test $P = 0.98$, Table 2).

Organic plots displayed a larger range in species richness, however, and had the potential to occasionally contain more species than conventional plots (range of estimated species richness 4 to ~11 in organic versus 4 to ~9 in conventional Figure 1).

Ant community composition was similar among organic and conventional treatments. Both treatments were dominated by three core species that made up 87% of all detected colonies (the American cornfield ant *Lasius neoniger* Emery, the winter ant *Prenolepis imparis* Say, and the exotic Eurasian pavement ant *Tetramorium immigrans* Santschi), and largely overlapped in ordination space (Supp. Figure S1). Organic plots had about 15% higher ant diversity than conventional plots, but both treatments had similar functional richness, functional diversity, and prevalence of exotic Eurasian pavement ants (functional richness Kruskal-Wallis $P = 0.52$, functional diversity Kruskal-Wallis $P = 0.20$, pavement ant prevalence *t*-test $P = 0.55$, Table 2).

Ant foraging activity

We recorded ant activity (worker ants per trap per 48 hours) from 637 pitfall traps capturing 1,725 worker ants. Conventional plots experienced twice as much foraging activity as organic plots over the growing season (median 1 worker per trap in organic, IQR = 3, versus 2 in conventional, IQR = 3, ANCOVA $F_{1,633} = 11.125$, $P = 0.0009$, Supp. Table S1a). But foraging activity varied through time (ANCOVA $F_{1,633} = 59.007$, $P < 0.0001$, Supp. Table S1a) and organic and conventional plots displayed different seasonal patterns (ANCOVA $F_{1,633} = 50.494$, $P < 0.0001$, Figure 2, Supp. Table S1a). Organic plots maintained relatively constant ant activity throughout the growing season (activity over time linear regression $P > 0.6$, $r^2 = 0.01$, Supp. Table S1b). Conventional plots, in contrast, experienced little or no ant foraging at the beginning of the season, with activity increasing thereafter (linear regression $P < 0.0001$, $r^2 = 0.2$) to a peak in late summer (September).

These patterns of overall ant activity were driven primarily by the three dominant species, which all displayed strong seasonal variation in foraging activity, presumably responding to changes in temperature and moisture (Supp. Figure S2, Figure 3). Activity patterns of these three species differed in organic versus conventional plots and among species. In organic plots the cold-tolerant winter ant *Prenolepis imparis* was most active at the beginning and end of the growing season when temperatures are cool (Talbot 1943). The more heat-tolerant cornfield ant *Lasius neoniger*, in contrast, increased its foraging activity throughout the growing season, with a dip in mid-summer (July), and reached its peak in late summer before descending at the end of the season. The exotic Eurasian pavement ant *Tetramorium immigrans* had high but variable activity throughout the warm part of the season, again with a possible but less clear dip in mid-summer. It displayed little activity during cool periods at the beginning and end of the growing season. Late-season patterns in conventional plots were similar to those in organic fields. During much of the early growing season, however, foragers of both native ants, *P. imparis* and *L. neoniger*, were nearly absent in conventional plots. The exotic pavement ant, in contrast, showed no clear difference in foraging activity between organic and conventional plots.

Potential for pest suppression

The variable timing of ant foraging activity in the agricultural treatments (constant moderate activity in organic versus initially low but increasing activity in conventional) has implications for pest suppression. In conventional plots most ant foraging activity occurred after the mid-summer harvest, such that only a small amount of total foraging occurred during crop growth (18% of total average *P. imparis* activity, 17% in *L. neoniger*, and 53% in *T. immigrans*) and could thereby contribute to pest suppression (Figure 3). In organic fields, in contrast, a much higher percentage of activity occurred during crop growth and was available for pest suppression

(65% of total average activity in *P. imparis*, 35% for *L. neoniger*, and 57% in *T. immigrans*). Combining the activity of the three most common species, 54% of total ant foraging activity occurred during crop growth in organic plots, versus only 25% in conventional plots.

Discussion

Ant foraging activity and potential pest suppression

We documented that when compared to conventional agriculture, organic agriculture supports higher pest suppression potential. This occurred despite overall similarities in ant community composition among organic and conventional fields growing rotating corn-soy-wheat crops. Organic plots supported higher species diversity, and occasionally higher species richness, than conventional plots, but otherwise shared similar ant species composition and average richness, functional richness and diversity, and prevalence of exotic ants. But the two management regimes differed in their seasonal patterns of ant foraging during the wheat year of the rotation. Conventional plots experienced higher ant activity overall, but 75% of that foraging occurred late in the growing season after the crop had already been harvested, precluding potential benefits for pest suppression. Organic plots, in contrast, experienced moderate levels of ant foraging activity throughout the growing season, but with most foraging activity occurring before crop harvest and therefore of potential value in pest suppression. By this measure, organic crops experienced over twice as much ant foraging during crop growth, and presumed pest suppression potential, relative to conventional plots. These effects were apparent despite the conventional plots receiving only low amounts of pesticides and fertilizers (one third the typical rates for the region).

The impacts on ant foraging activity of industrial fertilizers and pesticides are likely mediated not by direct effects of the chemicals on ants, but through bottom-up effects on crops and other plants. Although insecticides may reduce ant foraging activity (Wills et al. 2019), no insecticides were applied during our study period (pesticides were limited to herbicides and fungicides, although seeds in conventional plots were treated with insecticides prior to planting in the previous year, see Methods) and they have only rarely been applied throughout the 30-year study period (except through treated seeds, KBS LTER 2020), precluding most direct chemical-induced mortality of ants. Instead, the high overall foraging activity of ants in conventional plots and the skew in timing toward later in the growing season are probably due to changes in plant resource availability or quality. The high overall ant foraging activity in conventional plots, for example, may be due to synthetic fertilizers indirectly increasing the amount or quality of plant-derived honeydew (harvested from aphids or scale insects) or the abundance of herbivorous prey insects through increases in plant nutritional quality (Jacquemin et al. 2012; Bujan et al. 2016). Conventional fields also had a conspicuous lack of non-crop vegetation early in the growing season, due to spring applications of herbicides, and consisted of the wheat crop growing in mostly bare soil. Wheat in organic fields, in contrast, grew above a red clover cover crop (seeded in March into the overwintered wheat crop) and more abundant agricultural weeds. The denser and more species-rich vegetation in organic crops early in the growing season likely provided a more optimal mix of arthropod prey and plant-derived honeydew preferred by generalist ants (Helms et al. 2021). Similar cover crop boosts to early season activity have been demonstrated in carabid beetles, another group of generalist predators of crop pests (Carmona & Landis 1999). In this view, the herbicides applied to conventional crops, and the related necessity of planting cover crops after harvest rather than before, led to seasonal differences in non-crop productivity and ant foraging activity, despite the two regimes experiencing comparable annual yields and identical cover crop species. This emphasis on timing rather than annual totals helps reconcile apparently contrasting results that found no effect of agricultural cover crops on ant foraging activity (unidentified ants in conventional corn-soy fields, Dunbar et al. 2017) or diet (predatory trap-jaw ants *Odontomachus bauri* in banana plantations, Duyck et al. 2011). By enabling the presence of a cover crop or non-crop vegetation at a critical period early in the growing season (Regan et al. 2020; Rivers et al. 2020), organic management may boost the potential for pest suppression by ants, despite higher annual ant activity in conventional plots.

Although we document variation in potential pest suppression by ants, determined by the amount and timing of ant foraging activity relative to the period of crop growth, we did not directly measure pest mortality in this study. In previous work at our study site, we showed that higher ant species richness in agricultural fields can boost crop pest mortality by over 50% (Helms et al. 2020) and that ants are often apex predators in crop food webs (Helms et al. 2021). Complementary work at nearby sites in southern Michigan likewise found that ants are the most frequent predators of crop pests, responsible for up to ~90% of predator-prey encounters (Grieshop et al. 2012) and that modest dips in ant foraging activity cut pest mortality in half (Wills et al. 2019). We are therefore confident in linking ant foraging activity to pest suppression potential.

Ant communities and crop management

The ant foraging patterns we observed may not hold in other crops within the region and elsewhere. Native perennial crops, for example, including fields of switchgrass *Panicum virgatum* grown for cellulosic ethanol production, have drastically different ant communities than row crops and more benign disturbance regimes regardless of synthetic chemical use (Helms et al. 2020). Ant foraging in these systems may be less likely to be dominated by a few disturbance-tolerant species or to be strongly impacted by differences in management. Ant communities and ecosystem services may also vary with alternative crop rotations, tillage regimes, and insecticide application (Stinner et al. 1988; Dunbar et al. 2016) or with field size (Kravchenko et al. 2017), adjacent vegetation (Schulte et al. 2017; Assis et al. 2018; Zhang et al. 2020), or land-use history (Le Provost et al. 2020). Nevertheless, the lack of variation in ant community composition across management regimes in our study is consistent with a lack of strong effects of fire or grazing on grassland ant species composition in the same region (Debinski et al. 2011; Moranz et al. 2013; Nemec 2014) and mirrors a comparable lack of variation in community composition among organic and conventional farms in Hong Kong (Chan & Guénard 2020). Taken together, these patterns suggest that the impacts of organic management on ecosystem services provided by ants are more likely to be mediated by short-term processes like changes in ant foraging activity rather than by long-term changes in the presence or absence of particular species.

The ant communities in our study are composed of perennial species that have survived years of continual disturbance associated with annual planting, tilling, harvesting, and crop rotation. These challenging conditions may have filtered out disturbance-intolerant species, and further alterations (such as moderate fertilizer or pesticide application) may be unlikely to lead to gross changes in community composition. Intensive use of synthetic chemicals, however, as opposed to one third the regional amounts as in our experiment, might amplify the differences in ant activity relative to organic crops or lead to more notable differences in ant community composition. Since the potential for pest suppression depends on the timing of ant foraging relative to crop growth and harvest, it would likewise be useful to compare ant foraging patterns in crops harvested late in the season (corn and soy) rather than midsummer (wheat in our study).

In crops harvested at the end of the growing season, nearly all ant foraging would occur before harvest regardless of fertilizer or pesticide use, and the timing of ant activity may be less informative in determining pest suppression potential.

The impacts of synthetic chemical use on ant foraging activity are overlain on top of seasonal patterns driven by temperature and precipitation, presumably mediated by the specific thermal tolerances of each species (Albrecht & Gotelli 2001; Bujan et al. 2020; Roeder et al. 2021). The two most common native ants in our study displayed dips in foraging activity during the hottest part of midsummer, with one—the especially cold-tolerant *Prenolepis imparis* (Talbot 1943)—mostly limited to foraging during the beginning and end of the growing season. The exotic pavement ant *Tetramorium immigrans*, in contrast, appeared to better tolerate peak summer conditions and showed little to no sensitivity to conventional agricultural practices. Warmer temperatures or drier conditions, including those expected in the Corn Belt due to climate change (Pryor et al. 2014; Basso et al. 2021), may therefore favor the persistence of pavement ants or other heat-tolerant exotics over native ants, compounding or interacting with the impacts of synthetic chemical applications. Future experiments to disentangle the effects of temperature, precipitation, and synthetic chemicals on ant foraging activity would enable us to better predict the ecosystem services provided by organic and conventional agriculture in different landscapes or under future climate scenarios.

Summary

The management-driven differences in potential pest suppression we observe among otherwise similar ant communities suggest caution when assessing the ecosystem service impacts of land use change. Conspicuous biodiversity indicators like species richness or composition alone may not accurately predict ecosystem services that are mediated by subtle behavioral or physiological processes that can vary over short timescales. At the same time, we emphasize how adjustments to agricultural management can improve biodiversity and ecosystem function with only minor changes in crop yield or land use. Because the Corn Belt occupies such a large area, even minor changes implemented over a fraction of its total extent may restore ecosystem services over thousands of square kilometers.

Acknowledgments

Michigan State University and the Kellogg Biological Station occupy the ancestral, traditional, and contemporary Lands of the Anishinaabeg – Three Fires Confederacy of Ojibwe, Odawa, and Potawatomi peoples, in particular on lands ceded in the 1819 Treaty of Saginaw. We thank local communities and the state of Michigan for maintaining and allowing access to field sites. Support for this research was provided by the NSF Long-Term Ecological Research Program (DEB 1832042) at the Kellogg Biological Station and by Michigan State University AgBioResearch.

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Tables and Figures

Table 1. Ant species in organic and conventional agricultural fields

Species	Guild	Conventional	Organic
Aphaenogaster carolinensis	Seed disperser	1.4	-
Aphaenogaster rudis	Seed disperser	1.4	1.4
Brachymyrmex depilis	Honeydew	2.8	-
Crematogaster cerasi	Omnivore	-	2.8
Formica glacialis	Honeydew	1.4	4.2
Formica incerta	Honeydew	5.6	2.8
Formica subsericea	Honeydew	-	1.4
Formica vinculans	Honeydew	-	1.4
Lasius neoniger	Honeydew	94.4	83.3
Myrmica americana	Omnivore	9.7	26.4
Myrmica detritinodis	Honeydew	-	1.4
Prenolepis imparis	Honeydew	77.8	72.2
Solenopsis molesta	Thief	1.4	-
Tapinoma sessile	Omnivore	-	1.4
Tetramorium immigrans	Omnivore	61.1	68.1
Total		**10**	**12**

Numbers are percentages of pitfall trapping stations that captured a given species (72 stations in each habitat)

Table 2. Ant communities in organic and conventional agricultural fields

Treatment	Replicate Plots (*n*)	Sampling Stations	Species Richness (Chao2)	Diversity (Inverse Simpson's) *	Functional Richness (# Guilds)	Functional Diversity (Inverse Simpson's)	Ant Activity (# Workers) *	Pavement Ants (Proportion of Stations)
Organic	6	72	6.75 (2.8)	3.94 (0.5)	2 (0)	1.90 (0.06)	2.25 (2.6)	0.68 (0.1)
Conventional	6	72	6.71 (1.8)	3.35 (0.4)	2 (0.75)	1.82 (0.37)	3.16 (4.4)	0.61 (0.2)

* indicates treatments differ at $P = 0.05$

Values for *Functional Richness* and *Functional Diversity* are medians with interquartile ranges in parentheses, other variables are means with standard deviations. *Ant Activity* shows the average over the entire growing season.

Figure 1. Species accumulation curves of ants collected in pitfall traps in conventional versus organic agricultural fields. Each set of lines and symbols denotes one distinct plot (6 per treatment).

Figure 2. Ant foraging activity through the growing season in conventional and organic agricultural fields. Points and lines show average ant activity per trap across all sampling stations in a given week (maximum $n = 24$ per treatment per week), and shading shows one standard deviation. Red lines show the week the wheat crop was harvested.

Figure 3. Relative foraging activity through the growing season of the three most common ant species in conventional and organic agricultural plots. Points and lines show average ant activity per trap across all sampling stations per week, excluding stations at which the given species was never detected, and scaled to the maximum activity observed per species per treatment. Red lines show the week the wheat crop was harvested. The shaded area shows the summed total amount of foraging that occurred during crop growth and could potentially contribute to pest suppression, with the overlying numbers indicating the percentage this represents of the total season's foraging.