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Higher bat and prey abundance at organic than conventional soybean fields

Julia E. Put[a,*], Greg W. Mitchell[b], Lenore Fahrig[a]

[a] Geomatics and Landscape Ecology Research Laboratory (GLEL), Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada
[b] Wildlife Research Division, National Wildlife Research Centre, Environment and Climate Change Canada, 1125 Colonel By Drive, Ottawa, ON K1A 0H3, Canada

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ABSTRACT

Studies that have compared biodiversity at organic and conventional farms have generally found that there are more species in greater abundances at organic farms. One widespread problem with previous studies is that most do not control for differences in field structure and landscape composition at organic and conventional farms. Thus, the effects observed may be due to factors other than organic farming practices. We addressed this problem by selecting matched organic-conventional pairs of soybean fields such that in each pair the soybean fields were similar in size, hedgerow length, and surrounding landscape composition within 1 km, 2 km and 3 km of the fields. At each of our 16 field pairs (32 sites), we measured relative differences in bat species richness and abundance using acoustic bat recorders, and bat prey availability using black-light traps. We predicted that organic soybean fields would have greater bat species richness, bat abundance and bat prey abundance than conventional soybean fields due to the prohibition of synthetic pesticides and longer more diverse crop rotations in organic fields, both of which should benefit bat insect prey. We found that organic soybean fields had higher bat species richness, bat abundance and bat prey abundance than conventional fields, after controlling for the effect of differences in soybean height between conventional and organic fields. Our results suggest that the management practices used at organic farms benefit bats at least in part by providing greater bat prey availability.

1. Introduction

The use of agro-chemicals - pesticides and fertilizers - threatens biodiversity. Declines in plants (Geiger et al., 2010), invertebrates (Benton et al., 2002; Geiger et al., 2010) and vertebrates (Köhler and Triebskorn, 2013) have been attributed to agro-chemical use, which can have direct effects, through toxicity, or indirect effects. One indirect mechanism that is thought to have caused declines in insectivores is the reduction of invertebrate prey (Benton et al., 2002). Insecticides can target invertebrate prey directly, and herbicides can limit invertebrate host plants growing in fields or along field margins (Boatman et al., 2004). In locations where agro-chemicals are in greater use, there may be less invertebrate prey available to insectivores, resulting in lower abundance of insectivores in those areas.

Studies that compare biodiversity in organic versus conventionally farmed fields are often taken as support for the impacts of agro-chemicals on biodiversity. Organic farming prohibits the use of synthetic agro-chemicals, and organic farms have longer more diverse crop rotations than those under conventional farming (OMAFRA, 2009). While more studies have found greater biodiversity at organically farmed fields than conventionally farmed fields (Lichtenberg et al., 2017), there are large differences in results among and within taxonomic groups (Wickramasinghe et al., 2004; Fuller et al., 2005; Pocock and Jennings, 2008), among agricultural crop species or sampling locations within a farm (Wickramasinghe et al., 2003; Batáry et al., 2010), and among landscape contexts (Lichtenberg et al., 2017).

However, in most comparisons of biodiversity in organic versus conventional fields, the organic fields tend to be smaller (Freemark and Kirk, 2001; Norton et al., 2009), have more vegetated field margins (Wickramasinghe et al., 2003; Fuller et al., 2005), and are surrounded by more diverse landscapes (Norton et al., 2009; Winqvist et al., 2012) than the conventional fields. This raises the question whether lower reported biodiversity in conventional than organic fields is in fact due to the agro-chemical use in the conventional fields or to differences in field and landscape attributes between organic and conventional farming systems. Thus, if the goal is to uncover the effects of organic farming practices on animal abundance and diversity, substantial care is needed in site selection to avoid confounding these effects with other potentially influential variables.

Insectivorous bats are an important group in agricultural systems because they provide pest control services. Lactating bats have been found to eat approximately 75% to more than 100% of their

* Corresponding author.
E-mail addresses: julia.put@glel.carleton.ca (J.E. Put), gregory.mitchell@canada.ca (G.W. Mitchell), lenore_fahrig@carleton.ca (L. Fahrig).

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bodyweight in insects per night (Kunz et al., 2011), and their ability to forage opportunistically (Clare et al., 2009) allows them to target insect pest species that may be highly abundant for discrete periods of time (Davidai et al., 2015). Bats can suppress insect pest populations (Kunz et al., 2011), which should limit crop damage. In fact, bat agricultural pest control services have been estimated to be worth $3.7 to $53 billion per year in the United States (Boyles et al., 2011). Thus, farmers benefit from conservation actions that increase bat abundance in agricultural areas.

Our objective was to measure relative bat diversity and abundance and the abundance of their insect prey at organic and conventional fields, using a study design that controlled for potentially confounding field and landscape attributes. Specifically, we predicted that 1) the number of bat species and bat abundance, and 2) the number of nocturnal aerial insects, would be higher at organic fields than conventional fields in matched organic-conventional pairs selected to control for field and landscape attributes. Since we hypothesized that bats would be more abundant at organic fields than conventional fields because of their higher bat prey availability, we also predicted that 3) there would be a strong positive relationship between bat activity and the abundance of insects.

2. Methods

2.1. Overview

We estimated bat species richness and abundance and nocturnal aerial insect abundance in 16 pairs of soybean fields. Each pair contained an organic and a conventional field. The fields were selected to isolate the effects of farming practices (organic vs. conventional). We did this by selecting a conventional field that matched each organic field in terms of field size, length of hedgerows/treelines around the field, local habitat around the sampling equipment, and surrounding landscape composition measured as the proportion of the landscape in agriculture, forest and shrubland, water, and urban cover within 1, 2 and 3 km of the field. At each field we sampled bats using automated bat recorders, and we sampled insects using black-light traps. Bat activity (number of bat passes recorded) was used as an index of bat abundance. We performed generalized linear mixed modeling (GLMM) for bat species richness, total bat activity, individual bat species activity or presence/absence, total insect abundance, insect abundance in separate size classes, and insect abundance in separate Orders as response variables, and field type (organic versus conventional) as our predictor variable of interest. Presence/absence was used for the two least common bat species.

2.2. Study region

We conducted our study in the regions of eastern Ontario (29 fields) and Montérégie, Quebec (3 fields) in Canada (mean latitude: 45.23, mean longitude: −75.17, Fig. 1). Our study area covered a latitudinal span of ~65 km and a longitudinal span of ~160 km. Organic farming is relatively uncommon in this area with 1.7% of farms in Ontario and 4.4% of farms in Quebec that are certified organic or are transitioning to certified organic (Statistics Canada, 2016a). The dominant crops in Ontario and Quebec are corn (17.4% and 20.0%, respectively), hay (15.1% and 36.0%, respectively) and soybean (20.8% and 16.9%, respectively) (Statistics Canada, 2016b). Pesticide applications to conventionally farmed soybeans include treatment of seeds with neonicotinoids (imidacloprid, clothianidin or thiamethoxam), and direct application of pesticides to fields. The latest information available in Ontario indicates about 50% of soybean seeds are treated with neonicotinoids (Statistics Canada, 2016b; Government of Ontario, 2017), and about 1.8 kg of active ingredient of pesticides are applied per hectare of soybean, of which 98.8% is herbicide (Farm and Food Care Ontario, 2015).

2.3. Site selection

We identified farmers growing certified organic soybean, and quantified the attributes of the fields where they planned to grow soybean in the 2017 growing season. We chose soybean because it is commonly grown both organically and conventionally in our study area. We found organic soybean farmers through web directories, an organic seed seller, and through other organic soybean farmers. Using the most recent and detailed imagery we could find (MNR, 2014; 50-cm resolution), we delineated the sizes of the fields and the length of the hedgerows/treelines around the fields. We calculated the proportions of agriculture, forest and shrubland, water and urban cover within 1, 2 and 3 km of each field (Table A.1. and AAFC, 2017).

To identify a suitable conventional field to pair with each organic field, we first identified areas with similar land cover to that surrounding the organic field of interest. The conventional field was within 6 to 18 km of the organic field. We targeted areas that were at least 6 km from the organic field to ensure spatial independence, i.e. so that it was unlikely that the same individual bats would commute to both fields (Brigham, 1991; Henderson and Broders, 2008; Elmore et al., 2005; Sparks et al., 2005). Commuting distances of bats are not well known. One study found that the hoary bat (*Lasiurus cinereus*), likely the most mobile species in our area, commutes distances greater than 6 km for foraging (Barclay, 1989), but its mean commuting distance was estimated at 3.4 km in another study (Bonaccorso et al., 2015). We used a maximum distance of 18 km so that the fields would be in the same general region. We then created uniform points approximately 600 m apart in the 6 to 18 km area from each organic field, and calculated the proportions of agriculture, forest and shrubland, water and urban cover within 1, 2 and 3 km of each point (AAFC, 2017). We then identified points that shared similar proportions of land cover at the 1, 2 and 3 km radius landscape extents to the organic field of interest. Within this set of candidate areas we then identified fields of similar size and length of hedgerows/treelines around the field to the organic field of interest, and that were either soybean or corn the previous year (AAFC, 2017), because soybean and corn are commonly rotated on fields in Ontario. For each organic field, we followed this process of identifying potential paired conventional fields, and then ranked the potential conventional fields from the strongest match to the weakest match based on their similarity in land cover within 1, 2 and 3 km of the field, field size and hedgerow/treeline length. Ideally we would have also matched the paired fields based on hedgerow/treeline height (see Wickramasinghe et al., 2003), but this information was not available. For one organic field, we redid the selection process to consider areas farther from the organic field of interest (see directly below) after finding few options for potential matched conventional fields within 18 km. All spatial analyses were performed in ArcGIS 10.4.1 (ESRI, Redlands, California).

Starting with the top-matched candidate conventional field for each organic field, we first confirmed it would be planted with soybean in 2017 using conventional practices, and then requested permission to access the field for bat and insect surveys. The resulting conventional fields in each matched pair were in our top 4 candidate choices (mean = 2.4). The resulting pairs were between 6.6 and 25.4 km apart (mean = 12.7 km). No significant differences were detected in the field structure and landscape composition between the matched pairs (Fig. A.1 and Table A.2).

2.4. Field data collection

2.4.1. Acoustic sampling for bats

We selected two sampling locations on the edges of each field (A and B). These locations were paired in the matched organic-conventional field pairs based on the vegetation immediately surrounding the survey equipment (hedgerow/treeline versus open), and the land cover type adjacent to the field at the sample location (forest versus agricultural field, Fig. 2). The A and B survey locations at each field were at

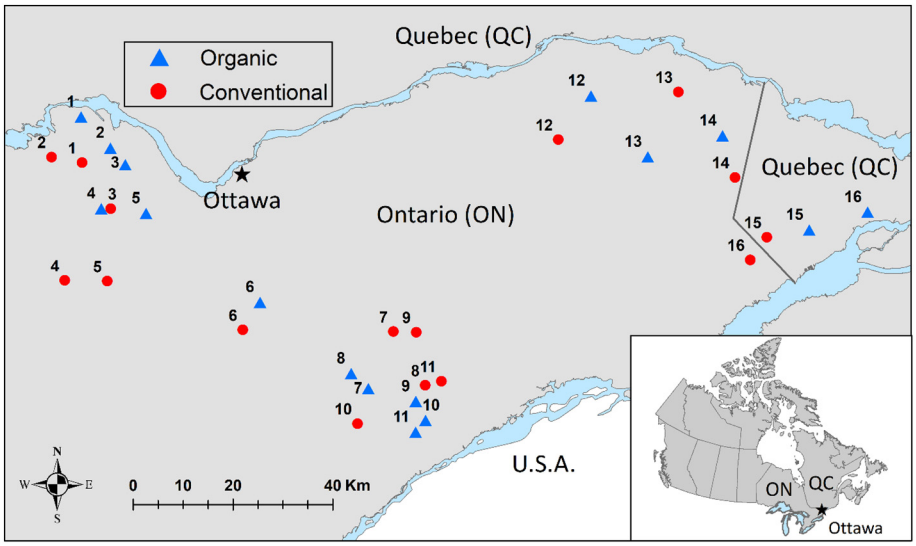

Fig. 1. Locations of the 16 matched organic-conventional soybean field pairs (32 fields in total) in eastern Ontario and western Québec, Canada, where we conducted bat and insect surveys. The inset indicates the location of the city of Ottawa in Canada. Pairs share the same number, where the organic site is in blue and the conventional site is in red. Pairs had similar proportions of agriculture, forest and shrubland, water and urban cover within 1 km, 2 km and 3 km of the soybean fields, field sizes and hedgerow lengths around the fields, and local habitat around the sampling equipment.

least 150 m apart, 100 m from wetlands, ponds and rivers, 50 m from buildings and paved roads, and 25 m from the corners of the field.

Between June 13th and July 28th, 2017, we sampled bats for two non-consecutive nights at each organic-conventional field pair. Each survey night we deployed four bat recorders (SM2 + BAT, Wildlife Acoustics), one at each survey location (A and B) at each field. Therefore, the total number of acoustic surveys was 128, i.e. 16 pairs × 2 fields per pair × 2 locations per field × 2 survey nights. The microphone (SMX-U1, Wildlife Acoustics) was mounted on a pole, approximately 1.5 m above the ground, and pointed toward the field. We sampled on nights with overnight temperatures above 10 °C and where there was little (< 1 mm) to no rain, because previous studies have shown that bat activity tends to be higher if both of these conditions are met (Erickson and West, 2002). Pairs were surveyed on the same nights, so that they would experience similar overnight temperatures and precipitation (if any), and to control for any other effects of date. The survey nights for each pair were an average of 23.8 days apart (range = 13–32 days).

We programmed the recorders for triggered settings to record full-spectrum bat passes from sunset (~20:30 to 21:00) to sunrise (~5:15 to 5:45). Recorders were set to record when sound above 12 dB and between 1 and 96 kHz was detected. They recorded for at least 2 s and up to a maximum of 20 s if sound continued to be detected.

A bat "pass" (each 2–20 s recording) is made up of 'chirps' that are made in quick succession. There are three types of chirps that can be found in a pass: search-phase, approach-phase and feeding buzzes (Gillam, 2007). Search-phase chirps are the most common and uniform type of chirps, and are made when a bat is commuting and searching for prey (Fenton and Bell, 1981).

We used search-phase chirps to identify bat passes to species. We made visual representations of the bat passes using the program Spek 0.8.2 (General Public Licence). We eliminated bat passes that did not contain bat chirps, recorded the number of feeding buzzes in each bat pass, and then we eliminated approach-phase chirps and feeding buzzes from the bat passes. The acoustic parameters of the chirps in the retained search-phase passes were measured using Scan'R 1.6.0 (Binary Acoustic Technology). To remove weak and fragmented chirps, we eliminated any passes that did not have at least two chirps above 16 dB with a duration of 0.99–30 ms and a minimum frequency of 15–60 kHz. To identify the search-phase passes to species, we used a quadratic discriminant function analysis model (QDFA) created by Ethier and Fahrig (2011). The QDFA uses seven acoustic parameters: chirp duration, interpulse interval, maximum frequency, minimum frequency, dominant frequency, slope, and curvature. Ethier and Fahrig (2011)

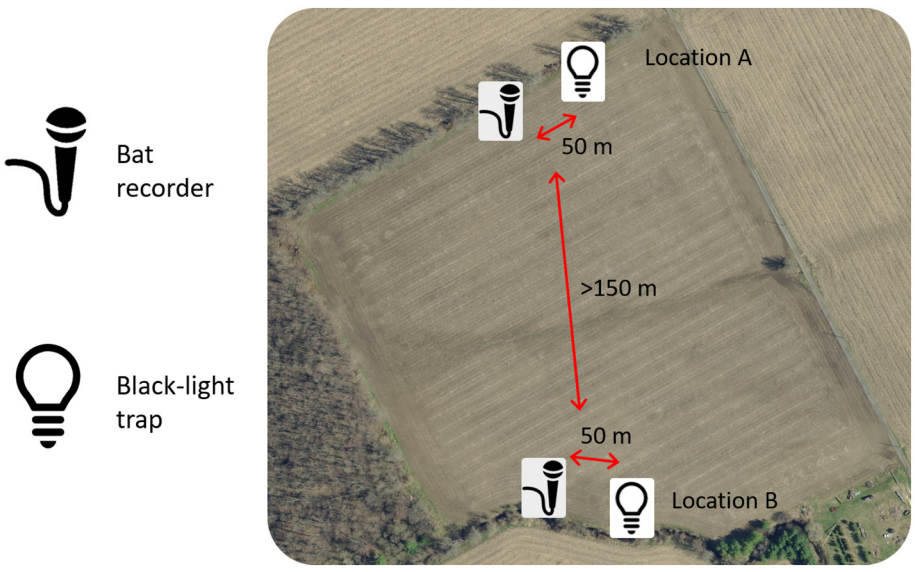

Fig. 2. Example layout of sampling equipment at each field. There were two locations (A and B) on the field edge of each field where an acoustic bat recorder and a black-light trap for catching nocturnal aerial insects were placed. At each location the bat recorder and black-light trap were placed 50 m from each other. The two locations on each field were at least 150 m apart. All sampling equipment was at least 100 m from wetlands, ponds and rivers, 50 m from buildings and paved roads, and 25 m from the corners of the field.

created the model using 269 reference bat passes recorded in Ontario that belong to the seven species found in our study area: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat, little brown bat (*Myotis lucifugus*), northern long-eared bat (*Myotis septentrionalis*), silver-haired bat (*Lasionycteris noctivagans*) and tri-colored bat (*Perimyotis subflavus*). The reference bat passes were obtained from the Fenton laboratory (Hooton, 2010; Adams, 2013). The QDFA has an overall correct species identification rate of 88.8%, and gives a posterior probability of the acoustic parameters of each chirp belonging to each species (0–1). We used the chirp with the highest signal-to-noise ratio from each bat pass in the QDFA. If there was high confidence (≥ 0.95) that it belonged to one species, then the pass was assigned to that species. If there was moderate confidence (0.50–0.95), then the chirp with the second highest signal-to-noise ratio was checked. If there was a posterior probability of > 0.5 for the same species as the first chirp, then the pass was assigned to that species. If not, the pass was classified as "unknown". The pass was also classified as "unknown" if the posterior probability of the chirp with the highest signal-to-noise ratio was < 0.5 for one species. We assigned 3.2% of passes as "unknown". The bat passes we recorded rarely contained more than one bat of the same or different species ($< 1.4\%$), so we did not modify our protocol for these instances. The QDFA model was run in R 3.3.2 (R Core Development Team, Boston, MA, USA).

2.4.2. Sampling for insects

We estimated nocturnal aerial insect abundance at the same time as our bat sampling, using two black-light traps (15 W - 368 Quantum Black Light, Leptraps LLC) on each field, one in each survey location 50 m along the field edge from the bat recorder at that location (Fig. 1). As for the bat recorders, the locations where the black-light traps were placed were paired for each organic-conventional pair, such that their habitat characteristics (see above) were similar.

To ensure that the black-light traps captured insects available to the bats, we programmed the black-light traps to turn on at sunset and turn off at sunrise. After an insect survey was over, we retrieved the sample from the trap and stored it in a freezer for later sorting.

We counted the number of insects collected in each insect sample. As insect size or Order may affect whether a bat readily consumes it (Aguirre et al., 2003; Clare et al., 2014; Valdez and O'Shea, 2014), we classified all insects by body length (0–5 mm, 5–10 mm, 10–15 mm, or > 15 mm) and Order (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera, other). We also measured the dry weight (biomass) of each Order in each sample.

Due to the very large number of insects collected in 85 of the 124 samples, we subsampled these samples. To subsample, we first counted, weighed and removed all large-sized moths (> 10 mm) from the sample, as macro-moths are an important food source for bats (Clare et al., 2009). Furthermore, macro-moths have been found to be a particularly important food source for hoary bats (Valdez and Cryan, 2009), which was the most common bat species recorded by other studies in our study region (Ethier and Fahrig, 2011; Monck-Whipp et al., 2018). The remaining sample was then placed in a standardized transparent rectangular container and shaken gently to evenly distribute the sample. Then the container was placed on top of a numbered 2-cm grid. We randomly chose grid cells to sample, and stopped subsampling when at least 500 insects had been counted. When a grid cell was selected we removed all the insects that fell in the boundaries of the grid cell and every second insect that crossed the boundaries. We determined that 500 insects was sufficient to reliably extrapolate to the contents of the rest of the sample (Fig. B.1, B.2 and B.3). To extrapolate, we divided the insects counted by the number of grid cells counted, and then multiplied by the total number of grid cells.

2.4.3. Measuring potentially confounding variables

Since the bat recorders and black-light traps were active at the same time for each matched organic-conventional pair, our study design inherently controlled for potential confounding variables, such as Julian date or weather conditions. Given the strong positive effects of distance to a river on bat activity found in another study (Froidevaux et al., 2017), we tested whether the distance to the nearest river or lake (Statistics Canada, 2011) was different between the paired recorder locations in the organic and conventional fields (mean = 3.5 km, range = 0.3–7.7 km), and found no significant difference (Wilcoxon paired test, $V = 307$, $p = 0.432$). Therefore, we did not include distance to river/lake as a confounding variable in our models.

However, during the spring we noticed that the conventional fields were often planted before the organic fields in each pair. This generally resulted in taller soybean at the conventional sites than at the organic sites, on a given sampling date. Differences in organic and conventional agricultural practices, such as weed control, fertilizer use or plant varieties, could also contribute to this difference in soybean height, as they are factors that contribute to lower crop yields in organic agriculture (Seufert et al., 2012). Previous studies have found a positive association between vegetation height and bat activity (Wickramasinghe et al., 2003; Jung et al., 2012; Froidevaux et al., 2017). Therefore, on the day of each survey, we measured the soybean height of three randomly selected soybean plants near each recorder (six measures/field per survey date). Soybean height was measured as the distance from where the soybean came out of the soil to the growing point. We averaged the six soybean height measurements for each field (organic and conventional) per survey date. Soybean was significantly taller at conventional fields than organic fields in pairs on a given date (Wilcoxon paired test, $V = 454.5$, $p < 0.001$), so we included soybean height as a potential confounding variable in all our models (below).

2.5. Data analysis

2.5.1. Effect of field type on bat species richness and activity

To test our prediction that bat species richness and activity is higher at organic fields than conventional fields (within pairs), we used GLMMs with bat species richness, total activity, and individual species activity or presence/absence as the response variables, and field type as our predictor variable of interest. We included soybean height as a potential confounding variable, and random effects for organic-conventional pair and for recorder location (A or B); recorder location was nested in pair. We used a normal distribution for bat species richness (Fig. C.1). For total activity we added species as a categorical variable to account for differences in activity among species and we used a negative binomial distribution to account for over dispersion in the count data (Fig. C.1). For the activity of each of the five most common bat species (big brown bat, eastern red bat, hoary bat, little brown bat and silver-haired bat) we used a negative binomial distribution (Fig. C.1). For the two least common bat species (northern long-eared bat and tri-colored bat) we used presence/absence data and a binomial distribution (logistic regression).

2.5.2. Effect of field type on insect abundance

To test our prediction that aerial insect abundance is higher at organic fields than conventional fields (within pairs), we used GLMMs with total insect abundance, abundance of each size class, and abundance of each Order as response variables, and field type (organic/conventional) as our predictor variable of interest. We included soybean height as a potential confounding variable, and random effects for organic-conventional pair and for recorder location (A or B); recorder location was nested in pair. All models used a negative binomial distribution (Fig. C.2 and C.3).

2.5.3. Relationship between bat species activity and insects

We performed Spearman's correlations between bat species activity and insect abundance and between bat species activity and insect dry weight to test our prediction that bat activity should be strongly positively correlated to insect prey availability. We did not include the

group of insects that were categorized as 'other' in insect abundance or insect weight for these correlations, because insects in the 'other' category are thought to contribute little to bat prey availability (Harvey et al., 2011). We conducted all statistical analysis in R version 3.3.2 (R Development Core Team, 2016) using the glmmADMB (Skaug et al., 2016) package. Our data is available through Mendeley Data (Put et al., 2018).

3. Results

Of the anticipated 128 acoustic surveys, three failed due to microphone malfunctioning. Over all remaining 125 surveys at 32 soybean fields, we recorded 15,430 bat passes. All seven species present in the study area were represented: big brown bat (2642 passes), eastern red bat (141), hoary bat (11,368), little brown bat (513), northern long-eared bat (35), silver-haired bat (144) and tri-colored bat (93). 494 bat passes were classified as 'unknown' (3.2% of passes). There were on average 123.4 bat passes per acoustic survey (range = 0–1015), and on average 3.8 species per survey (range = 0–7). There was a strong positive correlation across acoustic surveys ($r = 0.85$) between bat activity and feeding buzzes (Fig. F.1.). This indicates that in fields with greater bat activity, bats were foraging more.

Of the anticipated 128 insect surveys, five failed due to trap failure. Over all remaining 123 insect samples at 32 soybean fields, we collected an estimated 703,682 insects. Most insects were identified as Diptera (56.5%), Trichoptera (13.8%), Coleoptera (11.9%) and Lepidoptera (7.5%), and were in the 0–5 mm size class (87.3%). There was an average of 5721 insects per sample (range = 6–43,940).

Soybean plants at conventional fields were 5.8 cm taller, on average, than soybean plants at organic fields. Fields with taller soybean plants had greater bat species richness, total bat activity, activity levels for four bat species, insect abundance, and total insect weight (Fig. E.1, E.2 and E.3). Recall that the effect of soybean plant height was controlled for in tests of our predictions (below) by including soybean plant height as a co-variate.

Mean bat activity was not correlated with soybean field size ($r = 0.02$, $p = 0.924$; Fig. H.1a). There was a positive correlation between mean bat activity and hedgerow length per ha of field ($r = 0.49$, $p = 0.004$; Fig. H.1b). There was also a positive correlation between mean bat activity and forest cover ($r = 0.36$–0.41, $p = 0.045$–0.021, depending on spatial extent; Fig. H.1c, H.1d and H.1e). Recall that these effects of hedgerow length and forest cover were controlled for in tests of our predictions (below) through our paired sample site design (Fig. A.1 and Table A.2).

Consistent with our first prediction, bat species richness, total activity and activity levels for five bat species were significantly ($p < 0.05$) or nearly significantly ($p < 0.1$) greater at organic fields than conventional fields (Fig. 3 and Table G.1.). In addition, the direction of the effect was the same for the other two bat species. Based on the confidence intervals in Fig. 3 for the cross-species model, organic fields had approximately 31–75% more bat passes per survey than conventional fields. When bat passes from the most abundant bat species (i.e. hoary bats) were excluded in the cross-species model, the positive and significant response to organic soybean did not change (Table G.5.).

Consistent with our second prediction, total insect abundance, abundances of individual size classes, and abundances of individual Orders were significantly ($p < 0.05$) or nearly significantly ($p < 0.1$) higher at organic fields than conventional fields (Fig. 4 and Table G.2.). Based on the confidence intervals in Fig. 4, organic fields had approximately 41–114% more insects than conventional fields per survey. We found that the total dry weight and weight of individual Orders, except other, were also greater at organic fields than conventional fields (Fig. D.1. and Table G.3.). Consistent with our third prediction, bat abundance was positively correlated with total insect abundance (Spearman rank correlation, $r_s = 0.32$, $p < 0.001$) and total insect weight (Spearman rank correlation, $r_s = 0.47$, $p < 0.001$, Fig. 5), although the correlation had more unexplained variation than we had expected. With the variables log-transformed, bat abundance had a low percentage of variance explained by the model with total insect abundance ($R^2 = 0.08$) and total insect dry weight ($R^2 = 0.15$).

4. Discussion

Our results support our prediction that organic soybean fields have more bats and more bat prey than conventional soybean fields. There was greater bat species richness, total bat activity, and activity of big brown bats, eastern red bats, hoary bats, little brown bats and silver-haired bats, and higher total insect abundance, and insect abundance within separate size classes and Orders at organic fields than conventional fields. Our findings are consistent with most studies across a range of taxa (Hole et al., 2005). However, previous studies on bats have been variable: three studies observed more bats or foraging activity at organic sites (Wickramasinghe et al., 2003; Fuller et al., 2005; Davy et al., 2007), one study found a few bat species were more abundant at organic sites (MacDonald et al., 2012) and three studies observed no difference (Pocock and Jennings, 2008; Long and Kurta, 2014; Froidevaux et al., 2017).

We suggest that our ability to detect consistent effects of organic farming on bat species richness, bat abundance and bat prey abundance with a moderate sample size was due to our highly structured approach to site selection. This limited the effects of confounding variables and avoided spatial autocorrelation. Organic fields tend to be smaller than conventional fields (Freemark and Kirk, 2001; Norton et al., 2009); even in our study, where we put effort into controlling this variable, organic fields were slightly smaller (Table A.2.). Agricultural landscapes with smaller fields tend to have more vegetated field margins and more forest cover (Médiène et al., 2011). In our study, slight differences in field sizes among pairs were not responsible for the greater bat abundances at organic fields, because there was a weak relationship between bat abundance and field size. There was also no notable difference in hedgerow length and proportion of forest in the surrounding landscape between pairs. Our decision to ensure there was at least six km between organic and conventional fields within matched pairs was particularly important. Previous studies have recognized the importance of controlling for potentially confounding landscape variables (Winqvist et al., 2012), but they accomplished this by selecting organic-conventional field pairs such that the paired fields were close together and therefore in the same landscape context (Pocock and Jennings, 2008; Froidevaux et al., 2017). This creates spatial dependence of the organic and conventional fields and could be the reason that such studies did not find a difference in bat activity between organic and conventional fields. In other words, controlling for effects of landscape variables is important, but this should not be done in a way that compromises spatial independence of sites (Holland et al., 2004). Our paired fields were farther apart than the average commuting distance for the bat species in our study area (Brigham, 1991; Henderson and Broders, 2008; Sparks et al., 2005) making it unlikely that the same individual bats would commute to both fields.

Although bats and bat prey were both more abundant at organic fields than conventional fields, bat prey availability does not appear to be the only factor causing lower bat abundance at conventional fields. The relationship between insect abundance or insect weight and bat abundance was positive, but there was considerable unexplained variation (Fig. 5). Therefore, we speculate that conventional agriculture reduces bat activity through additional mechanism(s) beyond reduced prey availability. One possibility is that pesticides may have direct toxicological effects on bats. Harmful effects of organochlorine pesticides were documented on bats in the 1960s and 1970s (Clark, 1988). These highly toxic pesticides have been replaced by pesticides that are far less toxic (O'Shea and Johnston, 2009), but their effects on bats are not well studied. One study found that bats continued to forage in an

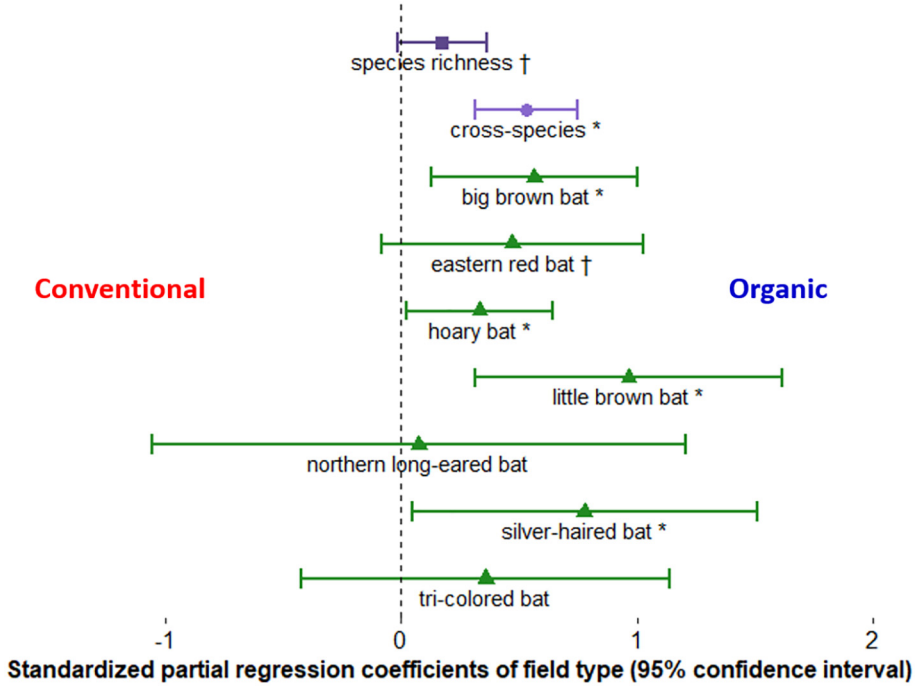

Fig. 3. Estimated effects of field type on bat species richness, cross-species activity and species-specific activity. The relationship for bat species richness was modeled using a linear mixed model. The relationships for cross-species activity and species-specific activity were modeled using GLMMs where the models for cross-species, big brown bat, eastern red bat, hoary bat, little brown bat and silver-haired bat used a negative binomial distribution and the models for northern long-eared bat and tri-coloured bat used a binomial distribution. All models included soybean height as a confounding variable. Positive slopes indicate that bat species richness, activity or presence is higher at organic than conventional sites in field pairs (*p-value < 0.05, †p-value < 0.10). The colour-symbol combinations group models with similar response variables.

apple orchard after it was sprayed with insecticide, and that the level of insecticide residues on bat prey items in the orchard were high enough to pose a potential reproductive risk to bats (Stahlschmidt and Brühl, 2012). In addition, the accumulation of small exposures to pesticides might reduce bat survival. Such an increase in mortality is not likely to be compensated by higher reproductive output, as most bat species produce only one young per year (Barclay and Harder, 2003). Another possible explanation for the high variation in the relationship we found between bat activity and insect abundance/weight is that bats and insects may respond to the amount of organic agricultural cover in the landscape at different spatial extents. We were not able to test for effects of amount of organic agriculture at different spatial extents because we could not obtain landscape-scale data on the distribution of organic agriculture, due to strong privacy laws that limit information availability in our study area.

We found that bat diversity, bat abundance and insect abundance increased with crop height. It is possible that taller crops provide more habitat for insects, thus increasing prey availability to bats. For example, McCracken et al. (1995) found that pastures with taller grass had more crane fly (*Tipulidae* sp.) larvae. Froidevaux et al. (2017) found

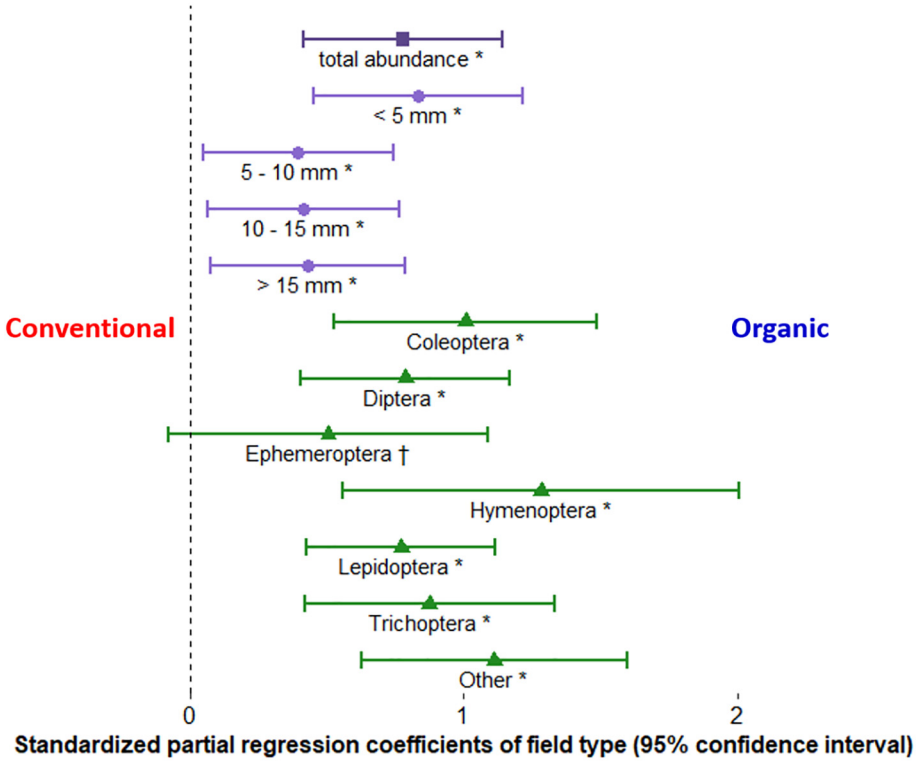

Fig. 4. Estimated effects of field type on total insect abundance, abundance in each size class and abundance in each insect Order. The relationships were modeled using GLMMs with a negative binomial distribution. In addition to field type, models included soybean height as a potential confounding variable, and random effects for organic-conventional pair and field location (A or B) nested in organic-conventional pair. Positive slopes indicate that insect abundance is higher at organic fields than conventional fields in field pairs (*p-value < 0.05, †p-value < 0.10). The colour-symbol combinations group models with similar response variables.

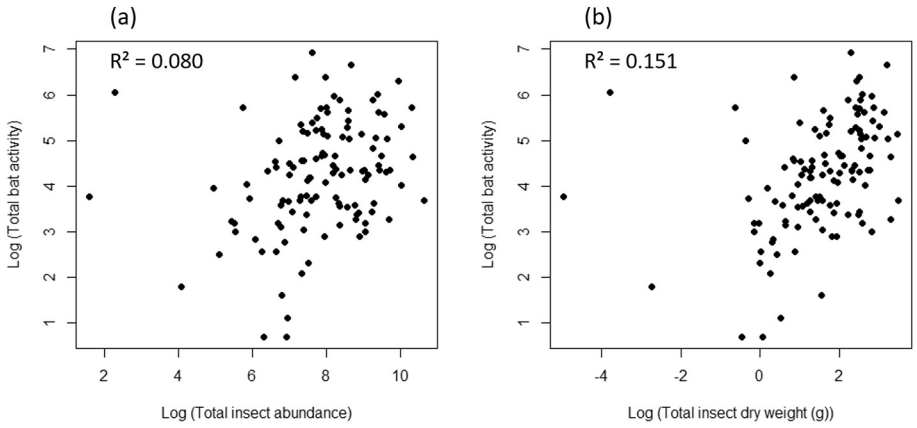

Fig. 5. Relationships between total bat activity (number of passes) and a) total insect abundance and b) total insect dry weight (not including 'other' insects; see Methods). Each plotted point represents data from a survey at a given sampling location (n = 120). Bat activity was recorded using acoustic recorders. Insect samples were collected using black-light traps, which target nocturnal aerial insects.

positive effects of vine row height in vineyards on one bat species. Heim et al. (2017) found positive effects of crop height on the foraging activity of two bat species, which had an interaction with insect diversity for one species and insect abundance for the other. An increase in prey habitat in taller crops could cause an increase in prey abundance either through increased survival or increased reproductive rate of prey. As we found no relationship between average insect weight (a proxy for insect reproductive potential) and soybean height (Fig. I.1), the former is more likely than the latter (Fig. E.2 and E.3; Honěk, 1993). Alternatively, the increase in bat abundance and bat species richness with increasing crop height may be a behavioural response, in that nocturnal bats may prefer to forage at higher elevations, as suggested by Heim et al. (2017).

The higher average soybean height in conventional fields was likely mainly due to the earlier planting of conventional fields in our area because it allows them more time for weed management (Coulter et al., 2010). However, other studies (Gomiero et al., 2011; Pimentel et al., 2005) have found higher yielding (and perhaps taller) soybean plants in conventional fields for other reasons, namely higher nitrogen-nutrient inputs and more aggressive weed control practices. If such differences in practices occur in our area, then it could be argued that these conventional practices (synthetic fertilizer use and herbicides) indirectly mitigate the effects of conventional farming practices on bats and insects, by causing an increase in soybean height. It is difficult to evaluate this possibility. Although the type of fertilizer differs between organic and conventional fields (natural vs. synthetic), the amounts applied may not be substantially different (Pimentel et al., 2005). In addition, while the application of herbicides may increase soybean height in conventional fields by reducing competition, it also decreases habitat for insect prey (i.e. plants). In any case, we note that even if we omit soybean plant height from models, the direction effect, i.e. more bats and insects in organic fields, remains constant, although the effect does become weaker (Table G.4.).

Although we detected all the bat species present in our study region, detectability likely varies among species. This is because some species vocalizations are more easily detected by bat detectors (Lumsden and Bennett, 2005), bat detector models have different detection rates (Adams et al., 2012), and species differ in behaviours, such as proximity to field edges and elevation of flight, which would affect their distances from the recorders. Such differences in detectability might have inflated the relative abundance of our most commonly detected species, hoary bat. However, this did not skew our overall results, because all species responded in the same way, i.e. higher activity in organic than conventional fields. In addition, the results for overall bat activity do not change if we exclude hoary bat calls from the cross-species model (Table G.5.).

We controlled for landscape attributes (i.e. proportion of agriculture, forest and shrubland, water and urban cover within 1, 2 and 3 km of each field) through our site selection approach, to estimate the effects of organic farming practices on bats and their prey. We did this because these landscape attributes are known to affect bats. Previous studies have found negative effects of average field size in the landscape (Monck-Whipp et al., 2018), landscape-scale agricultural cover (Put et al., 2018) and developed land cover (Dixon, 2012), and positive effects of hedgerows (Wickramasinghe et al., 2003; Pocock and Jennings, 2008; Boughey et al., 2011; Lentini et al., 2012), proximity to water (Russo and Jones, 2003) and forest cover in the landscape (Heim et al., 2015) on bat abundance. In addition, our data confirmed the positive effects of hedgerow length and forest cover per ha on bats. This highlights both the potential for modifying landscape structure to increase bat activity in farmlands, and the importance of controlling for these landscape effects when testing for effects of farming practices on bats.

Our study contributes to the growing body of literature that has found positive effects of organic farming on biodiversity (Lichtenberg et al., 2017), particularly to the small number of studies on bats (Park, 2015). Although studied through proxy, organic versus conventional studies allow us to understand the effects of synthetic agrochemical use on biodiversity. Synthetic agrochemicals reduce insect prey for insectivores, such as bats, and can potentially also have direct effects on them. Our results suggest that bat abundance and bat prey can be increased through policies that increase the extent of organic agricultural practices. Our results, combined with previous results, also suggest that bats can be promoted in agricultural landscapes by retaining forest and hedgerows.

Conflicts of interest

None.

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Appendix A. Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.biocon.2018.06.021.

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