Research Paper

Farmland heterogeneity benefits bats in agricultural landscapes

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Abstract

Pressure to increase food production poses a challenge for biodiversity conservation in agricultural landscapes. Previous studies suggest that one potential way to enhance biodiversity without taking land out of production is to increase the landscape heterogeneity of farmland by increasing the diversity of crop types in the landscape, and/or the complexity of the spatial pattern of the crop fields (e.g., by decreasing field sizes). Thus we hypothesize that farmland heterogeneity should also increase bat abundance and richness in agricultural landscapes. Here, we use data on bat activity and richness collected using acoustic surveys in rural eastern Ontario, Canada to test the predictions that there should be greater bat activity and greater species richness in agricultural landscapes with higher Shannon diversity of crops and smaller fields, when controlling for the effect of total crop cover. Bat activity increased with farmland heterogeneity, as predicted. Farmland heterogeneity was also positively related to species richness, although the relationship was not statistically supported. Positive effects of farmland heterogeneity on bats will be of interest to farmers and agricultural policy-makers, given the potential economic benefits of pest control by bats.

1. Introduction

Pressure to increase food production poses a challenge for biodiversity conservation. Conversion of natural and semi-natural land cover types to crops has been implicated in the declines of species in a number of taxa, including bats (Duchamp et al., 2004; Gorresen and Willig, 2004), birds (Billeter et al., 2008; Trzcinski et al., 1999), mammals (Nupp and Swihart, 2000), amphibians (Vallan, 2000), and arthropods (Aviron et al., 2005; Billeter et al., 2008). Thus removing land from agricultural production and replacing it with semi-natural land covers can benefit biodiversity (although time lags to full recovery can span decades to centuries; Flinn and Vellend, 2005). However, such conservation-motivated recommendations may be impractical in light of the pressure to increase food production. Thus the challenge is to find conservation actions that can maintain or increase biodiversity in agricultural landscapes without taking land out of production (Dobrovolski et al., 2011; Scherr and McNeely, 2008).

One potential way to enhance biodiversity in agricultural landscapes without taking land out of production is to increase farmland heterogeneity (Fahrig et al., 2011), where ‘farmland’ refers to the crop fields (including both annual row crops and perennial forage crops) in an agricultural landscape. There are two main ways that farmland heterogeneity can be increased. First, the compositional heterogeneity of crops can be increased by planting more types of crops and by ensuring each crop type is more evenly represented in the landscape. Second, farmland configurational heterogeneity can be increased by increasing the complexity of the spatial pattern of crop types, for example, by decreasing crop field sizes and by increasing the interspersion of different crop types (while holding the number of crop types and amounts constant; Lovett et al., 2005).

Farmland compositional and configurational heterogeneity could increase biodiversity in agricultural landscapes in a number of ways. Increasing the number of crop types may benefit biodiversity because different crop types can be used by different species, increasing the overall number of species that can inhabit a given landscape. A given species may also benefit from access to multiple crop types within the landscape (i.e., landscape complementation; Dunning et al., 1992); for example, hay fields may provide breeding grounds while row crops provide food for granivorous birds. Increasing interspersion of crop types may also increase accessibility of such complementary resources. Complex spatial patterns may further benefit wildlife by increasing movement success within the landscape; for example, wide fields may be riskier to cross than narrow fields. The majority of studies of landscape heterogeneity in agricultural landscapes have focused on overall
landscape heterogeneity (including all land cover types, e.g., Bolívar-Cimé et al., 2013) or semi-natural habitat heterogeneity (e.g., Billette et al., 2008), rather than farmland heterogeneity. However, support for the farmland heterogeneity hypothesis has been found in a number of taxa, including butterflies, spiders, carabid beetles, birds, amphibians, and plants (Bertrand et al., 2016; Collins and Fahrig, 2017; Fahrig et al., 2015; Josefsson et al., 2017).

We hypothesize that farmland compositional and configurational heterogeneity should also increase bat abundance and richness in agricultural landscapes. Greater farmland heterogeneity may benefit insectivorous bat communities by supporting more diverse and abundant communities of prey insects (Bertrand et al., 2016; Fahrig et al., 2015). Some insect species use one or more crops as part of their life cycle (e.g., for food, breeding areas, or as cover; Kallio, 2014), and a greater variety of crops will likely support a greater variety of these insects within an agricultural landscape. Greater prey diversity should benefit bat communities by making prey abundance more stable through time, both in the short-term, because different insects are active at different times of night (Rydell et al., 1996), and seasonally, because abundances of different species peak at different times. Having smaller fields should also benefit bat communities because bats prefer to forage and commute along linear landscape elements, such as the hedgerows or grassy/herbaceous vegetation strips at the interface between crop fields (Boughhey et al., 2011; Frey-Ehrenbold et al., 2013; Lentini et al., 2012; Limpens et al., 1989; Verboom and Hultema, 1997). Positive effects of rural landscape heterogeneity (including all land cover types) and habitat fragmentation on bat activity and richness suggest that bats benefit from landscape complementation (e.g., Bolívar-Cimé et al., 2013; Ethier and Fahrig, 2011, but see also Fuentes-Montemayor et al., 2013); thus bats may also benefit from farmland heterogeneity because it reduces distances between foraging and roosting habitats.

Insectivorous bats are an important component of agricultural landscapes. They are a critical link in the food web because they are nocturnal aerial insectivores, a niche only occupied by bats, small owls, and caprimulgiform birds (Humphrey, 1975). Additionally, healthy bat populations can provide an ecosystem service – pest control – for farmers, contributing potentially massive amounts of pest insect removal in farmlands (Boyles et al., 2011; Whitaker, 1995) and suppressing pest insect populations (Boyles et al., 2013; Kunz et al., 2011). Thus conservation actions that increase bat biodiversity in agricultural landscapes can benefit both the wildlife community and farmers.

Here, we tested the hypothesis that bat abundance and richness in agricultural landscapes increases with farmland compositional and configurational heterogeneity, independent of the effect of total crop cover. We used data on bat activity and richness collected using acoustic surveys near the centres of 46, 3 × 3 km landscapes in rural eastern Ontario, Canada (Fig. 1). Specifically, we tested the predictions that there should be greater bat activity (estimated as an index of relative bat abundance among landscapes) and more bat species recorded in agricultural landscapes with higher crop diversity (i.e., Shannon diversity of crops) and smaller fields. We chose these two farmland heterogeneity metrics because they represent aspects of the landscape that could, at least in principle, be directly targeted by agricultural policy-makers, i.e., policies to encourage more crop types and smaller fields. We also tested for relationships between flying insect abundance and the compositional and configurational heterogeneity of farmland in these same landscapes, to test our underlying assumption that farmland heterogeneity benefits bats, at least in part, by increasing the abundance of their prey.

2. Methods

2.1. Study region

We conducted our study in rural eastern Ontario, Canada, which is located in the easternmost portion of the Lake Simcoe-Rideau Ecoregion (Crins et al., 2009; Fig. 1). This Ecoregion has a mild, moist climate, with mean annual temperatures ranging from 5 to 8 °C, mean precipitation from 76 to 109 cm, and a mean growing season of 205 to 230 days (Crins et al., 2009). This is the most densely populated Ecoregion in Ontario, and its land use is dominated by agriculture. In eastern Ontario, ~ 5400 km² is used in crop production, dominated by hay, corn, and soybean fields (OMAFRA, 2011).

2.2. Landscape selection

Our 46, 3 × 3 km landscapes were the 2012 subset of the 93 landscapes used by Fahrig et al. (2015) in a larger project focused on effects of farmland heterogeneity on biodiversity of birds, plants, butterflies, syrphids, bees, carabids, and spiders. We used the 3 × 3 km scale because it encompasses the average commuting distance between foraging and roosting habitat for all local bat species (Brigham, 1991; Broders et al., 2006; Campbell et al., 1996; Elmore et al., 2005; Menzel et al., 2003; Sparks et al., 2005).

The objectives of landscape selection in this larger project were to select agricultural landscapes that: (1) were spatially independent, i.e., non-overlapping with minimal spatial autocorrelation of the values of each farmland heterogeneity metric (crop diversity and mean field size) across landscapes; (2) represented the regional variability in these heterogeneity metrics; and (3) had low cross-landscape collinearity between the two heterogeneity metrics, and between each metric and the crop amount. Landscape selection was based on a classified land cover map (30 m pixel size) created by Pasher et al. (2013) from Landsat-5 images from the 2007 growing season (30 m pixel; obtained from the USGS Earth Explorer, https://earthexplorer.usgs.gov/) and SPOT-4 panchromatic imagery (10 m pixel; obtained from the Government of Canada GeoBase, http://open.canada.ca/data/en/dataset/d799c202-603d-4e5c-b16b-d058093b909f). For full details of landscape selection see Pasher et al. (2013).

Fahrig et al. (2015) also created a finer-resolution (40-cm pixel) land cover data set for the year of data collection, i.e., 2012. Land cover was classified for each 3 × 3 km landscape based on aerial photographs (40-cm resolution) commissioned by Fahrig et al. (2015), and was validated by field observations. Individual crop fields were defined based on visible boundaries between crop and non-crop, or between different crop types. Thus, areas of the same crop type separated by a non-crop land cover (e.g., field margin, road) were considered separate fields, and areas of different crop types were considered separate fields, even if they were not separated by a non-crop land cover. For examples, see Fig. 2.

We measured three continuous landscape variables in each landscape, using the finer-resolution 2012 land cover data: the crop amount (i.e., the proportion of the landscape covered by crop fields), crop diversity, and mean field size (in ha). We note that correlations among our three landscape variables were stronger than expected from landscape selection ($r = -0.34$ to 0.73, all $p \leq 0.02$; Fig. A1 in Supplementary file). This is because the land cover data changed between the coarser-resolution 2007 data used to select landscapes (Pasher et al., 2013) and the finer-resolution 2012 data used in this study. However, we note that collinearity between crop amount and our two measures of farmland heterogeneity did not explain the observed relationships between bat activity and farmland heterogeneity (see 4 Discussion).

2.3. Field data collection

2.3.1. Acoustic surveys for echolocation calls

We selected two survey locations per landscape, within the 1 × 1 km area at the center of each 3 × 3 km landscape. Each survey location was randomly located along a field boundary at least 50 m long, with at least 25 m of continuous boundary on either side of the
survey location (Fig. 3). To limit the influence of non-crop land cover types on bat activity/richness, each survey location was ≥ 100 m from roads, water features, and buildings, and ≥ 50 m from any other non-crop land cover type. The two survey locations within each landscape were at least 200 m apart.

We conducted acoustic surveys between May 23 and August 1, 2012. We surveyed, on average, two landscapes per night, in random order. We did not conduct surveys if the overnight temperature

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Fig. 1. Locations of the 46, 3 × 3 km landscapes in rural eastern Ontario, Canada. Crop, urban, and road covers were taken from Agriculture and Agri-foods Canada (2012).

Fig. 2. Four examples selected from our set of 46, 3 × 3 km landscapes, one representing each of the four combinations of high and low crop diversity, and high and low mean field size. We use the 40-cm-resolution land cover map created by Fahrig et al. (2015), based on aerial photographs and field observations taken in the year of bat sampling (2012). White areas represent non-farmland cover types, including both developed areas and natural habitats.
2.3.2. Sticky-trap sampling for flying insects

We estimated the relative abundance of flying insects on the same night as a bat acoustic survey. We sampled each of the two survey locations in a landscape once. We used a custom-made cylindrical sticky trap consisting of a sheet of 33 cm × 29.5 cm white paper secured around a PVC pipe, which was mounted on a 2-m-high pole (Barclay, 1985). The outside surface of the paper was coated with Tangletrap (Contech Enterprises Inc., Victoria, BC, Canada). One trap was placed 10 m from the acoustic recording station and retrieved the following morning (Fig. 3). We estimated relative insect abundance as the number of insects collected. As insect size or type may influence its quality as a bat food source (e.g., Aguirre et al., 2003), we classified all insects by body length (0–5 mm, 5–10 mm, 10–15 mm, or > 15 mm; Threlfall et al., 2012). We also counted the numbers in each of the four main orders: Lepidoptera, Coleoptera, Hymenoptera, and Diptera.

2.3.3. Measuring potentially confounding variables

Weather conditions may influence the detectability and/or activity of bats and insects. If such conditions were correlated with our landscape variables (crop diversity, mean field size, and crop amount), then they might confound interpretation of models relating bat activity/bat richness/insect abundance to these variables. We measured mean temperature, precipitation, and wind speed on the night of each acoustic survey using a WS-2080 Wireless Home Weather Station (Ambient Weather, Chandler, Arizona, USA). The weather station was erected beside the insect sticky trap (see 2.3.2 Sticky-trap sampling for flying insects; Fig. 3). The weather station recorded temperature, precipitation, and wind speed every 15 min until we collected the station the following morning.

Additionally, the amount of moonlight has been linked to activity and habitat use by insectivorous bats (Hecker and Brigham, 1999). Moon illumination was measured as the product of the percentage of moon illumination × the number of minutes the moon was above the horizon during the acoustic survey. These two measurements were taken from local weather networks.

Finally, estimated species activity and richness may depend on when a landscape was sampled during the sampling period. For example, one would expect bat abundance (and thus activity) to increase over the sampling period, because late-season samples are more likely to include both adult and juvenile bats than early-season samples. Thus, we also recorded the Julian date of sampling for each acoustic survey.

2.4. Data analysis

2.4.1. Bat species identification from acoustic survey

There are two typical types of bat call sequences: search-phase call sequences and feeding buzz call sequences (Schnitzler and Kalko, 2001), where a ‘call’ refers to an individual pulse of sound. We used only search-phase call sequences for species identification because these have less within-species variability than feeding buzz call sequences. A search-phase call sequence was distinguished from a feeding buzz call sequence by the interval between individual calls, with 50–100 ms between search-phase calls and ≤ 10 ms between feeding buzz calls (Griffin et al., 1960). We then selected one call from each recorded search-phase call sequence that included at least two calls. We limited recordings to those with at least two calls to ensure the sound was part of a bat call sequence and not due to other noise present in the landscape (Thomas, 1988). The call with the highest signal-to-noise ratio was selected from the set of all calls within the call sequence for identification (Parsons and Jones, 2000). We visualized call sequences and selected individual calls for species identification in SPECT'R, using the full-spectrum WAV files.

We classified each search-phase call sequence to species using a quadratic discriminant function analysis model (QDFA; Minitab Inc., using

We compared the selected call to a library of reference call sequences (Hooton and Adams, University of Western Ontario, unpublished data), comparing the call duration, inter-pulse interval, maximum frequency, minimum frequency, bandwidth, dominant frequency, characteristic frequency, slope, and curvature between calls. It then provides a posterior probability (0–1) of the call belonging to each species in the call sequence library. If the posterior probability for one species was ≥ 0.95, the call sequence was assigned to that species, and if the largest
posterior probability was < 0.50 it was classified as “Unidentified”. Otherwise, we assessed all remaining calls in the search-phase call sequence and either assigned a call sequence to a species, if there were at least twice as many calls assigned to that species than any others, or classified it as Unidentified. Six percent of call sequences were Unidentified.

2.4.2. Effects of potentially confounding variables on relationships between bat activity/bat species richness/insect abundance and the landscape variables

We had intended to include any potentially confounding variables that were highly correlated to the landscape variables in our analyses (see Sections 2.4.3 and 2.4.4, below). However, correlations between our landscape variables (crop diversity, mean field size, and crop cover) and our five potentially confounding variables (mean temperature, precipitation, wind speed, moon illumination, and sampling date) were all low (all Spearman rank correlations ≤ 0.38; Table B1 in Supplementary file). Thus these variables should not confound interpretation of models relating bat activity/bat richness/insect abundance to these variables. Supplementary analyses confirmed this: our conclusions were the same whether we included the potentially confounding variables or not (Tables B2–B5 in Supplementary file). Additionally, inclusion of these variables reduced our sample size because only 43 of our 46 landscapes had estimates of all five confounding variables. Therefore, we do not include any of the potentially confounding variables in the presented analyses of effects of farmland heterogeneity on bat activity/bat species richness/insect abundance.

2.4.3. Effects of landscape variables on bat activity and species richness

We used model selection, based on the small-sample Akaike Information Criterion (AICc, also called the second-order AIC; Burnham and Anderson, 1998), to test our prediction of greater bat activity in agricultural landscapes with higher crop diversity and smaller mean field sizes, independent of the crop amount. We included three candidate farmland heterogeneity models that predicted the cross-landscape bat activity as a linear function of (1) crop diversity + mean field size + crop amount, (2) crop diversity + crop amount, and (3) mean field size + crop amount, and compared these to (4) a model including crop amount only, and (5) the null (intercept-only) model. Relationships were modeled using generalized linear models with a negative binomial distribution and log link. We included species as a categorical variable in each candidate model, to account for differences in overall activity among species. Effects of farmland heterogeneity on bat activity were supported if a model including crop diversity or mean field size had a smaller AICc than both the crop-amount-only model and the null model. This support was considered ‘strong’ if a farmland heterogeneity model had a ΔAICc ≥ 2 relative to the crop-amount-only model and null model. The response variable, bat activity, was the number of call sequences identified for each species in acoustic surveys, averaged for all visits of the two survey locations in each landscape. Mean values were rounded to the nearest integer for analysis.

In the analysis above, we assumed that each bat species responded to farmland heterogeneity in a similar way. To determine whether these cross-species models of bat activity were representative of the individual species’ responses to farmland heterogeneity, we reran the above analysis, including landscape variable × species interactions in the candidate model set.

We tested our prediction of more bat species in agricultural landscapes with higher crop diversity and smaller mean field sizes, independent of the crop amount, using the same model selection procedure and candidate model set as above, with the exception that here we used generalized linear models with a Poisson distribution and log link. The response variable, species richness, was the number of bat species identified in acoustic surveys, averaged for all visits of the two survey locations in each landscape and rounded to the nearest integer.

We chose to use model selection because our goal was to directly compare among multiple, competing candidate models to explain the variation in bat activity/richness among our sampling locations (Burnham and Anderson, 1998). However, we recognize that some readers prefer to rely on p-values for interpretation of variable significance. Therefore, we also report the statistical significance of landscape variable effects in each candidate model for the above analyses, and those in the section below, based on an analysis of variance with Type III sum of squares.

We conducted these analyses, and those in the section below, in R version 3.4.0 (R Core Team, 2017) using the MASS (Venables and Ripley, 2002), MuMln (Barton, 2016), and car (Fox and Weisberg, 2011) packages. Data used in these analyses are available through Mendeley Data (Monck-Whipp et al., 2017).

2.4.4. Effects of landscape variables on flying insect abundance

We used model selection to test for relationships between relative insect abundance and farmland heterogeneity. We used the same model selection procedure and set of five candidate models as described above (see 2.4.3 Effects of landscape variables on bat activity and species richness) to test for effects of farmland heterogeneity on insect abundance. The response variable was the number of insects in each size class (0–5 mm, 5–10 mm, 10–15 mm, and > 15 mm), averaged for the two survey locations within a landscape and rounded to the nearest integer. Relationships were modeled using generalized linear models with a negative binomial distribution and log link. We included size class as a categorical variable in each candidate model, to account for differences in overall abundance among size classes. To ensure that these models of insect abundance were representative of the responses of different size classes to farmland heterogeneity, we reran the above analysis, including landscape variable × size class interactions in the candidate model set. We also repeated these analyses using mean insect abundances for each order (Lepidoptera, Coleoptera, Hymenoptera, and Diptera) instead of size class.

3. Results

3.1. Effects of landscape variables on bat activity and species richness

We completed 108 acoustic surveys. The number of acoustic surveys ranged from 1 to 5 surveys/landscape: seven landscapes had one survey each, 23 had two surveys, 10 had three surveys, five had four surveys, and one had five surveys. We assessed calls from 2864 search-phase call sequences collected during these surveys, of which 2688 (94%) were identified to one of seven species: Lasius septentrionalis (1529 call sequences), Eptesicus fuscus (834), Myotis lucifugus (127), Lasius borealis (61), Lasionycteris noctivagans (61), Perimyotis subflavus (41), and Myotis septentrionalis (35; Fig. Cl in Supplementary file). There was an average of 27 search-phase call sequences per acoustic survey (range 0–214), and an average of three species found per acoustic survey (range 0–7). L. cinereus was the most common species (57% of identified call sequences) and was detected in all landscapes. M. septentrionalis was the least common species in our landscapes, detected in 30% (14/46) of the landscapes. Correlations among our three landscape variables ranged from r = −0.34 to 0.73 (all p ≤ 0.02; Table A1 in Supplementary file), and crop amount was strongly and negatively correlated with the dominant non-crop land cover, i.e., forest (r = −0.72, p < 0.001).

Bat activity increased with farmland heterogeneity, as predicted (Fig. 4, Fig. D1a,b in Supplementary file). Models including crop diversity and/or mean field size had more support than both the crop-amount-only model (ΔAICc ≥ 4.22) and the null (intercept-only) model (ΔAICc ≥ 11.48; Table 1). Candidate models including heterogeneity variables alone or in combination had similar support (ΔAICc ≤ 0.33; Table 1); thus, we cannot draw conclusions about the relative importance of crop diversity versus mean field size from this analysis.

Our supplementary analysis of the landscape variable × species interactions found that responses to farmland heterogeneity were
generally consistent across our seven study species. Although the most supported model set included candidate models with a mean field size × species interaction, these models had similar levels of support as models excluding interactions (Table E1 in Supplementary file). This is because farmland heterogeneity had the same direction of effect on five of the seven species for crop diversity and six of the seven species for mean field size (Fig. 4). And, with the exception of the response of *M. lucifugus* to mean field size, the 95% CI of the predicted farmland heterogeneity effect for each species overlapped with the effect predicted from models assuming a similar response across species (Fig. 4).

We did not find strong support for effects of farmland heterogeneity on bat richness (Fig. D1c,d in Supplementary file). The best supported model of bat species richness was the null model (Table 2).

### 3.2. Effects of landscape variables on flying insect abundance

We captured an average of 25 insects per survey (range 1–105; Fig. F1 in Supplementary file). The most supported model predicted insect abundance as a function of crop diversity + crop amount + size class (Table 3), with a positive effect of crop diversity on insect abundance (Fig. 5). However, we note that there was only moderate support for this model over the null model (ΔAICc = 1.17; Table 3). Landscape variable × size class interactions were not supported (ΔAICc ≥ 3.57; Table G1 in Supplementary file). We also found no support for relationships between insect abundance and farmland heterogeneity when accounting for insect order (Tables G2–G3 in Supplementary file).

### 4. Discussion

We found support for the hypothesis that bat abundance in agricultural landscapes increases with farmland compositional and structural characteristics (Table 3).
configural heterogeneity. Our prediction that bat activity increases with farmland heterogeneity was strongly supported, with higher bat activity in landscapes with more diverse crops and smaller crop fields. Effects of farmland heterogeneity on species richness were not statistically supported, although we note that farmland heterogeneity had the same direction of effect on both bat activity and species richness (Fig. D1 in Supplementary file). The lack of statistical support for effects of farmland heterogeneity on species richness was likely, at least in part, due to low variability in richness across landscapes (Fig. C1h in Supplementary file). Given this, we would have required a much larger sample size to increase statistical power and allow us to detect a farmland heterogeneity effect on species richness. Additionally, because farmland heterogeneity generally had the same direction of effect across individual species we were better able to detect effects in models of bat activity because these aggregated effects across species.

There are three main factors that may lead bat abundance to increase with farmland heterogeneity. First, farmland heterogeneity may benefit bats if prey is more abundant, and its availability more stable through time, in more heterogeneous landscapes. Previous studies have found significant positive effects of farmland heterogeneity on highly mobile insects (Bertrand et al., 2016; Fabrig et al., 2015), supporting this explanation. On the other hand, we found only moderate support for a relationship between insect abundance and crop diversity in our study landscapes. We note that our limited sampling effort for insects may have resulted in poor estimates of actual insect abundance, especially for high-flying species eaten by bats, and thus the effects of farmland heterogeneity on insects may have been underestimated. Nevertheless, this result suggests that insects are more abundant in agricultural landscapes with greater farmland compositional heterogeneity. Second, higher farmland configurational heterogeneity may benefit bat communities by increasing the length of field boundaries, especially those with hedgerows including tall vegetation such as shrubs or trees. A previous study has shown that bats are highly sensitive to the loss of field boundaries (including hedgerows; Pocock and Jennings, 2008), which bats can use as flight corridors, foraging habitat, and refuge from wind or predators (Verboom and Huijtema, 1997). Finally, bats may benefit from farmland heterogeneity because it reduces distances between foraging and roosting habitats. Future research is needed to determine the relative importance of these factors for bat activity in agricultural landscapes, using a set of landscapes that minimizes the correlations among heterogeneity metrics (e.g., crop diversity, mean field size, and field-forest interspersion).

The observed positive effects of farmland heterogeneity on bats may also, at least in part, result from an association between higher farmland heterogeneity and bat-friendly farming practices (e.g., reduced pesticide use, reduced hedgerow mowing/pruning). For example, several studies found more bat species and greater activity levels on organic than conventional farms (Fuller et al., 2005; Wickramasinghe et al., 2003), and organic farms tend to have smaller field sizes than conventional farms (Freemark and Kirk, 2001; Fuller et al., 2005). However, it is not clear from these correlational relationships whether bats benefit from organic farming because of farming practices, or because organic farms tend to have high farmland heterogeneity, or both. We note that organic farming is likely rare or absent in our landscapes, as only 1.5% of farms in Ontario are certified organic or are in the process of becoming certified (Statistics Canada, 2011). However, this does not preclude correlations between farming practices and farmland heterogeneity among conventional farms. Thus further research is required to determine the relative importance of farming practices and farmland heterogeneity for bats in agricultural landscapes.

In our landscapes, the amount of crop cover was negatively correlated with crop diversity and positively correlated with mean field size (Fig. A1 in Supplementary file); however, this collinearity does not explain the observed relationships between bat activity and our two measures of farmland heterogeneity. If crop amount was driving these relationships, we should have seen little improvement in model support between models including crop diversity or mean field size and the crop-amount-only model. This was not the case. Additionally, if crop amount was driving our observed relationships between bat activity and crop diversity, the direction of effect should have been opposite for crop amount and crop diversity because they are negatively correlated. This is opposite to what we observed: both showed positive effects on bat activity. If crop amount was driving our observed relationships between bat activity and mean field size, the direction of effects should have been the same for these two variables, because they are positively correlated. Instead, crop amount had a positive effect on bat activity, and mean field size had a negative effect. Therefore, correlations with crop amount were not responsible for the effects of farmland heterogeneity we observed.

Contrary to expectation, bat activity increased with the amount of crop cover in our study landscapes. This is surprising, given that a previous study suggested that bat activity is lower in agricultural landscapes with more open land cover types (including crop fields) and less tree cover (Kalda et al., 2014). Additionally, some studies suggest that bats are negatively affected by forest loss (e.g., Gorresen and Willig, 2004) and, in our landscapes, increasing crop cover was strongly related to a decline in forest cover. Indeed, the bat species we studied are all generally associated with forested or woodland habitats – which provide both roosting and foraging opportunities – although they are also known to forage in areas with more open canopies (Van Zyll de Jong, 1985). For example, P. subflavus activity has previously been shown to decline with loss of forest cover (Farrow and Broders, 2011), and M. septentrionalis preferentially forages in forested areas instead of farm fields (Henderson and Broders, 2008). However, a previous study in our study area found that the activity levels of some of our bat species – including P. subflavus – were higher in landscapes with less forest cover (Ethier and Fahrig, 2011). We speculate that bats may be more active in landscapes with more crop cover because, in our agriculture-dominated study area (on average 69% of the landscape in crops), crops were better foraging habitat than the small remnants of semi-natural land cover. Alternatively, bat activity may have appeared higher in landscapes with more crop cover because foraging activity in
landscapes with more crops is concentrated along hedgerows rather than forest edges (Jantzen and Fenton, 2013). If true, we may have underestimated bat activity in landscapes with less crop cover because we did not survey along forest edges.

In closing, our results support the hypothesis that farmland heterogeneity increases bat abundance in agricultural landscapes. Although previous studies have investigated effects of crop type and farming practices on bats in agricultural landscapes (Davy et al., 2007; Fuller et al., 2005; Lentini et al., 2012; Wickramasinghe et al., 2003), and effects of overall landscape heterogeneity (including all land cover types) on bats (Bolivar-Cimé et al., 2013; Fuentes-Montemayor et al., 2013), to our knowledge this is the first to look at the effects of the heterogeneity of the cropped portion of the landscape (i.e., farmland).

Positive effects of farmland heterogeneity on bats may be particularly interesting to farmers and agricultural policy makers, given the benefit of bats for pest removal from farms (Boyles et al., 2011). Pest removal services may become increasingly important in temperate climates, where pest outbreaks are predicted to become more frequent as the climate warms and pest insect ranges expand to higher latitudes (e.g., Bebber et al., 2013).

Our study also adds to the growing body of literature supporting the hypothesis of positive effects of farmland heterogeneity on biodiversity (Bertrand et al., 2016; Collins and Fahrig, 2017; Fahrig et al., 2015; Josefsson et al., 2017). Pressure to increase food production to satisfy a growing global human population poses a challenge for biodiversity conservation, because conversion of natural and semi-natural land covers to crop fields results in habitat loss and biodiversity declines (e.g., Billette et al., 2008; Duchamp et al., 2004; Nupp and Swithart, 2000). Thus the challenge for conservation is to find actions that can maintain or increase biodiversity without taking land out of production. Studies, including ours, suggest that one way to enhance biodiversity in farmlands is to increase landscape heterogeneity of crop cover, by increasing the diversity of crop types in farmlands and reducing the average size of crop fields.

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Appendices A–G Supplementary data
Supplementary data associated with this article can be found in the online version, at https://doi.org/10.1016/j.agee.2017.11.001.
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