Effects of organic farming and agricultural landscape
composition on relative bat diversity and abundance

by

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A thesis submitted to the Faculty of Graduate and Postdoctoral
Affairs in partial fulfillment of the requirements for the degree of

Master of Science

in

Biology

Carleton University
Ottawa, Ontario

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Abstract

Some ways that agricultural areas have intensified, include increased agro-chemical inputs, use of annual row crops and agricultural extent. These changes would be expected to reduce insect prey for bats, causing smaller bat populations to be supported. Chapter 1 examines the influence that the proportion of the landscape in agriculture and the proportion of agricultural lands in annual crops (vs. perennial forage crops) has on relative bat abundance and diversity. We found that bat abundance was highest in landscapes that had a low proportion of agriculture and where the proportion of agriculture in annual crops was about equal to the proportion in perennial forage. Chapter 2 examines the influence of organic versus conventional farming practices using match-organic conventional soybean field pairs on bat diversity, bat abundance and bat prey abundance. We found organic fields had higher bat diversity, bat abundance and bat prey abundance than conventional fields.

Acknowledgements

First and foremost, I would like to thank my supervisors, Dr. Lenore Fahrig and Dr. Greg W. Mitchell, for patiently guiding me through the process of research. I am grateful to them for developing my overall research skills, and specifically for making me a better scientific writer. I started my MSc thinking I would never go on to do a PhD, and now they have compelled me to strongly consider it.

I would like to thank my other committee member, Dr. Charles Francis for guiding me and previous students in the world of bat research. Although Dr. Scott Wilson did not have an official role on my project, I received influential comments and support from him throughout.

The Geomatics and Landscape Ecology Research Laboratory (GLEL) has been an excellent group to be a part of. Hearing people's comments on papers during Friday discussions has always given me ideas and realizations about my thesis. I would like to thank Dan Bert for his help with ordering equipment and computer-related issues.

I would like to thank all the landowners who allowed me to conduct my research on their properties. Without them my second chapter would not have been possible. Sometimes it was scary how quickly they could tell that I did not grow up on a farm. I will have to work on that.

Lastly, I would like to thank my field assistants, friends and family, which seemed to cross over into these different roles during my project. During my first field season, I was helped by Michelle Vala and my husband, Laurens Put. During my second field season my friend, Patrick Gilhooly, moved to Ottawa for the season to be my assistant. I was also helped by Erik Pervin and an army of volunteers, including Jennifer Murray,

Sara Khan, Anon Rashid, Angelica Ramos and Xiomara Alfaro. I would like to thank my family, who have always been interested in what I study, even though their careers are completely different than mine.

My husband, Laurens, has supported me every step of the way. I would like to thank him for picking me up from the university at midnight when those pesky bugs took their time drying, making dinner for us when I worked late, giving me feedback on writing and analysis, listening to my worries, and all the other ways he helped me while I worked on my thesis.

My thesis was supported by an NSERC Discovery Grant to L. Fahrig and by Environment and Climate Change Canada.

Table of Contents

Abstract.....	ii
Acknowledgements	iii
Table of Contents	v
List of Tables	vii
List of Figures.....	viii
List of Appendices.....	xii
Chapter 1: Bats respond negatively to increases in the amount and homogenization of agricultural land cover	1
1.1 Abstract	1
1.2 Introduction	2
1.3 Methods.....	4
1.3.1 Overview	4
1.3.2 Study region	5
1.3.3 Landscape selection	5
1.3.4 Field data: bat recordings	8
1.3.5 Evaluating bat activity.....	9
1.3.6 Bat species identification	10
1.3.7 Landscape predictor variables.....	11
1.3.8 Statistical analysis	13
1.4 Results	15
1.5 Discussion.....	23
1.5.1 Conclusions	25
Chapter 2: Higher bat abundance and bat food abundance at organic than conventional soybean fields.....	26

2.1	Abstract	26
2.2	Introduction	27
2.3	Methods	29
2.3.1	Overview	29
2.3.2	Study region	30
2.3.3	Site selection	31
2.3.4	Field data collection: acoustic sampling for bats	33
2.3.5	Field data collection: black-light trap sampling for nocturnal aerial insects.....	36
2.3.6	Field data collection: measuring potentially confounding variables.....	38
2.3.7	Data analysis: effect of organic versus conventional farming on bat species richness and activity	39
2.3.8	Data analysis: effect of organic versus conventional farming on aerial insect abundance.....	39
2.3.9	Data analysis: relationship between bat species activity and aerial insects	40
2.4	Results	40
2.4.1	Effect of organic versus conventional farming on bat species richness and activity	40
2.4.2	Effect of organic versus conventional farming on insect abundance	42
2.4.3	Relationship between bat abundance and insect abundance	44
2.5	Discussion.....	45
Appendices.....		49
References		75

List of Tables

Table 1.1	Model estimates and associated measures from GLMMs predicting the effect of the proportion of the landscape in agriculture (Proportion agriculture) and the proportion of agriculture in annual crops (Annual crops / Agriculture) on number of bat species (species richness), total bat activity, activity of big brown bat, hoary bat, and little brown bat, presence/absence of eastern red bat, silver-haired bat, northern long-eared bat, and tri-colored bat (* indicates p-value <0.05, † indicates p-value <0.10). The estimated scale of effect that was used in each GLMM (see Figure 1.5) for the landscape predictors is indicated under 'Scale'. For proportion of agriculture in annual crops we either included a linear term only or a linear term and a quadratic term, determined by comparing the AICc values of GLMMs that included either the linear term only or a linear term and a quadratic term (see Appendix 1.E). If the GLMM with the quadratic term had a lower AICc value than the one without, then we included it in our final GLMM for that response variable.....	21
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List of Figures

- Figure 1.1** Focal point locations (black dots in centre of coloured circles) of the 32 agricultural landscapes in eastern Ontario where bat surveys were conducted using bat recorders. The inset indicates the city of Ottawa within Canada. The agricultural landscapes were located within 100 km of Ottawa. Landscapes that had more of their agricultural cover in annual crops than perennial forages are indicated in red 1 km-radius circles, and those that had more agriculture in forages than annual crops are indicated in blue 1 km-radius circles. 6
- Figure 1.2** Example landscapes with a 1 km radius extent depicting the variation in the proportion of the landscape in agriculture (red (annual crops) plus blue (perennial forage) areas) and the proportion of agriculture that is annual crops (red areas divided by red plus blue areas). In all, 32 agricultural landscapes were sampled for bats, to determine how bat species richness, total bat activity and individual bat species activity or presence are related to (1) the proportion of the landscape in agriculture and (2) the proportion of agriculture that is annual crops. Non-agriculture (white) areas in the landscapes are mainly forested..... 7
- Figure 1.3** Example of land cover in one of the 32 sample agricultural landscapes. Bat surveys were conducted at the centre focal point of the landscape. The land cover is mapped within each of 15 circular landscapes (0.125, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5 and 6 km radius), to estimate the scale of effect of landscape predictor variables on bat response variables. Land cover information is from the 2016 Annual Crop Inventory layer (AAFC 2017)..... 12

Figure 1.4 Relationship between total bat activity (number of passes) and bat feeding rate (total feeding buzzes). Bats vocalize feeding buzzes just prior to capturing an insect, which can be seen visually in acoustic recordings. As a result, feeding buzzes can be used to measure the number of insects captured by bats. Total bat activity is the total number of bat passes recorded at an acoustic recorder. At 32 agricultural landscapes, acoustic bat recorders were deployed twice for 3 to 4 nights each, from which 2 sampling nights were chosen from each round for bat identification analysis for a total of 4 sampling nights. In this plot, each point represents data from a landscape with the total feeding buzzes and total bat activity averaged across the 4 sampling nights..... 16

Figure 1.5 Estimation of the scale of effect of each of two landscape variables - the proportion of the landscape in agriculture (triangles) and the proportion of agriculture in annual crops (squares) - on bat richness and abundance response variables measured at the centre points of 32 landscapes. The estimated scale of effect is the spatial extent of the landscape within which the effect of the landscape predictor on the bat response is strongest, as indicated by the where the $\Delta AICc$ value equals 0 (vertical arrows). Filled-in symbols indicate statistical significance at the 0.05 level..... 19

Figure 1.6 Relationships between bat responses and landscape predictor variables - the proportion of the landscape in agriculture and the proportion of agriculture in annual crops - at their identified scales of effect (Figure 1.5). Each data point in the plots represents the data from one landscape (32 landscapes in total) averaged over four sampling nights, except for plots that use presence/absence, where there are 4 data points per landscape - one from each sampling night. Bat responses were measured at the centre of each landscape. Bat species richness is the number of different bat species recorded

during a survey. Total bat activity is the summed number of bat passes recorded during a survey. The estimated scale of effect for each landscape predictor variable with a given response variable (Figure 1.5) is indicated in brackets on the x-axis. The natural log was used in the plots for total bat activity, big brown bat activity, hoary bat activity and little brown bat activity. 20

Figure 2.1 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 aerial insect surveys. The inset indicates the location of the city of Ottawa in Canada. Matched organic-conventional pairs share the same number, where the organic site is in blue and the conventional site is in red. Matched organic-conventional pairs had similar a) proportions of agriculture, forest and shrubland, water and urban cover within 1 km, 2 km and 3 km of the soybean fields, b) field sizes and hedgerow lengths around the fields, and c) local habitat around the bat and insect sampling equipment. 31

Figure 2.2 Example layout of bat and insect 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 and ponds or rivers, at least 50 m from buildings and paved roads, and at least 25 m from the corners of the field. 34

Figure 2.3 Estimated effects of field type (organic versus conventional) on bat richness, cross-species activity and species-specific activity. The relationship for bat richness was modeled using a linear mixed model. The relationships for cross-species activity and

species-specific activity were modeled using generalized linear mixed models 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 richness, activity or presence is higher at organic than conventional sites in matched organic-conventional soybean field pairs (* indicates p-value <0.05, † indicates p-value <0.10)...... 41

Figure 2.4 Estimated effects of field type (organic versus conventional) on total insect abundance, abundance in each size class (< 5 mm, 5-10 mm, 10-15 mm and >15 mm) and abundance in each insect Order (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera and ‘other’). The relationships were modeled using generalized linear mixed models 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 matched organic-conventional soybean field pairs (* indicates p-value <0.05, † indicates p-value <0.10)...... 43

Figure 2.5 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). Samples where either bat acoustic data or insect data were missing are not included here (n=8). Bat activity was recorded using acoustic recorders. Insect samples were collected using black-light traps, which target nocturnal aerial insects. 44

List of Appendices

Appendix 1.A Land-use types in eastern Ontario, Canada, classified from the 2016 Annual Crop Inventory (AAFC 2017).....	49
Appendix 1.B Spearman's correlations between ordinal date (date of sampling) and average temperature, and landscape predictor variables.....	50
Appendix 1.C Moran's I test results for the number of bat species (species richness), total bat passes (total bat activity), activity of big brown bat, hoary bat, and little brown bat, and presence/absence of eastern red bat, silver-haired bat, northern long-eared bat, and tri-colored bat.....	51
Appendix 1.D Relationships between Shannon diversity of crops and agriculture in annual row crops at 0.125, 0.25, 0.5, 0.75, 1, 2, 3, 4, 5, 6 km radius extents in agricultural landscapes.....	52
Appendix 1.E Comparison of AICc values between GLMMs for each response variable that either included a linear term only or a linear term and a quadratic term for the proportion of agriculture in annual crops.....	53
Appendix 2.A Classification of land-use categories and comparison of local and landscape-level variables between organic and conventional soybean fields	53
Appendix 2.B Effectiveness of subsampling method of nocturnal aerial insect samples.....	56
Appendix 2.C Frequency distributions of bat species richness, bat activity, insect abundances and insect weights across 16 matched organic-conventional pairs (32 sites).....	60

Appendix 2.D Standardized partial regression coefficients of field type from models with insect weights as response variables.....	63
Appendix 2.E Standardized partial regression coefficients of soybean height from models with species richness, bat activity, insect abundances and insect weights as response variables	64
Appendix 2.F Model estimates and associated measures from models predicting the effect of field type on species richness, bat activity, insect abundance and insect weight.....	66
Appendix 2.G Model estimates and associated measures from models predicting the effect of field type on species richness, bat activity, insect abundance and insect weight without soybean height as a confounding variable.....	70
Appendix 2.H Relationships between bat activity and field structure and landscape composition variables	73
Appendix 2.I Relationship between soybean height and average insect weight.....	74

Chapter 1: Bats respond negatively to increases in the amount and homogenization of agricultural land cover

1.1 Abstract

Changes in agricultural landscapes due to intensification, such as loss of natural areas, loss of grazing lands to annual row crops, and increased use of pesticides, have led to widespread declines in biodiversity. Bats are expected to respond negatively to agricultural intensification because of reductions in prey abundance and roosting habitat availability. We measured relative bat abundance with acoustic bat recorders in landscapes that varied in (1) the proportion of agriculture and (2) the proportion of agriculture that is in annual row crops vs. perennial forages (pasture and hay). We predicted that relative bat abundance would be highest where (1) the proportion of agriculture was low and (2) the agriculture was dominated by perennial forage. Consistent with our first prediction, the abundance or presence of four bat species, total bat abundance and bat species richness declined with increasing agricultural cover. Counter to our second prediction, we did not find a negative relationship between species richness or relative bat abundance or presence and the proportion of agricultural land that is in annual row crops. Instead we found that the abundance of three bat species, total bat abundance and bat species richness were greatest where the proportion of agriculture in annual crops was about equal to the proportion in perennial forage. Based on these results, we suggest that bat abundance and richness can be increased in agricultural landscapes by reducing the conversion of natural areas to agriculture and by maintaining a balance of perennial forage and annual crop agricultural cover types.

1.2 Introduction

Agricultural intensification is occurring globally. Intensification involves (i) loss of natural areas to agriculture, (ii) loss of grazing lands to annual crops and (iii) increasing intensity of crop management, e.g. increased use of pesticides (Matson et al. 1997). This increase in intensity of crop management is partly due to a gradual replacement of perennial forage crops, such as pasture and hay, with annual row crops, such as corn and soybean (Bianchi et al. 2006, Blank et al. 2016). Perennial forage lands (often termed extensive agriculture) receive very little inputs (e.g. herbicide), are disturbed infrequently, and contain perennial plant species (Boutin and Jobin 1998). Conversely, annual row crops (often termed intensive agriculture) typically receive chemical inputs, are disturbed more frequently (e.g. tillage), and fields are actively managed to contain a single annual crop (Tschardt et al. 2005, Boehmel et al. 2008). Agriculture makes up the largest land use worldwide at about 38% (FAOSTAT 2017) and the conversion of natural areas to agriculture increased by approximately 3% between 1985 to 2005 (Foley et al. 2011).

Bats should be sensitive to these shifts in agriculture, because natural areas are expected to have greater abundances of insect prey than agricultural areas, and high-intensity annual crops typically use intensive pest management regimes that should reduce insect prey abundance (Meehan et al. 2011). Pest management regimes used on high-intensity annual crops may decrease insects directly through the use of insecticides, and indirectly through the removal of weeds either manually or using herbicide (Stoate et al. 2001, Robinson and Sutherland 2002). A greater variety of vegetation in a field should

support more insect diversity (Knops et al. 1999), because of the availability of more varied habitats (Tews et al. 2004). Insectivorous bats should benefit from greater insect diversity, as higher diversity should provide a more stable level of prey availability throughout a night because different insect species can be active at different times during the night (Rydell et al. 1996), and throughout a season (Davidai et al. 2015). Natural areas might also provide more roosting habitat (trees) than agricultural areas, particularly for bat species that do not roost in human-made structures such as houses. An understanding of how changes in agricultural landscapes affect bat populations is important for efforts in conserving bat populations, particularly in areas where white-nose syndrome is causing declines. Insectivorous bats also provide ecosystem services to farmers by removing insect pests and preventing pest outbreaks (Boyles et al. 2011, Kunz et al. 2011).

From 2001 to 2016 in Ontario, Canada, high-intensity annual crops, primarily corn and soybean, increased by 11.4%, and low-intensity perennial forage lands decreased by 34.3% (OMAFRA 2017), reflecting similar trends in other areas globally (Monfreda et al. 2008, Dauber et al. 2010, Haughton et al. 2015). In Ontario, hay land is typically planted in alfalfa once every 3 years, and the fields receive no inputs (Farm and Food Care Ontario 2015). In contrast, annual row crops are planted each season and often receive both herbicides and insecticides. For example, in Ontario in 2013, 86.2% of all pesticides used were applied to annual row crops and only 0.6% were applied to perennial forage land (Farm and Food Care Ontario 2015). These changes in agricultural practices through time, combined with recent precipitous population declines in bats in North America (Frick et al. 2010, Hammerson et al. 2017), point to a need to understand

how land use practices and land cover can be best managed to support remaining bat populations.

Our objective was to measure relative bat abundance and diversity in a set of landscapes selected such that the proportion of the landscape in agriculture and the proportion of agricultural lands in annual crops (vs. perennial forage crops) varied independently. As described above, forest cover provides roosting habitat for bats, and in eastern Ontario, landscapes with more agriculture typically have less forest (Wilson et al. 2017), so we expected lower relative bat abundance in landscapes with a higher proportion of agricultural land cover. With respect to our second objective, vegetation is generally more diverse in perennial forage lands, which may give rise to a greater diversity of prey for bats relative to annual crop fields. As a result, we expected more bats in landscapes where the agriculture is dominated by perennial forages relative to landscapes where the agriculture is dominated by annual crops. We predicted that bat species richness, abundance, and individual species presence would be highest in landscapes where (1) the proportion of agriculture was low and (2) the agriculture was dominated by perennial forage agriculture.

1.3 Methods

1.3.1 Overview

To test these predictions we used acoustic recordings to estimate relative bat species richness, total bat abundance and individual bat species abundance or presence in 32 landscapes that varied in (1) the proportion of agriculture and (2) the proportion of agriculture that was in annual row crops vs. perennial forages (pasture and hay). The

latter was measured as the amount of cover in annual crops divided by the total amount of agricultural cover, as in our region almost all non-annual crop cover is perennial forage. Total bat activity was used as an index of total bat abundance. We then performed generalized linear mixed models (GLMM) with bat species richness, total bat activity, species-specific activity or presence as response variables and the proportion of the landscape in agriculture and the proportion of agriculture in annual crops as predictor variables.

1.3.2 Study region

We conducted our study in eastern Ontario, to the southwest of Ottawa, Canada. During the 18th and 19th centuries, extensive forest clearing took place in this area to make space for agricultural lands, but within the past 70 years, some forest regeneration has occurred. For example, from 2001 to 2016 in Ontario, agricultural area decreased by 8.6% (OMAFRA 2017). In the 1970s, corn and soybean were first grown in the area, and now agricultural land in annual row crop production exceeds perennial forages. In 2016, the agricultural land in eastern Ontario was composed of 370,919 ha of annual row crops and 297,661 ha of perennial forage land (pasture: 131,739 ha, hay: 165,922 ha) (OMAFRA 2017).

1.3.3 Landscape selection

32 landscapes were selected in eastern Ontario that varied in (1) the proportion of the landscape that was in agriculture and (2) the proportion of agriculture that was in annual row crops. Landscapes were circular areas with a 1 km radius each, centred on a focal point where bats were recorded (Figure 1.1 and 1.2). The focal point of each landscape was a vegetated edge of a country road. The proportions of land cover around

each focal point within the 1 km radius was calculated in ArcGIS 10.3.1 (ESRI 2015) using the 2013 Annual Crop Inventory (AAFC 2013) data layer.

Figure 1.1 Focal point locations (black dots in centre of coloured circles) of the 32 agricultural landscapes in eastern Ontario where bat surveys were conducted using bat recorders. The inset indicates the city of Ottawa within Canada. The agricultural landscapes were located within 100 km of Ottawa. Landscapes that had more of their agricultural cover in annual crops than perennial forages are indicated in red 1 km-radius circles, and those that had more agriculture in forages than annual crops are indicated in blue 1 km-radius circles.

Figure 1.2 Example landscapes with a 1 km radius extent depicting the variation in the proportion of the landscape in agriculture (red (annual crops) plus blue (perennial forage) areas) and the proportion of agriculture that is annual crops (red areas divided by red plus blue areas). In all, 32 agricultural landscapes were sampled for bats, to determine how bat species richness, total bat activity and individual bat species activity or presence are related to (1) the proportion of the landscape in agriculture and (2) the proportion of agriculture that is annual crops. Non-agriculture (white) areas in the landscapes are mainly forested.

We began with 313 candidate 1-km radius landscapes that were at least 2 km apart edge to edge and centred on vegetated sites along country roads in eastern Ontario within 100 km of the city of Ottawa. To narrow down our set of 313 candidate landscapes to a number that we could feasibly survey for bats, we first selected landscapes having at least 35% agriculture. This was also done because we noticed that landscapes with a low percentage of agriculture often contained only agriculture in perennial forage crops. From

these we then sub-selected landscapes to reduce variation in the proportions of the landscapes in water/wetland and developed area, to control for the effects that these land cover types have on bat activity (Geggie and Fenton 1985, Gehrt and Chelsvig 2003, 2004, Walters et al. 2007, Ethier and Fahrig 2011). Our remaining 87 landscapes had <25% water/wetland and <20% developed area within a 1 km radius of the focal point. We sub-selected from these landscapes to limit any correlation between our two landscape variables of interest, i.e. the proportion of the landscape in agriculture and the proportion of agriculture in annual crops ($R^2 = 0.0018$). This resulted in 32 landscapes (Figure 1.1 and 1.2). The focal points of the landscapes were on average 6.4 km (range 3.7 – 17.6 km) apart. Some focal points were moved slightly when in-situ verification revealed that the original locations lacked a nearby tree or shrub, which was necessary for equipment setup (below).

1.3.4 Field data: bat recordings

From June 13th to July 29th 2016, one bat recorder (SM2+BAT, Wildlife Acoustics) was deployed at the focal point of each of the 32 landscapes for two deployment periods. Each deployment period was 3 or 4 sampling nights long. From each deployment period, recordings from 2 nights were chosen for analysis. We selected the nights with 1) no precipitation and 2) the highest overnight temperatures because previous studies have found that precipitation and low overnight temperatures decrease bat activity (Erickson and West 2002). The time between deployment periods at each landscape was on average 20 days (range 7 – 27 days). We ensured that the order in which we visited the landscapes was independent of our two predictor variables, the

proportion of the landscape in agriculture and the proportion of agriculture in annual crops.

The bat recorders were on average 3.2 m from the edge of the road (range 0.8 – 10.8 m). The microphones were approximately 1.5 m above the ground, mounted on a tree or shrub between the road and a field edge (e.g., in a hedgerow), and pointed away from vegetation to avoid sound interference. Microphones were pointed either towards or away from the road, depending on which orientation best obscured the equipment from passers-by, to avoid tampering. The microphones we used (SMX-US, Wildlife Acoustics) have little directionality, so this would have had little effect on the number of bat recordings.

The bat recorders were programmed to record full-spectrum echolocation passes from sunset (~20:30 to 21:00) to sunrise (~5:15 to 5:45). When sound above 12 dB and between 1 and 96 kHz was detected, the unit was set to record for a minimum of 2 seconds and up to a maximum of 20 seconds if sound continued to be detected.

1.3.5 Evaluating bat activity

Each 2-20 second recording is called a bat "pass". A bat pass is made up of a quick succession of repetitive 'chirps'. Within a pass there can be three types of chirps: search-phase, approach-phase and feeding buzzes (Gillam 2007, Harvey et al. 2011). Search-phase chirps are made when a bat is commuting and searching for prey. If a bat finds a prey item, the chirps will increase in repetition (approach-phase chirps), and just prior to prey capture the bat will vocalize a "feeding buzz" (Schnitzler and Kalko 2001). A feeding buzz occurs when the chirps are so rapid that they are not easily distinguishable from each other (Gillam 2007).

1.3.6 Bat species identification

Search-phase chirps are consistently different for different bat species, while approach-phase chirps and feeding buzzes are not. Therefore, search-phase chirps are typically used to identify bat passes to species (Fenton and Bell, 1981). We identified bat species based on the acoustic parameters (below) of search-phase chirps. The program Spek 0.8.2 (General Public Licence 2017) was used to create visual representations of the bat passes we recorded. We first manually identified and eliminated any recording that did not contain bat chirps (false-positives: 10.9% of recordings). We included only search-phase passes containing at least two chirps above 16 dB, with a duration of 0.99 – 30 ms and a minimum frequency of 15 – 60 kHz, to remove weak and fragmented chirps. We measured the acoustic parameters of the chirps in the retained search-phase passes using Scan'R 1.6.0 (Binary Acoustic Technology 2008) and entered them in a quadratic discriminate function analysis model (QDFA) created by Ethier and Fahrig (2011). This model was created using 269 reference bat passes from throughout Ontario, obtained from the Fenton laboratory (Hooton 2010, Adams 2013), that belong to the seven species found in our study area: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), northern long-eared bat (*Myotis septentrionalis*), little brown bat (*Myotis lucifugus*), silver-haired bat (*Lasionycteris noctivagans*) and tri-colored bat (*Perimyotis subflavus*). The acoustic parameters in the model are chirp duration, interpulse interval, maximum frequency, minimum frequency, dominant frequency, slope, and curvature. The QDFA gives a posterior probability of the parameters of the chirp being attributed to each species in our region (0 – 1). Using the reference calls, the model has an overall correct species identification rate of 88.8%.

From each bat pass, we used the chirp with the highest signal-to-noise ratio in the QDFA. If the posterior probability was ≥ 0.95 for one species, the pass was assigned to that species. If the posterior probability was $0.50 - 0.95$ for one species, then we checked the posterior probability of the chirp with the second highest signal-to-noise ratio. If the posterior probability of the second chirp was > 0.5 for the same species as the first chirp, we assigned the pass to that species; otherwise, we classified the pass as “Unknown”. If the posterior probability of the chirp with the highest signal-to-noise ratio was < 0.5 for one species, we also classified the pass as “Unknown”. Four percent of all passes were categorized as "Unknown." We ran the QDFA model in R 3.2.3 (R Core Development Team, Boston, MA, USA).

1.3.7 Landscape predictor variables

The landscape predictor variables were the proportion of the landscape in agriculture and the proportion of agriculture in annual crops.

As described above, landscape selection was based on 1 km-radius landscapes. This radius was selected because it is within the average commuting distances between roosting and foraging habitat for our local bat species, as measured by radio-tracking studies (Brigham 1991, Campbell et al. 1996, Elmore et al. 2005). However, previous studies have shown that detection of landscape context effects on bats can vary with the landscape size used in the analysis, where some effects are strongest at extents larger than a 1-km radius (Ethier and Fahrig 2011, Monck-Whipp et al. 2018). We therefore estimated the landscape predictor variables within a range of spatial extents (15 extents ranging from 0.125 km to 6 km from each landscape’s focal point) using the 2016 Annual Crop Inventory (AAFC 2017) land cover data (Figure 1.3 and Appendix 1.A).

Figure 1.3 Example of land cover in one of the 32 sample agricultural landscapes. Bat surveys were conducted at the centre focal point of the landscape. The land cover is mapped within each of 15 circular landscapes (0.125, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5 and 6 km radius), to estimate the scale of effect of landscape predictor variables on bat response variables. Land cover information is from the 2016 Annual Crop Inventory layer (AAFC 2017).

Although we controlled for potential confounding variables through landscape selection (see above) and limited variation in overnight temperatures by selecting the 2 warmest nights from each deployment period, the bat surveys still varied considerably in survey date and overnight temperature (range 13.7 – 22.8 °C), which can affect bat activity (Erickson and West 2002). To determine whether these variables might confound the interpretation of our results, we performed Spearman’s correlations between the landscape predictor variables and ordinal date and average temperature (per hour from sunset to sunrise). The correlations ranged between -0.08 and 0.42 (Appendix 1.B). We

included any potentially confounding variables in our final GLMMs that were correlated with either of the landscape predictor variables to reduce the unexplained variation in our models.

1.3.8 Statistical analysis

To check for potential spatial autocorrelation of the response variables, we calculated Moran's I in ArcGIS 10.3.1 (ESRI 2015). We detected no significant spatial autocorrelation for any of our response variables (see Results).

To test our predictions, we performed GLMMs with bat species richness, total bat activity, species-specific activity or presence as response variables, the proportion of the landscape in agriculture, the proportion of agriculture in annual crops as predictor variables, and any potentially confounding variables that were significantly correlated to either of the landscape predictors, and landscape ID and recorder ID as random effects. As we did not know a priori the most appropriate spatial extent for measuring the landscape predictors (their scales of effect), we conducted the GLMMs in two stages. First, for each response variable and each landscape predictor we did a series of 15 models, one model for each of the 15 spatial extents, with the landscape predictor measured at that spatial extent, and including landscape ID and recorder ID. The estimated scale of effect for each response-predictor combination was then the landscape radius for that landscape predictor variable with the lowest small-sample Akaike Information Criterion (AICc). Once the scale of effect was estimated for each response-predictor combination, the predictions were tested by conducting a GLMM for each response variable, containing both landscape predictor variables, each measured at its estimated scale of effect, any potential confounding variable(s) that were correlated to a

landscape predictor at its estimated scale of effect, and landscape ID and recorder ID as random effects. The GLMMs for the species richness of bats used a Poisson distribution. For the GLMMs for total bat activity and the activity of the three most common bats (big brown bat, hoary bat, little brown bat) we used a negative binomial distribution. Logistic regressions were used on presence/absence data for the four least common bats (eastern red bat, northern long-eared bat, silver-haired bat, tri-colored bat). Recorder ID was not used as a random effect in any models with northern long-eared bat presence due to issues with model convergence. For each model that used a Poisson or negative binomial distribution, we assessed the homogeneity of variance by examining the plots of the residuals versus fitted values. We conducted these analyses in R version 3.2.4 (R Core Team 2017) using the glmmADMB (Skaug et al. 2016), lme4 (Bates et al. 2015), MASS (Venables and Ripley 2002) and MuMIn (Barton 2014) packages. The data set used in our analysis is available through Mendeley Data (Put et al., 2017). Prediction 1 would be supported if the proportion of the landscape in agriculture had a negative relationship with the bat response variables. Prediction 2 would be supported if the proportion of agriculture in annual crops had a negative relationship with the bat response variables.

After visually inspecting the plots between the proportion of agriculture in annual crops and the bat response variables we noticed that some relationships had a quadratic-shaped pattern. Since different nocturnal aerial insects can be pests of particular crop types (Davidai et al. 2015), landscapes with a greater number of crop types may have greater availability of bat prey throughout the season. With few types of crops commonly planted in our study area (OMAFRA 2017), a landscape with a mixture of perennial forages and annual row crops would have high Shannon diversity of crops at small spatial

scales (Appendix 1.D). However, since the land cover data (AAFC 2017) we used did not separate pasture and hay land, values for Shannon diversity of crops may be artificially lower in landscapes with low agriculture in annual row crops (e.g. high agriculture in perennial forage). For these response variables we tested whether a quadratic term for the proportion of agriculture in annual crops would better predict the responses we observed. Finally, we plotted the relationship between bat activity (number of passes) and bat feeding rate (number of feeding buzzes) per site to determine the extent to which bat activity reflects feeding success.

1.4 Results

Over all 128 acoustic surveys within the 32 landscapes, we recorded 13,245 bat passes. All seven species present in the study area were represented, with the majority of passes identified as hoary bat (56.7%) and big brown bat (35.4%). There was an average of 103.5 bat passes per acoustic survey (range 0 – 785), and an average of 3.3 species per survey (range 0 – 7). 531 bat passes were classified as ‘Unknown’, making up 4% of the total bat passes we recorded. As a result, 12,714 (96%) were identified to one of seven species. No significant spatial autocorrelation was detected for any of our response variables (Moran’s I from -0.12 to 0.13, $P > 0.05$) (Appendix 1.C). There was a strong positive correlation across acoustic surveys ($r = 0.85$) between total bat activity and total feeding buzzes (Figure 1.4), indicating that in locations with greater bat activity, bats are foraging more.

Figure 1.4 Relationship between total bat activity (number of passes) and bat feeding rate (total feeding buzzes). Bats vocalize feeding buzzes just prior to capturing an insect, which can be seen visually in acoustic recordings. As a result, feeding buzzes can be used to measure the number of insects captured by bats. Total bat activity is the total number of bat passes recorded at an acoustic recorder. At 32 agricultural landscapes, acoustic bat recorders were deployed twice for 3 to 4 nights each, from which 2 sampling nights were chosen from each round for bat identification analysis for a total of 4 sampling nights. In this plot, each point represents data from a landscape with the total feeding buzzes and total bat activity averaged across the 4 sampling nights.

The proportion of the landscape in agriculture ranged from 36.9% to 84.3% and the proportion of agriculture in annual crops ranged from 1.3% to 96.9% at the 1 km radius landscape extent (used to select the landscapes). The scales of effect of the landscape predictors on the response variables ranged from 0.125 km to 4.5 km for the proportion of the landscape in agriculture and 0.25 km to 6 km for the proportion of agriculture in annual crops (Figure 1.5). We acknowledge that for many of the relationships the delta AICc values were small, so the scale of effect was often not well

estimated. The correlation between the proportion of the landscape in agriculture and the proportion of agriculture in annual crops ranged from -0.06 to 0.53, and was highest at the largest spatial extents (Appendix 1.B).

Consistent with our first prediction, bat species richness, total bat activity and the activity levels or presences of 4 bat species had significant ($p < 0.05$) or near significant ($p < 0.1$) negative responses to the proportion of the landscape in agriculture, and the direction of the effect was negative for all the other species except silver-haired bats (Figure 1.6 and Table 1.1).

Contrary to our second prediction, the activity levels or presence of bats was not highest in landscapes with agriculture dominated by perennial forage crops. Bat species richness, total bat activity and 3 bat species had significant ($p < 0.05$) or near significant ($p < 0.1$) quadratic responses to the proportion of agriculture that is annual crops, where the activity was greatest where there was a combination of agriculture in annual crops and perennial forage crops (Figure 1.6 and Table 1.1).

Figure 1.5 Estimation of the scale of effect of each of two landscape variables - the proportion of the landscape in agriculture (triangles) and the proportion of agriculture in annual crops (squares) - on bat richness and abundance response variables measured at the centre points of 32 landscapes. The estimated scale of effect is the spatial extent of the landscape within which the effect of the landscape predictor on the bat response is strongest, as indicated by the where the $\Delta AICc$ value equals 0 (vertical arrows). Filled-in symbols indicate statistical significance at the 0.05 level.

Figure 1.6 Relationships between bat responses and landscape predictor variables - the proportion of the landscape in agriculture and the proportion of agriculture in annual crops - at their identified scales of effect

(Figure 1.5). Each data point in the plots represents the data from one landscape (32 landscapes in total) averaged over four sampling nights, except for plots that use presence/absence, where there are 4 data points per landscape - one from each sampling night. Bat responses were measured at the centre of each landscape. Bat species richness is the number of different bat species recorded during a survey. Total bat activity is the summed number of bat passes recorded during a survey. The estimated scale of effect for each landscape predictor variable with a given response variable (Figure 1.5) is indicated in brackets on the x-axis. The natural log was used in the plots for total bat activity, big brown bat activity, hoary bat activity and little brown bat activity.

Table 1.1 Model estimates and associated measures from GLMMs predicting the effect of the proportion of the landscape in agriculture (Proportion agriculture) and the proportion of agriculture in annual crops (Annual crops / Agriculture) on number of bat species (species richness), total bat activity, activity of big brown bat, hoary bat, and little brown bat, presence/absence of eastern red bat, silver-haired bat, northern long-eared bat, and tri-colored bat (* indicates p-value <0.05, † indicates p-value <0.10). The estimated scale of effect that was used in each GLMM (see Figure 1.5) for the landscape predictors is indicated under ‘Scale’. For proportion of agriculture in annual crops we either included a linear term only or a linear term and a quadratic term, determined by comparing the AICc values of GLMMs that included either the linear term only or a linear term and a quadratic term (see Appendix 1.E). If the GLMM with the quadratic term had a lower AICc value than the one without, then we included it in our final GLMM for that response variable.

Response variable	Predictor variable	Scale	Estimate	SE	z	P
Species richness	Intercept		1.469	0.40	3.67	< 0.001 *
	Proportion agriculture	1 km	-0.759	0.42	-1.82	0.069 †
	Annual Crops / Agriculture	1 km	1.538	0.82	1.88	0.060 †
	Annual Crops / Agriculture ²	1 km	-1.568	0.82	-1.91	0.056 †
	Average temperature		-0.005	0.02	-0.26	0.796
Total bat activity	Intercept		4.223	0.60	7.07	< 0.001 *
	Proportion agriculture	0.125 km	-1.089	0.62	-1.76	0.079 †
	Annual Crops / Agriculture	1 km	4.785	2.05	2.33	0.020 *
	Annual Crops / Agriculture ²	1 km	-5.021	2.06	-2.44	0.015 *
Big brown bat	Intercept		3.348	0.82	4.11	< 0.001 *
	Proportion agriculture	0.125 km	-1.509	0.87	-1.74	0.082 †
	Annual Crops / Agriculture	1 km	5.066	2.90	1.75	0.080 †
	Annual Crops / Agriculture ²	1 km	-5.507	2.90	-1.90	0.058 †
Eastern red bat	Intercept		1.877	2.30	0.81	0.420
	Proportion agriculture	1.5 km	-2.536	2.96	-0.86	0.390
	Annual Crops / Agriculture	2 km	-1.920	1.80	-1.07	0.290
	Average temperature		-0.084	0.12	-0.72	0.470
Hoary bat	Intercept		3.579	0.53	6.78	< 0.001 *
	Proportion agriculture	0.125 km	-0.966	0.53	-1.82	0.068 †
	Annual Crops / Agriculture	1 km	4.541	1.76	2.58	0.010 *
	Annual Crops / Agriculture ²	1 km	-4.646	1.76	-2.64	0.008 *
Little brown bat	Intercept		1.454	1.64	0.89	0.374
	Proportion agriculture	1 km	-4.860	2.15	-2.27	0.023 *
	Annual Crops / Agriculture	2 km	7.698	4.30	1.79	0.073 †
	Annual Crops / Agriculture ²	2 km	-8.063	4.68	-1.72	0.085 †
	Average temperature		-0.020	0.06	-0.34	0.732
Northern long-eared bat	Intercept		0.370	1.29	0.29	0.774
	Proportion agriculture	0.75 km	-4.233	1.99	-2.13	0.034 *
	Annual Crops / Agriculture	0.5 km	1.110	0.82	1.36	0.175
Silver-haired bat	Intercept		-7.354	3.73	-1.97	0.049 *
	Proportion agriculture	4.5 km	0.500	2.55	0.20	0.844
	Annual Crops / Agriculture	0.25 km	3.381	3.40	1.00	0.320
	Annual Crops / Agriculture ²	0.25 km	-3.180	3.10	-1.03	0.305
	Ordinal date		0.028	0.02	1.38	0.168
Tri-colored bat	Intercept		-12.191	5.24	-2.33	0.020 *
	Proportion agriculture	1 km	-3.351	3.45	-0.97	0.332
	Annual Crops / Agriculture	6 km	0.451	1.90	0.24	0.813
	Ordinal date		0.084	0.03	2.99	0.003 *
	Average temperature		-0.199	0.12	-1.63	0.103

1.5 Discussion

We found support for our prediction that landscapes containing more agriculture would have fewer bats. There was greater species richness, higher total bat abundance, higher abundance of big brown bats, hoary bats and little brown bats, and a higher probability of presence for northern long-eared bats in landscapes with lower proportions of agriculture. Consistent with these findings, studies have found higher bat abundances closer to vegetated linear strips in agricultural landscapes (Estrada et al. 1993, Verboom and Huitema 1997, Boughey et al. 2011), and also found that agricultural landscapes with more hedgerows and woodlots have higher bat abundance (Verboom and Huitema 1997). These studies are consistent with our result of a negative effect of the proportion of a landscape in agriculture on bat abundance, because (i) landscapes with higher proportions of agriculture typically have larger field sizes (Roschewitz et al. 2005b, Fahrig et al. 2015) and thus fewer vegetated field boundaries, and (ii) landscapes with higher proportions of agriculture have less forest and other woody vegetation ($r = -0.88$ across our landscapes at 6-km radius).

Although the relationships between agricultural cover and the presence of eastern red bats and tri-colored bats were not significant, they were all negative. The relationship was positive for silver-haired bats, but also not significant. The weak relationships for these species may indicate that availability of roosting habitat may not be as important a factor limiting bat populations in our study area as we had thought, as most of these species depend on natural roosting sites (Campbell et al. 1996, Willis and Brigham 2005,

Limpert et al. 2007, Poissant et al. 2010), which would be reduced in landscapes containing more agriculture (and thus less forest).

We did not find support for our prediction that landscapes where the agriculture is dominated by perennial forages would have greater bat abundances. We suggest the most likely explanation for our results is that the perennial forages in our landscapes consisted of more hay land than pasture. Similar to annual row crop fields, hay land is typically planted with one crop species, whereas pasture can contain a number of plant species that would be expected to provide more varied habitat for insects supporting a greater diversity of insect species. If pasture does support greater bat abundances than hay land, and hay land supports similar bat abundances to annual row crops, then in our study area where there is less pasture than hay land, we might not expect a strong response of bats to the proportion of agriculture in annual row crops in the landscape. Note that we were unable to test this idea (post hoc) because our land cover data do not distinguish between pasture and hay land.

On the other hand, we did find a peaked relationship between the proportion of agriculture in annual row crops and species richness, total bat abundance and the abundance or presence of big brown bats, hoary bats and little brown bats, with the maxima occurring at about equal amounts of perennial forage and annual row crops. We suggest that bats may benefit from these landscapes through the combination of abundant short-term food in annual row crops due to insect pest outbreaks and greater insect diversity and stability through time in perennial forage fields. Perennial forage crops are disturbed less frequently than annual row crops, allowing natural enemies to persist year to year (Landis et al. 2000). With fewer natural enemies persisting through time in annual

crop fields, outbreaks are more common (Wissinger 1997). Bat abundances can respond to these crop pest outbreaks, as was found for the corn earworm moth (*Helicoverpa zea*) in Texas (Davidai et al. 2015). With higher insect diversity in perennial forage fields (Werling et al. 2014), there is more stability in insect populations through the season. Thus we speculate that in landscapes with a mixture of agriculture in annual row crops and perennial forage fields there is a higher availability of bat prey through time.

A potential concern in interpreting our results using bat activity levels as a measure of abundance is that, if bats spend more time searching for prey when prey are scarce, this could artificially inflate our bat abundance estimates (number of bat passes) in sites with low prey abundance. If true, this would call into question the relationships between agriculture and bat abundance that we detected. However, we argue that this not a problem in our study because bat activity was strongly positively correlated with the amount of prey captured (total feeding buzzes) (Figure 1.4), opposite what we would have seen if bat activity were elevated in low-prey sites.

1.5.1 Conclusions

Given our findings, we suggest that bat abundances can be increased in agricultural landscapes by reducing the conversion of natural areas to agriculture and maintaining a balance between perennial forages and annual row crops. A balance of perennial forages and annual row crops may benefit bats due to the combination of stable insect availability at perennial forage fields with short-term insect pest outbreaks at annual row crops which together would provide high availability of prey for bats in these landscapes.

Chapter 2: Higher bat abundance and bat food abundance at organic than conventional soybean fields

2.1 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 solved 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 through their greater bat prey availability.

2.2 Introduction

The use of agro-chemicals - pesticides and fertilizers - threatens biodiversity. Declines in plants (Roschewitz et al. 2005a, Geiger et al. 2010, Gaba et al. 2016), invertebrates (Benton et al. 2002, Geiger et al. 2010, Potts et al. 2010) and vertebrates (Benton et al. 2002, Boatman et al. 2004, Boone et al. 2007, Poulin et al. 2010, Köhler and Triebkorn 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, whereas 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. 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, Bengtsson et al. 2005, Fuller et al. 2005, Froidevaux et al. 2017), among agricultural crop species or sampling locations within a farm (Wickramasinghe et al. 2003, 2004, Batáry et al. 2010), and among landscape contexts (Gabriel et al. 2010, Winqvist et al. 2012, 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, Fuller et al. 2005, Norton et al. 2009), have more vegetated field margins (Wickramasinghe et al. 2003, Fuller et al. 2005, Norton et al. 2009), and are surrounded by more diverse landscapes (Bengtsson et al. 2005, 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 species 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 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. It is also important to understand other factors that contribute to reductions in bat population sizes in light of the presence of white-nose syndrome in our study area.

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 nocturnal aerial insects.

2.3 Methods

2.3.1 Overview

We estimated bat 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 bat and insect sampling equipment, and surrounding landscape composition measured as the proportion of the landscape in agriculture, forest and shrubland, water, and urban cover within 1 km, 2 km and 3 km of the field. At each field we sampled bats using bat recorders and insects using black-light traps. We performed generalized linear mixed modeling 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.

2.3.2 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; Figure 2.1). 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 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).

Figure 2.1 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 aerial insect surveys. The inset indicates the location of the city of Ottawa in Canada. Matched organic-conventional pairs share the same number, where the organic site is in blue and the conventional site is in red. Matched organic-conventional pairs had similar a) proportions of agriculture, forest and shrubland, water and urban cover within 1 km, 2 km and 3 km of the soybean fields, b) field sizes and hedgerow lengths around the fields, and c) local habitat around the bat and insect sampling equipment.

2.3.3 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 asking 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 km, 2 km and 3 km of each field using the 2016 Annual Crop Inventory (AAFC 2017) data layer.

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, Campbell et al. 1996, Elmore et al. 2005, Henderson and Broders 2008). We used a maximum distance of 18 km so that the fields would be in the same general region. We then created uniform points spaced 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 km, 2 km and 3 km of the fields using the 2016 Annual Crop Inventory (AAFC 2017) data layer. We then identified points that shared similar proportions of agriculture, forest and shrubland, water and urban cover at the 1 km, 2 km and 3 km radius landscape spatial extents to the organic field of interest. Within this set of candidate fields we then identified fields of similar field 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 according to the 2016 Annual Crop Inventory (AAFC 2017) data layer. We focused on fields that had been either soybean or corn, because these two crops 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 1) agriculture, forest and shrubland, water and urban cover within 1 km, 2 km and 3 km of the field, 2) field size and 3) hedgerow/treeline length. For one organic field, we redid the selection process to consider areas farther from the organic field of interest after finding that there were few options for potential matched conventional fields within 18 km of the organic field. All spatial analyses were performed in ArcGIS 10.4.1 (ESRI 2016).

Starting with the top-matched candidate conventional field for each organic field, we first confirmed that it would be planted with soybean in 2017 and would be conventionally farmed, 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 matched organic-conventional pairs were between 6.6 km and 25.4 km apart, with an average distance of 12.7 km. No significant differences were detected in the field structure and landscape composition variables between the matched organic-conventional field pairs (see Appendix 2.A).

2.3.4 Field data collection: 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) (Figure 2.2). The A and B survey locations at each field were at 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.

Figure 2.2 Example layout of bat and insect 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 and ponds or rivers, at least 50 m from buildings and paved roads, and at least 25 m from the corners of the field.

Between June 13th to 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 organic-conventional pairs x 2 fields per pair x 2 locations per field x 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). Matched organic-conventional pairs were surveyed on the same nights, so that they would experience similar overnight temperatures and precipitation (if any). The survey nights for each organic-conventional pair were an average of 23.8 days apart (min=13 days, max=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 seconds and up to a maximum of 20 seconds if sound continued to be detected.

A bat "pass" (each 2-20 second 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, Harvey et al. 2011). 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 2017). We eliminated bat passes that did not contain bat chirps, and we eliminated chirps from the bat passes if they were not search-phase chirps. The acoustic parameters of the chirps in the retained search-phase passes were measured using Scan'R 1.6.0 (Binary Acoustic Technology 2008). 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) 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 (*Lasiurus cinereus*), 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 QDFA model was run in R 3.3.2 (R Core Development Team, Boston, MA, USA).

2.3.5 Field data collection: black-light trap sampling for nocturnal aerial insects

We estimated nocturnal aerial insect abundance at the same time as our bat sampling, using two black-light traps (15 Watt - 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 (Figure 2.2). 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 recorded, 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), 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 (> 10mm) from the sample, as macro-moths are an important food source for bats (Clare et al. 2009, Valdez and Cryan 2009). 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 by 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 and every other insect that crossed the boundaries. We determined that 500 insects was sufficient to reliably extrapolate to the

contents of the rest of the sample (see Appendix 2.B). To extrapolate, we divided the insects counted by the number of grids counted, and then multiplied by the total number of grids.

2.3.6 Field data collection: 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 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 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. Previous sites have found a positive association between vegetation height and bat activity (Ford et al. 2005, Jung et al. 2012, Froidevaux et al. 2017). 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 confounding variable in all our models (below).

2.3.7 Data analysis: effect of organic versus conventional farming on bat species richness and activity

To test our prediction that bat richness and activity is higher at organic fields than conventional fields (within pairs), we performed generalized linear mixed modelling 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 organic-conventional pair. We used a normal distribution for bat species richness (Figure 2.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 (Figure 2.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 (Figure 2.C.1.). Logistic regressions were performed on presence/absence data for the two least common bat species (northern long-eared bat and tri-colored bat).

2.3.8 Data analysis: effect of organic versus conventional farming on aerial insect abundance

To test our prediction that aerial insect abundance is higher at organic fields than conventional fields (within pairs), we performed generalized linear mixed models (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 organic-conventional pair. All models used a negative binomial distribution (Figure 2.C.2.).

2.3.9 Data analysis: relationship between bat species activity and aerial insects

We performed Spearman's correlations between bat species activity and aerial insect abundance and between bat species activity and aerial 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. We conducted all statistical analysis in R version 3.3.2 (R Core Team 2017) using the glmmADMB (Skaug et al. 2016) package.

2.4 Results

2.4.1 Effect of organic versus conventional farming on bat species richness and activity

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 (2,642 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’, making up 3.2% of the total passes recorded. 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). Consistent with our prediction, bat species richness, total activity and activity levels for five bat species were significantly ($p < 0.05$) or near significantly ($p < 0.1$) greater at organic fields than conventional fields (Figure 2.3 and Table 2.F.1.). In addition, the direction of the effect was the same for the other two bat species. Based on the confidence intervals in Figure 2.3 for the cross-species model, organic fields had approximately 31-75% more bat passes per survey than conventional fields.

Figure 2.3 Estimated effects of field type (organic versus conventional) on bat richness, cross-species activity and species-specific activity. The relationship for bat richness was modeled using a linear mixed model. The relationships for cross-species activity and species-specific activity were modeled using

generalized linear mixed models 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 richness, activity or presence is higher at organic than conventional sites in matched organic-conventional soybean field pairs (* indicates p-value <0.05, † indicates p-value <0.10).

2.4.2 Effect of organic versus conventional farming on insect abundance

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%) and Coleoptera (11.9%), and in the 0–5 mm size class (87.3%). There was an average of 5,721 insects per sample (range 6 – 43,940).

Figure 2.4 Estimated effects of field type (organic versus conventional) on total insect abundance, abundance in each size class (< 5 mm, 5-10 mm, 10-15 mm and >15 mm) and abundance in each insect Order (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera and 'other'). The relationships were modeled using generalized linear mixed models 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 matched organic-conventional soybean field pairs (* indicates p-value <0.05, † indicates p-value <0.10).

Consistent with our prediction, total insect abundance, abundances of individual size classes, and abundances of individual Orders were significantly ($p < 0.05$) or near significantly ($p < 0.1$) higher at organic fields than conventional fields (Figure 2.4 and

Table 2.F.2.). Based on the confidence intervals in Figure 2.4, organic fields had approximately 41-114% more nocturnal aerial 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, so we have placed these results in the supplementary material (see Appendix 2.D and Table 2.F.3.).

2.4.3 Relationship between bat abundance and insect abundance

Bat abundance was positively correlated with total insect abundance ($r=0.32$, $p < 0.001$) and total insect weight ($r=0.47$, $p < 0.001$) (Figure 2.5).

Figure 2.5 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 ($n=120$). Samples where either bat acoustic data or insect data were missing are not included here ($n=8$). Bat activity was recorded using acoustic recorders. Insect samples were collected using black-light traps, which target nocturnal aerial insects.

2.5 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 richness, bat abundance and bat prey abundance was due to our highly structured approach to site selection, which limited the effects of confounding variables and avoided spatial autocorrelation. 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 (Wickramasinghe et al. 2003, 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).

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 weight and bat abundance was positive, but there was considerable unexplained variation. 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 (Jefferies 1972, Geluso et al. 1976, Clark et al. 1978). These highly toxic pesticides have been replaced by modern 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 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 bats 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 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 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. We found no relationship between average insect weight and soybean height (see Appendix 2.I), indicating the latter is more likely than the former (see Figure 2.E.2. and 2.E.3.). Alternatively, the increase in bat abundance and 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).

Even though we demonstrated effects of organic farming on bats independent of field and landscape attributes, these attributes are also known to affect bats. Therefore, bat abundance and richness can be increased not only by organic farming practices but also by modifications to field and landscape attributes. For example, 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. in review) and developed land cover (Dixon 2012, Coleman and Barclay 2013), and positive effects of hedgerows (Lentini et al. 2012), proximity to water (Russo and Jones 2003) and forest cover in the landscape (Heim et al. 2015) on bat abundance. Our data confirm these field and landscape effects, as the correlation between mean bat activity and hedgerow length per ha of field was 0.49 and between mean bat activity and forest cover was 0.36 - 0.41 (depending on spatial extent) (see Appendix 2.H). These correlations confirm the importance of controlling for these effects through our matched organic-conventional paired field study design, to isolate the effects of organic versus conventional farming. Our results, combined with previous results, suggest that bat abundance can be increased through policies that increase the extent of organic agricultural practices, and that alter fields and landscapes in ways that favour bats, eg. by reducing field sizes and retaining hedgerows.

Appendices

Appendix 1.A

Table 1.A.1 Land-use types in eastern Ontario, Canada, classified from the 2016 Annual Crop Inventory (AAFC 2017). For each class, the code used by the Annual Crop Inventory is given.

Land-use types	Code	AAFC land-cover classes
Agriculture	110	Grassland
	122	Pasture / Forages
	131	Fallow
	133	Barley
	136	Oats
	137	Rye
	145	Winter Wheat
	146	Spring Wheat
	147	Corn
	153	Canola / Rapeseed
	156	Safflower
	158	Soybeans
	162	Peas
	167	Beans
	179	Other Vegetables
	183	Cranberry
	185	Other Berry
	195	Buckwheat
Annual crops	133	Barley
	136	Oats
	137	Rye
	145	Winter Wheat
	146	Spring Wheat
	147	Corn
	153	Canola / Rapeseed
	156	Safflower
	158	Soybeans
	162	Peas
	167	Beans
Forages	179	Other Vegetables
	183	Cranberry
	185	Other Berry
	195	Buckwheat
	110	Grassland

	122	Pasture / Forages
Water	20	Water
	80	Wetland
Trees and shrubs	50	Shrubland
	210	Coniferous
	220	Broadleaf
	230	Mixedwood
Developed	34	Urban / Developed

Appendix 1.B

Table 1.B.1 Spearman's correlations between ordinal date (date of sampling) and average temperature, and landscape predictor variables - proportion of the landscape in agriculture and proportion of agriculture in annual crops, at landscape spatial extents (radii) estimated as the scale of effect for at least one response-predictor combination (see Figure 1.5). Correlations contain one data point for each landscape (n=32). For each landscape, the mean has been used for the values across sampling nights for ordinal date and average temperature. The correlations in bold indicate $p < 0.05$.

	Ordinal date	Average temperature	Annual crops / Agriculture				
			0.25 km	0.5 km	1 km	2 km	6 km
Ordinal date		0.31	0.19	0.17	0.20	0.30	0.38
Average temperature	0.31		0.14	0.20	0.19	0.22	0.19
Proportion agriculture	0.125 km	-0.08	0.19		-0.06		
	0.75 km	-0.07	0.26	0.01			
	1 km	0.11	0.35		0.30	0.35	0.33
	1.5 km	0.14	0.37			0.53	
	4.5 km	0.42	0.33	0.47			

Appendix 1.C

Table 1.C.1 Moran's *I* test results for the number of bat species (species richness), total bat passes (total bat activity), activity of big brown bat, hoary bat, and little brown bat, and presence/absence of eastern red bat, silver-haired bat, northern long-eared bat, and tri-colored bat. The Moran's *I* test was used to test the level of potential spatial autocorrelation of the response variables. Values near 0 indicate absence of spatial autocorrelation.

Response variable	Moran's <i>I</i>	z-score	P
species richness	-0.04	-0.04	0.97
total bat activity	-0.06	-0.30	0.77
big brown bat	-0.05	-0.20	0.84
eastern red bat	-0.05	-0.21	0.83
hoary bat	-0.06	-0.25	0.80
little brown bat	0.08	0.23	0.22
northern long-eared bat	-0.12	-0.83	0.41
silver-haired bat	0.13	1.54	0.12
tri-colored bat	-0.01	0.26	0.79

Appendix 1.D

Figure 1.D.1 Relationships between Shannon diversity of crops and agriculture in annual row crops at 0.125, 0.25, 0.5, 0.75, 1, 2, 3, 4, 5, 6 km radius extents in agricultural landscapes. Each data point in the

plots represents the land cover data from one landscape (32 landscapes in total) where bat surveys took place.

Appendix 1.E

Table 1.E.1 Comparison of AICc values between GLMMs for each response variable that either included a linear term only or a linear term and a quadratic term for the proportion of agriculture in annual crops. We did this comparison after noticing that our data plots between some response variables and the proportion of agriculture in annual crops appeared to show a peaked relationship instead of the predicted negative linear relationship. The AICc values indicated below are for the GLMM with the proportion of agriculture in annual crops at the landscape radius that was estimated as the scale of effect (Figure 1.5). In the final GLMMs we either included a linear term only or a linear term and a quadratic term depending on which of these GLMMs had the lowest AICc value.

Response variable	AICc - linear model	AICc - quadratic model
species richness	470.3 (2 km)	470.2 (1 km)
total bat activity	1407.4 (0.5 km)	1404.2 (1 km)
big brown bat	1113.9 (0.5 km)	1112.8 (1 km)
eastern red bat	140.9 (2 km)	143.0 (2km)
hoary bat	1261.5 (2.5 km)	1257.8 (1 km)
little brown bat	400.9 (6 km)	400.3 (2 km)
northern long-eared bat	111.7 (0.5 km)	112.1 (1 km)
silver-haired bat	140.0 (1.5 km)	137.9 (0.25 km)
tri-colored bat	150.0 (6 km)	150.3 (1 km)

Appendix 2.A Classification of land-use categories and comparison of local and landscape-level variables between organic and conventional soybean fields.

Table 2.A.1 Land-use types in eastern Ontario and western Québec, Canada, classified from the 2016 Annual Crop Inventory (AAFC 2017) into 4 general land-use types of interest – agriculture, water, trees and shrubs, and developed land. For each class, the code used by the Annual Crop Inventory is given.

Land-use types	Code	AAFC land-cover classes
Agriculture	110	Grassland
	122	Pasture / Forages
	131	Fallow
	133	Barley
	136	Oats
	137	Rye
	138	Spelt
	141	Switchgrass
	142	Sorghum
	145	Winter Wheat
	146	Spring Wheat
	147	Corn
	153	Canola / Rapeseed
	156	Safflower
	157	Sunflower
	158	Soybeans
	162	Peas
	167	Beans
	176	Tomatoes
	177	Potatoes
	179	Other Vegetables
	182	Blueberry
	183	Cranberry
	185	Other Berry
	188	Orchards
	189	Other Fruits
	190	Vineyards
	191	Hops
	194	Nursery
	195	Buckwheat
	197	Hemp
	199	Other Crops
Water	20	Water
	80	Wetland
Trees and shrubs	50	Shrubland
	210	Coniferous
	220	Broadleaf
	230	Mixedwood
Developed	34	Urban / Developed

Figure 2.A.1 Box plots of field structure and landscape composition variables in organic and conventional soybean fields. These variables were controlled for in each matched organic-conventional pair during site selection. Matched organic-conventional soybean fields were paired to have similar a) field sizes (ha), b)

hedgerow lengths, and c) proportions of agriculture, forest and shrubland, urban and water within 1 km, 2 km and 3 km of the soybean fields.

Table 2.A.2 Comparison of field structure and landscape composition variables between organic and conventional soybean fields. The landscape composition variables were measured within 1 km, 2 km and 3 km of each soybean field.

	metric	organic			conventional		
		mean (SD)	min	max	mean (SD)	min	max
	field size (ha)	10.9 (7.4)	3.0	27.2	11.4 (7.3)	3.3	24.3
	hedgerow length (m)	791.9 (596.1)	0.0	2138.6	814.9 (634.3)	6.6	2400.8
proportion of	agriculture (1 km)	72.9 (12.9)	52.3	93.8	74.9 (13.5)	49.4	96.4
	agriculture (2 km)	67.9 (16.5)	32.3	87.8	69.8 (16.6)	38.7	92.9
	agriculture (3 km)	64.2 (18.3)	25.8	86.9	66.2 (17.5)	35.8	89.9
	forest (1 km)	19.7 (12.1)	1.6	42.9	19.3 (13.4)	0.3	46.8
	forest (2 km)	22.8 (14.6)	2.5	57.2	22.9 (15.3)	2.6	49.9
	forest (3 km)	24.6 (14.0)	2.5	46.8	25.0 (14.5)	6.3	51.9
	urban (1 km)	3.7 (2.4)	0.9	9.5	3.1 (1.8)	0.9	7.5
	urban (2 km)	5.1 (4.4)	1.0	18.1	3.7 (2.3)	1.6	9.3
	urban (3 km)	5.5 (4.7)	2.0	20.7	4.4 (3.1)	1.7	11.7
	water (1 km)	1.1 (1.0)	0.1	4.3	1.1 (1.1)	0.0	3.4
	water (2 km)	2.1 (2.0)	0.3	7.9	2.0 (2.3)	0.1	8.8
	water (3 km)	3.7 (4.1)	0.3	14.2	2.7 (3.5)	0.3	12.7

Appendix 2.B Effectiveness of subsampling method of nocturnal aerial insect samples.

Three samples were selected to test whether the subsampling method was effective. After subsampling each sample, we counted the rest of the contents of the three samples. The samples contained the following number of insects in total: sample one – 794, sample

two – 3103, sample three – 3094. ‘Subsample’ (in blue) represents the portion of the sample that was subsampled (at least 500 insects), and ‘Total’ (in green) represents the complete contents in the sample. To subsample, the sample was put in a standardized container over a numbered grid. We chose grids to sample at random, and stopped subsampling once 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 and every other insect that crossed the boundaries.

Figure 2.B.1 The proportion of insects from each size class in the subsample compared to the whole sample using three samples where the subsampling method was tested.

Figure 2.B.2 The proportion of insects from each Order in the subsample compared to the whole sample using three samples where the subsampling method was tested.

Figure 2.B.3 The proportion of the total dry weight by Order in the subsample compared to the whole sample using three samples where the subsampling method was tested. The Lepidoptera > 10 mm are not included in this figure, and the Lepidoptera < 10 mm in sample 1 are also not included.

Appendix 2.C Frequency distributions of bat species richness, bat activity, insect abundances and insect weights across 16 matched organic-conventional pairs (32 sites).

Figure 2.C.1 Frequency distributions of bat species richness/sample (a) and bat passes/sample, for each of the seven bat species in our study (b-h). A “sample” refers to the recordings collected from one bat recorder at either location A or B at a field over one night.

Figure 2.C.2 Frequency distributions of total insect abundance/sample (a), insect abundance/sample of four size classes (b-e), and insect abundance/sample of six insect orders and other category (f-l). A “sample” refers to the insects collected from one black-light trap at either location A or B at a field over one night.

Figure 2.C.3 Frequency distributions of total insect dry weight/sample (a), and insect dry weight/sample of four insect orders and other category (f-l). A “sample” refers to the insects collected from one black-light trap at either location A or B at a field over one night.

Appendix 2.D Standardized partial regression coefficients of field type from models with insect weights as response variables.

Figure 2.D.1 Estimated effects of field type at matched organic-conventional soybean pairs on total insect dry weight and dry weight in insect Orders (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera and 'other'). The relationships were modeled using GLMMs with soybean height as a confounding variable, recorder location (A or B) nested in organic-conventional pair as random effects, and a negative binomial distribution. Positive slopes indicate that insect abundance is higher at organic sites in matched organic-conventional soybean pairs.

Appendix 2.E Standardized partial regression coefficients of soybean height from models with species richness, bat activity, insect abundances and insect weights as response variables.

Figure 2.E.1 Estimated bat species richness and cross-species effects of soybean height (cm) at matched organic-conventional soybean pairs. The bat species richness relationship was modeled using a linear mixed model with recorder location (A or B) nested in organic-conventional pair as random effects. The cross-species relationships were modeled using GLMMs with bat species as a fixed effect and recorder location (A or B) nested in organic-conventional pair as random effects. We also show the modeled relationships of field type on the individual species of bats in our study area. All models included field type as a fixed effect and soybean height as a confounding variable. Positive slopes indicate that bat richness, activity or presence is higher at soybean fields with taller soybean.

Figure 2.E.2 Estimated effects of soybean height (cm) at matched organic-conventional soybean pairs on total insect abundance, abundance in size classes (< 5 mm, 5-10 mm, 10-15 mm and >15 mm) and abundance in insect Orders (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera and 'other'). The relationships were modeled using GLMMs with field type as a fixed effect, soybean height as a confounding variable and recorder location (A or B) nested in organic-conventional pair as random effects. Positive slopes indicate that insect abundance is higher at soybean fields with taller soybean.

Figure 2.E.3 Estimated effects of soybean height (cm) at matched organic-conventional soybean pairs on total insect dry weight and dry weight in insect Orders (Coleoptera, Diptera, Lepidoptera, Trichoptera and ‘other’). The relationships were modeled using GLMMs with field type as a fixed effect, soybean height as a confounding variable and recorder location (A or B) nested in organic-conventional pair as random effects. Positive slopes indicate that insect abundance is higher at soybean fields with taller soybean.

Appendix 2.F Model estimates and associated measures from models predicting the effect of field type on species richness, bat activity, insect abundance and insect weight.

Table 2.F.1 Estimates and associated measures from models estimating the effect of field type on the number of bats species (species richness), cross-species activity, activity of big brown bat, eastern red bat, hoary bat, little brown bat and silver-haired bat, and presence/absence of northern long-eared bat and tri-colored bat (* indicates p-value <0.05, † indicates p-value <0.10).

Response variable	Predictor variable	Estimate	SE	z	P
species richness	Intercept	1.24	0.07	16.82	< 0.001 *
	Field type - organic	0.17	0.10	1.81	0.070 †
	Soybean height (cm)	0.12	0.05	2.55	0.011 *
cross-species	Intercept	2.24	0.24	9.26	< 0.001 *
	Eastern red bat	-2.59	0.18	-14.37	< 0.001 *
	Hoary bat	1.79	0.15	11.94	< 0.001 *
	Little brown bat	-1.72	0.16	-10.46	< 0.001 *
	Northern long-eared bat	-4.28	0.24	-17.74	< 0.001 *
	Silver-haired bat	-2.86	0.18	-16.01	< 0.001 *
	Tri-colored bat	-3.19	0.19	-16.46	< 0.001 *
	Field type - organic	0.53	0.11	4.80	< 0.001 *
	Soybean height (cm)	0.37	0.06	5.97	< 0.001 *
big brown bat	Intercept	2.07	0.37	5.54	< 0.001 *
	Field type - organic	0.57	0.22	2.53	0.012 *
	Soybean height (cm)	0.43	0.13	3.41	< 0.001 *
eastern red bat	Intercept	-0.35	0.26	-1.37	0.172
	Field type - organic	0.47	0.28	1.68	0.093 †
	Soybean height (cm)	0.59	0.17	3.49	< 0.001 *
hoary bat	Intercept	4.04	0.23	17.64	< 0.001 *
	Field type - organic	0.33	0.16	2.10	0.036 *
	Soybean height (cm)	0.39	0.09	4.44	< 0.001 *
little brown bat	Intercept	0.14	0.35	0.39	0.694
	Field type - organic	0.97	0.33	2.90	0.004 *
	Soybean height (cm)	0.22	0.18	1.20	0.231
northern long-eared bat	Intercept	-2.15	0.49	-4.42	< 0.001 *
	Field type - organic	0.08	0.58	0.13	0.890
	Soybean height (cm)	0.04	0.30	0.14	0.890
silver-haired bat	Intercept	-0.78	0.39	-2.01	0.044 *
	Field type - organic	0.78	0.37	2.09	0.037 *
	Soybean height (cm)	0.45	0.21	2.12	0.034 *
tri-colored bat	Intercept	-0.74	0.30	-2.49	0.013 *
	Field type - organic	0.36	0.40	0.90	0.367
	Soybean height (cm)	0.24	0.20	1.18	0.237

Table 2.F.2 Model estimates and associated measures from GLMMs estimating the effect of field type on total insect abundance, abundance in size classes (< 5 mm, 5-10 mm, 10-15 mm and >15 mm) and abundance in insect Orders (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera and ‘other’) (* indicates p-value <0.05, † indicates p-value <0.10).

Response variable	Predictor variable	Estimate	SE	z	P
total abundance	Intercept	7.98	0.20	40.37	< 0.001 *
	Field type - organic	0.78	0.19	4.18	< 0.001 *
	Soybean height (cm)	0.65	0.12	5.41	< 0.001 *
< 5 mm	Intercept	7.80	0.21	38.13	< 0.001 *
	Field type - organic	0.83	0.20	4.27	< 0.001 *
	Soybean height (cm)	0.66	0.13	5.18	< 0.001 *
5 - 10 mm	Intercept	5.95	0.20	29.25	< 0.001 *
	Field type - organic	0.39	0.18	2.22	0.026 *
	Soybean height (cm)	0.61	0.11	5.38	< 0.001 *
10 - 15 mm	Intercept	3.90	0.21	19.03	< 0.001 *
	Field type - organic	0.41	0.18	2.33	0.020 *
	Soybean height (cm)	0.56	0.12	4.78	< 0.001 *
> 15 mm	Intercept	3.15	0.14	21.99	< 0.001 *
	Field type - organic	0.43	0.18	2.36	0.018 *
	Soybean height (cm)	0.42	0.10	4.06	< 0.001 *
Coleoptera	Intercept	5.50	0.33	16.86	< 0.001 *
	Field type - organic	1.01	0.25	4.10	< 0.001 *
	Soybean height (cm)	0.70	0.18	3.93	< 0.001 *
Diptera	Intercept	7.38	0.20	36.33	< 0.001 *
	Field type – organic	0.79	0.20	4.03	< 0.001 *
	Soybean height (cm)	0.64	0.12	5.24	< 0.001 *
Ephemeroptera	Intercept	3.49	0.37	9.55	< 0.001 *
	Field type – organic	0.50	0.30	1.68	0.092 †
	Soybean height (cm)	0.45	0.18	2.45	0.014 *
Hymenoptera	Intercept	2.39	0.31	7.78	< 0.001 *
	Field type – organic	1.28	0.37	3.48	< 0.001 *
	Soybean height (cm)	0.76	0.23	3.32	< 0.001 *
Lepidoptera	Intercept	5.34	0.21	25.54	< 0.001 *
	Field type – organic	0.77	0.18	4.34	< 0.001 *
	Soybean height (cm)	0.78	0.12	6.27	< 0.001 *
Trichoptera	Intercept	5.60	0.27	21.11	< 0.001 *
	Field type – organic	0.87	0.23	3.75	< 0.001 *
	Soybean height (cm)	0.98	0.16	6.29	< 0.001 *
Other	Intercept	5.07	0.30	16.87	< 0.001 *

Field type – organic	1.11	0.25	4.49	< 0.001 *
Soybean height (cm)	1.17	0.19	6.07	< 0.001 *

Table 2.F.3 Model estimates and associated measures from GLMMs estimating the effect of field type on total insect dry weight and dry weight in insect Orders (Coleoptera, Diptera, Lepidoptera, Trichoptera and ‘other’) (* indicates p-value <0.05, † indicates p-value <0.10).

Response variable	Predictor variable	Estimate	SE	z	P
total weight	Intercept	1.64	0.17	9.88	< 0.001 *
	Field type – organic	0.52	0.16	3.17	0.002 *
	Soybean height (cm)	0.52	0.10	5.00	< 0.001 *
Coleoptera	Intercept	-1.00	0.39	-2.58	0.010 *
	Field type – organic	0.60	0.34	1.75	0.080 †
	Soybean height (cm)	0.26	0.21	1.24	0.217
Diptera	Intercept	-1.90	0.43	-4.39	< 0.001 *
	Field type – organic	1.05	0.36	2.96	0.003 *
	Soybean height (cm)	0.55	0.17	3.23	0.001 *
Lepidoptera	Intercept	0.84	0.19	4.44	< 0.001 *
	Field type – organic	0.59	0.19	3.06	0.002 *
	Soybean height (cm)	0.63	0.12	5.22	< 0.001 *
Trichoptera	Intercept	-1.36	0.45	-3.04	0.002 *
	Field type – organic	0.70	0.33	2.11	0.035 *
	Soybean height (cm)	0.78	0.21	3.80	< 0.001 *
Other	Intercept	-1.21	0.43	-2.82	0.005 *
	Field type – organic	0.30	0.46	0.66	0.511
	Soybean height (cm)	0.35	0.27	1.30	0.193

Appendix 2.G Model estimates and associated measures from models predicting the effect of field type on species richness, bat activity, insect abundance and insect weight without soybean height as a confounding variable.

Table 2.G.1 Estimates and associated measures from models estimating the effect of field type on the number of bats species (species richness), cross-species activity, activity of big brown bat, eastern red bat, hoary bat, little brown bat and silver-haired bat, and presence/absence of northern long-eared bat and tri-colored bat without soybean height as a confounding variable (* indicates p-value <0.05, † indicates p-value <0.10).

Response variable	Predictor variable	Estimate	SE	z	P
species richness	Intercept	1.29	0.07	18.40	< 0.001 *
	Field type - organic	0.10	0.09	1.10	0.270
cross-species	Intercept	2.41	0.22	10.80	< 0.001 *
	Eastern red bat	-2.56	0.18	-14.00	< 0.001 *
	Hoary bat	1.79	0.16	11.60	< 0.001 *
	Little brown bat	-1.74	0.17	-10.40	< 0.001 *
	Northern long-eared bat	-4.30	0.24	-17.70	< 0.001 *
	Silver-haired bat	-2.84	0.18	-15.70	< 0.001 *
	Tri-colored bat	-3.21	0.20	-16.40	< 0.001 *
	Field type - organic	0.29	0.11	2.80	0.005 *
big brown bat	Intercept	2.29	0.34	6.67	< 0.001 *
	Field type - organic	0.28	0.22	1.30	0.190
eastern red bat	Intercept	-0.05	0.23	-0.20	0.840
	Field type - organic	0.18	0.29	0.65	0.520
hoary bat	Intercept	4.23	0.21	19.85	< 0.001 *
	Field type - organic	0.10	0.16	0.61	0.540
little brown bat	Intercept	0.24	0.34	0.72	0.471
	Field type - organic	0.83	0.31	2.67	0.008 *
northern long-eared bat	Intercept	-2.14	0.48	-4.46	< 0.001 *
	Field type - organic	0.05	0.55	0.10	0.920
silver-haired bat	Intercept	-0.50	0.36	-1.39	0.170
	Field type - organic	0.49	0.35	1.38	0.170
tri-colored bat	Intercept	-0.66	0.28	-2.36	0.018 *
	Field type - organic	0.22	0.38	0.57	0.567

Table 2.G.2 Model estimates and associated measures from GLMMs estimating the effect of field type on total insect abundance, abundance in size classes (< 5 mm, 5-10 mm, 10-15 mm and >15 mm) and abundance in insect Orders (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, Trichoptera and ‘other’) without soybean height as a confounding variable (* indicates p-value <0.05, † indicates p-value <0.10).

Response variable	Predictor variable	Estimate	SE	z	P
total abundance	Intercept	8.281	0.178	46.41	< 0.001 *
	Field type - organic	0.499	0.203	2.46	0.014 *
< 5 mm	Intercept	8.098	0.185	43.81	< 0.001 *
	Field type - organic	0.564	0.211	2.67	0.008 *
5 - 10 mm	Intercept	6.2449	0.1958	31.9	< 0.001 *
	Field type - organic	0.0758	0.1886	0.4	0.690
10 - 15 mm	Intercept	4.145	0.195	21.21	< 0.001 *
	Field type - organic	0.133	0.184	0.72	0.470
> 15 mm	Intercept	3.387	0.131	25.9	< 0.001 *
	Field type - organic	0.16	0.184	0.87	0.390
Coleoptera	Intercept	5.799	0.295	19.67	< 0.001 *
	Field type - organic	0.664	0.249	2.66	0.008 *
Diptera	Intercept	7.697	0.192	40.05	< 0.001 *
	Field type – organic	0.469	0.209	2.25	0.025 *
Ephemeroptera	Intercept	3.636	0.35	10.38	< 0.001 *
	Field type – organic	0.386	0.3	1.29	0.200
Hymenoptera	Intercept	2.791	0.313	8.91	< 0.001 *
	Field type – organic	0.751	0.346	2.17	0.030 *
Lepidoptera	Intercept	5.7	0.19	29.93	< 0.001 *
	Field type – organic	0.432	0.196	2.21	0.027 *
Trichoptera	Intercept	6.065	0.266	22.82	< 0.001 *
	Field type – organic	0.5	0.265	1.88	0.060 †
Other	Intercept	5.753	0.246	23.41	< 0.001 *
	Field type – organic	0.525	0.263	1.99	0.046 *

Table 2.G.3 Model estimates and associated measures from GLMMs estimating the effect of field type on total insect dry weight and dry weight in insect Orders (Coleoptera, Diptera, Lepidoptera, Trichoptera and ‘other’) (* indicates p-value <0.05, † indicates p-value <0.10).

Response variable	Predictor variable	Estimate	SE	z	P
total weight	Intercept	1.90	0.14	13.14	< 0.001 *
	Field type – organic	0.25	0.18	1.44	0.150
Coleoptera	Intercept	-0.89	0.37	-2.44	0.015 *
	Field type – organic	0.48	0.33	1.45	0.146
Diptera	Intercept	-1.58	0.43	-3.72	< 0.001 *
	Field type – organic	0.64	0.34	1.91	0.056 †
Lepidoptera	Intercept	1.17	0.17	6.91	< 0.001 *
	Field type – organic	0.26	0.21	1.28	0.200
Trichoptera	Intercept	-0.88	0.40	-2.19	0.029 *
	Field type – organic	0.32	0.34	0.93	0.354
Other	Intercept	-1.01	0.39	-2.61	0.009 *
	Field type – organic	0.11	0.43	0.26	0.795

Appendix 2.H Relationships between bat activity and field structure and landscape composition variables.

Figure 2.H.1 Relationships between bat activity (number of passes) and (a) soybean field size (ha), (b) hedgerow length per ha of soybean field, (c-e) proportion of the landscape in forest within 1 km, 2 km and 3 km of the fields. At 32 soybean fields (16 matched organic-conventional pairs), 2 bat recorders were deployed on 2 non-consecutive nights. In these plots, each point represents data from a soybean field with bat activity averaged across the 2 sampling nights and 2 sampling locations on the field.

Appendix 2.I Relationship between soybean height and average insect weight.

Figure 2.I.1 Relationship between soybean height (in centimeters) and average insect weight (in grams). Each plotted point represents averaged data from a survey at a field ($n=64$), where the values of insect abundance and weight have been averaged between the two survey locations to get average insect weight. Insect samples were collected using black-light traps, which target nocturnal aerial insects. We did not include the group of insects that were categorized as ‘other’ in the total insect abundance or total insect dry weight. Soybean height was measured as the distance from where the soybean plant came out of the soil to the growing point, and 6 random plants/field were measured.

References

- Adams, A. M. 2013. Assessing and analyzing bat activity with acoustic monitoring: challenges and interpretations. Ph.D. Thesis, The University of Western Ontario, London.
- Agriculture and Agri-Food Canada (AAFC). 2013. Annual Crop Inventory 2013. <http://open.canada.ca/data/en/dataset/4b1d45b0-5bfe-4c6d-bcd3-96c9d821ad3b> (Accessed 5 May 2016).
- Agriculture and Agri-Food Canada (AAFC). 2017. Annual Crop Inventory 2016. <http://open.canada.ca/data/en/dataset/b8e4da73-fb5f-4e6e-93a4-8b1f40d95b51> (Accessed 1 March 2017).
- Aguirre, L., A. Herrel, R. Van Damme, and E. Matthysen. 2003. The implications of food hardness for diet in bats. *Functional Ecology* 17:201–212.
- Barclay, R. M., and L. D. Harder. 2003. Bat ecology. Pages 209–253 *in* Kunz, TH and Fenton, MB, editor. University of Chicago Press Chicago.
- Barton, K. 2014. Package “MuMIn”: multi-model inference. R package. Version 1.9. 13.
- Batáry, P., T. Matthiesen, and T. Tscharntke. 2010. Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. *Biological Conservation* 143:2020–2027.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67:1–48.
- Bengtsson, J., J. Ahnström, and A. C. Weibull. 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42:261–269.
- Benton, T. G., D. M. Bryant, L. Cole, and H. Q. Crick. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39:673–687.
- Bianchi, F., C. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society of London B: Biological Sciences* 273:1715–1727.
- Blank, P. J., C. L. Williams, D. W. Sample, T. D. Meehan, and M. G. Turner. 2016. Alternative scenarios of bioenergy crop production in an agricultural landscape and implications for bird communities. *Ecological Applications* 26:42–54.

- Boatman, N. D., N. W. Brickle, J. D. Hart, T. P. Milsom, A. J. Morris, A. W. Murray, K. A. Murray, and P. A. Robertson. 2004. Evidence for the indirect effects of pesticides on farmland birds. *Ibis* 146:131–143.
- Boehmel, C., I. Lewandowski, and W. Claupein. 2008. Comparing annual and perennial energy cropping systems with different management intensities. *Agricultural Systems* 96:224–236.
- Boone, M. D., R. D. Semlitsch, E. E. Little, and M. C. Doyle. 2007. Multiple stressors in amphibian communities: effects of chemical contamination, bullfrogs, and fish. *Ecological Applications* 17:291–301.
- Boughey, K. L., I. R. Lake, K. A. Haysom, and P. M. Dolman. 2011. Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation* 144:1790–1798.
- Boutin, C., and B. Jobin. 1998. Intensity of agricultural practices and effects on adjacent habitats. *Ecological Applications* 8:544–557.
- Boyles, J. G., P. M. Cryan, G. F. McCracken, and T. H. Kunz. 2011. Economic importance of bats in agriculture. *Science* 332:41–42.
- Brigham, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology* 69:117–121.
- Campbell, L. A., J. G. Hallett, and M. A. O’Connell. 1996. Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. *Journal of Mammalogy* 77:976–984.
- Clare, E. L., E. E. Fraser, H. E. Braid, M. B. Fenton, and P. D. Hebert. 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Molecular Ecology* 18:2532–2542.
- Clark, D. R., R. K. LaVal, and D. M. Swineford. 1978. Dieldrin-induced mortality in an endangered species, the gray bat (*Myotis grisescens*). *Science* 199:1357–9.
- Coleman, J. L., and R. M. Barclay. 2013. Prey availability and foraging activity of grassland bats in relation to urbanization. *Journal of Mammalogy* 94:1111–1122.
- Dauber, J., M. B. Jones, and J. C. Stout. 2010. The impact of biomass crop cultivation on temperate biodiversity. *GCB Bioenergy* 2:289–309.
- Davidai, N., J. K. Westbrook, J.-P. Lessard, T. G. Hallam, and G. F. McCracken. 2015. The importance of natural habitats to Brazilian free-tailed bats in intensive agricultural landscapes in the Winter Garden region of Texas, United States. *Biological*

- Conservation 190:107–114.
- Davy, C. M., D. Russo, and M. B. Fenton. 2007. Use of native woodlands and traditional olive groves by foraging bats on a Mediterranean island: consequences for conservation. *Journal of Zoology* 273:340–397.
- Dixon, M. D. 2012. Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosystems* 15:683–695.
- Elmore, L. W., D. A. Miller, and F. J. Vilella. 2005. Foraging area size and habitat use by red bats (*Lasiurus borealis*) in an intensively managed pine landscape in Mississippi. *The American Midland Naturalist* 153:405–417.
- Erickson, J. L., and S. D. West. 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. *Acta Chiropterologica* 4:17–24.
- Estrada, A., R. Coates-Estrada, and D. Meritt. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* 16:309–318.
- Ethier, K., and L. Fahrig. 2011. Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landscape Ecology* 26:865–876.
- Fahrig, L., J. Girard, D. Duro, J. Pasher, A. Smith, S. Javorek, D. King, K. F. Lindsay, S. Mitchell, and L. Tischendorf. 2015. Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment* 200:219–234.
- Farm and Food Care Ontario. 2015. Survey of Pesticide Use In Ontario, 2013/2014 Estimates of Pesticides Used on Field Crops and Fruit and Vegetable Crops. Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA), Guelph, Canada. 22 pages.
- Fenton, M. B., and G. P. Bell. 1981. Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy* 62:233–243.
- Foley, J., N. Ramankutty, K. Brauman, E. Cassidy, J. Gerber, M. Johnston, N. Mueller, C. O’Connell, D. Ray, P. West, C. Balzer, E. Bennett, S. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockström, J. Sheehan, S. Siebert, D. Tilman, and D. Zaks. 2011. Solutions for a cultivated planet. *Nature* 478:337–42.
- Food and Agriculture Organization of the United Nations (FAOSTAT). 2017. FAOSTAT. [http:// faostat.fao.org/site/567/default.aspx#ancor](http://faostat.fao.org/site/567/default.aspx#ancor) (Accessed 1 July 2017).

- Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation* 126:528–539.
- Freemark, K. E., and D. A. Kirk. 2001. Birds on organic and conventional farms in Ontario: partitioning effects of habitat and practices on species composition and abundance. *Biological Conservation* 101:337–350.
- Frick, W. F., J. F. Pollock, A. C. Hicks, K. E. Langwig, D. S. Reynolds, G. G. Turner, C. M. Butchkoski, and T. H. Kunz. 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679–682.
- Froidevaux, J. S., B. Louboutin, and G. Jones. 2017. Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. *Agriculture, Ecosystems & Environment* 249:112–122.
- Fuller, R. J., L. R. Norton, R. E. Feber, P. J. Johnson, D. E. Chamberlain, A. C. Joys, F. Mathews, R. C. Stuart, M. C. Townsend, W. J. Manley, M. S. Wolfe, D. W. Macdonald, and L. G. Firbank. 2005. Benefits of organic farming to biodiversity vary among taxa. *Biology letters* 1:431–434.
- Gaba, S., E. Gabriel, J. Chadœuf, F. Bonneu, and V. Bretagnolle. 2016. Herbicides do not ensure for higher wheat yield, but eliminate rare plant species. *Scientific Reports* 6:30112.
- Gabriel, D., S. M. Sait, J. A. Hodgson, U. Schmutz, W. E. Kunin, and T. G. Benton. 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters* 13:858–869.
- Geggie, J., and M. Fenton. 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology* 63:263–266.
- Gehrt, S. D., and J. E. Chelvig. 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. *Ecological Applications* 13:939–950.
- Gehrt, S. D., and J. E. Chelvig. 2004. Species-specific patterns of bat activity in an urban landscape. *Ecological Applications* 14:625–635.
- Geiger, F., J. Bengtsson, F. Berendse, W. W. Weisser, M. Emmerson, M. B. Morales, P. Ceryngier, J. Liira, T. Tschardt, C. Winqvist, S. Eggers, R. Bommarco, T. Pärt, V. Bretagnolle, M. Plantegenest, L. W. Clement, C. Dennis, C. Palmer, J. J. Oñate, I. Guerrero, V. Hawro, T. Aavik, C. Thies, A. Flohre, S. Hänke, C. Fischer, P. W. Goedhart, and P. Inchausti. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied*

- Ecology 11:97–105.
- Geluso, K. N., J. S. Altenbach, and D. E. Wilson. 1976. Bat mortality: pesticide poisoning and migratory stress. *Science* 194:184–186.
- Gillam, E. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. *Canadian Journal of Zoology* 85:795–801.
- Government of Ontario. 2017. Neonicotinoid regulations for seed vendors. <https://www.ontario.ca/page/neonicotinoid-regulations-seed-vendors> (Accessed 9 January 2018).
- Hammerson, G., M. Kling, M. Harkness, M. Ormes, and B. Young. 2017. Strong geographic and temporal patterns in conservation status of North American bats. *Biological Conservation* 212:144–152.
- Harvey, M. J., J. S. Altenbach, and T. L. Best. 2011. *Bats of the United States and Canada*. John Hopkins University Press, Baltimore.
- Haughton, A. J., D. A. Bohan, S. J. Clark, M. D. Mallott, V. Mallott, R. Sage, and A. Karp. 2015. Dedicated biomass crops can enhance biodiversity in the arable landscape. *GCB Bioenergy* 8:1071–1081.
- Heim, O., L. Lorenz, S. Kramer-Schadt, K. Jung, C. C. Voigt, and J. A. Eccard. 2017. Landscape and scale-dependent spatial niches of bats foraging above intensively used arable fields. *Ecological Processes* 6:24.
- Heim, O., J. T. Treitler, M. Tschapka, M. Knörnschild, and K. Jung. 2015. The Importance of Landscape Elements for Bat Activity and Species Richness in Agricultural Areas. *PloS one* 10:e0134443.
- Henderson, L. E., and H. G. Broders. 2008. Movements and Resource Selection of the Northern Long-Eared Myotis (*Myotis septentrionalis*) in a Forest—Agriculture Landscape. *Journal of Mammalogy* 89:952–963.
- Hole, D., A. Perkins, J. Wilson, I. Alexander, P. Grice, and A. D. Evans. 2005. Does organic farming benefit biodiversity? *Biological Conservation* 122:113–130.
- Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. *Bioscience* 54:227–233.
- Hooton, L. A. 2010. Identifying critical stopover sites for migratory bats. M.Sc. Thesis, The University of Western Ontario, London.

- Jefferies, D. 1972. Organochlorine insecticide residues in British bats and their significance. *Journal of Zoology* 166:245–263.
- Jung, K., S. Kaiser, S. Böhm, J. Nieschulze, and E. K. Kalko. 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *Journal of Applied Ecology* 49:523–531.
- Knops, J. M., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286–293.
- Köhler, H.-R., and R. Triebkorn. 2013. Wildlife ecotoxicology of pesticides: can we track effects to the population level and beyond? *Science* 341:759–65.
- Kunz, T. H., E. Braun de Torrez, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. *Annals of the New York Academy of Sciences* 1223:1–38.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45:175–201.
- Lentini, P. E., P. Gibbons, J. Fischer, B. Law, J. Hanspach, and T. G. Martin. 2012. Bats in a farming landscape benefit from linear remnants and unimproved pastures. *PloS one* 7:e48201.
- Lichtenberg, E. M., C. M. Kennedy, C. Kremen, P. Batáry, F. Berendse, R. Bommarco, N. A. Bosque-Pérez, L. G. Carvalheiro, W. E. Snyder, N. M. Williams, R. Winfree, B. K. Klatt, S. Åström, F. Benjamin, C. Brittain, R. Chaplin-Kramer, Y. Clough, B. Danforth, T. Diekötter, S. D. Eigenbrode, J. Ekroos, E. Elle, B. M. Freitas, Y. Fukuda, H. R. Gaines-Day, H. Grab, C. Gratton, A. Holzschuh, R. Isaacs, M. Isaia, S. Jha, D. Jonason, V. P. Jones, A. M. Klein, J. Krauss, D. K. Letourneau, S. Macfadyen, R. E. Mallinger, E. A. Martin, E. Martinez, J. Memmott, L. Morandin, L. Neame, M. Otieno, M. G. Park, L. Pfiffner, M. J. O. Pocock, C. Ponce, S. G. Potts, K. Poveda, M. Ramos, J. A. Rosenheim, M. Rundlöf, H. Sardiñas, M. E. Saunders, N. L. Schon, A. R. Sciligo, C. S. Sidhu, I. Steffan-Dewenter, T. Tschamntke, M. Veselý, W. W. Weisser, J. K. Wilson, and D. W. Crowder. 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology* 23:4946–4957.
- Limpert, D. L., D. L. Birch, M. S. Scott, M. Andre, and E. Gillam. 2007. Tree selection and landscape analysis of eastern red bat day roosts. *Journal of Wildlife Management* 71:478–486.

- Long, B. L., and A. Kurta. 2014. Activity and diet of bats in conventional versus organic apple orchards in southern Michigan. *The Canadian Field-Naturalist* 128:158–164.
- MacDonald, M., A. Morris, S. Dodd, I. Johnstone, A. Beresford, R. Angell, K. Haysom, S. Langton, G. Tordoff, T. Brereton, R. Hobson, C. Shellswell, N. Hutchinson, T. Dines, E. M. Wilberforce, R. Parry, and V. Matthews. 2012. Welsh Assembly Government Contract 183/2007/08 to Undertake Agri-environment Monitoring and Services. Lot 2–Species Monitoring. Welsh Government, 250 pages.
- Matson, P. A., W. J. Parton, A. Power, and M. Swift. 1997. Agricultural intensification and ecosystem properties. *Science* 277:504–509.
- McCracken, D. I., G. N. Foster, and A. Kelly. 1995. Factors affecting the size of leatherjacket (Diptera: Tipulidae) populations in pastures in the west of Scotland. *Applied Soil Ecology* 2:203–213.
- Meehan, T. D., B. P. Werling, D. A. Landis, and C. Gratton. 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proceedings of the National Academy of Sciences of the United States of America* 108:11500–5.
- Ministry of Natural Resources (MNR). 2014. Digital Raster Acquisition Project for the East (DRAPE) <https://library.carleton.ca/find/gis/geospatial-data/eastern-ontario-air-photos-drape-2008-2014> (Accessed 1 March 2017).
- Monck-Whipp, L., A. E. Martin, C. M. Francis, and L. Fahrig. 2018. Farmland heterogeneity benefits bats in agricultural landscapes. *Agriculture, Ecosystems & Environment* 253:131–139.
- Monfreda, C., N. Ramankutty, and J. A. Foley. 2008. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles* 22:GB1022.
- Norton, L., P. Johnson, A. Joys, R. Stuart, D. Chamberlain, R. Feber, L. Firbank, W. Manley, M. Wolfe, B. Hart, F. Mathews, D. Macdonald, and R. J. Fuller. 2009. Consequences of organic and non-organic farming practices for field, farm and landscape complexity. *Agriculture, Ecosystems & Environment* 129:221–227.
- Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA). 2017. http://www.omafra.gov.on.ca/english/stats/agriculture_summary.htm#area (Accessed 1 August 2017).
- O’Shea, T. J., and J. J. Johnston. 2009. Environmental contaminants and bats: Investigating exposure and effects. In: Parsons S (ed) Kunz TH. *Ecological and behavioral methods for the study of bats*. John Hopkins University Press, Baltimore, pp 500–528.

- Pocock, M. J., and N. Jennings. 2008. Testing biotic indicator taxa: the sensitivity of insectivorous mammals and their prey to the intensification of lowland agriculture. *Journal of Applied Ecology* 45:151–160.
- Poissant, J. A., H. G. Broders, and G. M. Quinn. 2010. Use of lichen as a roosting substrate by *Perimyotis subflavus*, the tricolored bat, in Nova Scotia. *Écoscience* 17:372–378.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–53.
- Poulin, B., G. Lefebvre, and L. Paz. 2010. Red flag for green spray: adverse trophic effects of Bti on breeding birds. *Journal of Applied Ecology* 47:884–889.
- Put, J. E., L. Fahrig, and G. W., Mitchell. 2017. Data from: Bats respond negatively to increases in the amount and homogenization of agricultural land cover. Mendeley Data, v1. <https://doi.org/10.17632/b2mfw6fgyy.1>.
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Robinson, R. A., and W. J. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39:157–176.
- Roschewitz, I., D. Gabriel, T. Tscharntke, and C. Thies. 2005a. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology* 42:873–882.
- Roschewitz, I., C. Thies, and T. Tscharntke. 2005b. Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields? *Agriculture, Ecosystems & Environment* 105:87–99.
- Russo, D., and G. Jones. 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* 26:197–209.
- Rydell, J., A. Entwistle, and P. A. Racey. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* 76:243–252.
- Schnitzler, H.-U., and E. K. Kalko. 2001. Echolocation by insect-eating bats *Bioscience* 51:557–569.
- Skaug, H., D. Fournier, B. Bolker, A. Magnusson, and A. Nielsen. 2016. Generalized linear mixed models using “AD Model Builder.” R package version 0.8.4.

- Stahlschmidt, P., and C. A. Brühl. 2012. Bats at risk? Bat activity and insecticide residue analysis of food items in an apple orchard. *Environmental Toxicology and Chemistry* 31:1556–63.
- Statistics Canada. 2011. Water File - Lakes and Rivers (polygons) - 2011 Census. <http://open.canada.ca/data/en/dataset/448ec403-6635-456b-8ced-d3ac24143add> (Accessed 19 January 2018).
- Statistics Canada. 2016a. Census of Agriculture, organic products for sale. <http://www5.statcan.gc.ca/cansim/a26?lang=eng&retrLang=eng&id=0040211&&pattern=&stByVal=1&p1=1&p2=-1&tabMode=dataTable&csid=> (Accessed 3 January 2018).
- Statistics Canada. 2016b. Estimated areas, yield, production, average farm price and total farm value of principal field crops, in metric and imperial units. <http://www5.statcan.gc.ca/cansim/a26?lang=eng&retrLang=eng&id=0010017&&pattern=&stByVal=1&p1=1&p2=-1&tabMode=dataTable&csid=> (Accessed 3 January 2018).
- Stoate, C., N. D. Boatman, R. J. Borralho, C. R. Carvalho, G. R. de Snoo, and P. Eden. 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63:337–65.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31:79–92.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters* 8:857–874.
- Valdez, E. W., and P. M. Cryan. 2009. Food habits of the hoary bat (*Lasiurus cinereus*) during spring migration through new Mexico. *Southwestern Naturalist* 54:195–200.
- Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer, New York.
- Verboom, B., and H. Huitema. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12:117–125.
- Walters, B. L., C. M. Ritzi, D. W. Sparks, and J. O. Whitaker Jr. 2007. Foraging behavior of eastern red bats (*Lasiurus borealis*) at an urban-rural interface. *The American Midland Naturalist* 157:365–373.

- Werling, B. P., T. L. Dickson, R. Isaacs, H. Gaines, C. Gratton, K. L. Gross, H. Liere, C. M. Malmstrom, T. D. Meehan, L. Ruan, B. A. Robertson, G. P. Robertson, T. M. Schmidt, A. C. Schrotenboer, T. K. Teal, J. K. Wilson, and D. A. Landis. 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 111:1652–7.
- Wickramasinghe, L. P., S. Harris, G. Jones, and N. Vaughan Jennings. 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conservation Biology* 18:1283–1292.
- Wickramasinghe, L. P., S. Harris, G. Jones, and N. Vaughan. 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *Journal of Applied Ecology* 40:984–993.
- Willis, C. K. R., and R. M. Brigham. 2005. Physiological and Ecological Aspects of Roost Selection by Reproductive Female Hoary Bats (*Lasiurus cinereus*). *Journal of Mammalogy* 86:85–94.
- Wilson, S., G. W. Mitchell, J. Pasher, M. McGovern, M. -A. R. Hudson, and L. Fahrig. 2017. Influence of crop type, heterogeneity and woody structure on avian biodiversity in agricultural landscapes. *Ecological Indicators* 83, 218–226.
- Winqvist, C., J. Ahnström, and J. Bengtsson. 2012. Effects of organic farming on biodiversity and ecosystem services: taking landscape complexity into account. *Annals of the New York Academy of Sciences* 1249:191–203.
- Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biological Control* 10:4–15.