



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

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Abstract

Context Agricultural intensification has led to widespread declines in biodiversity. An important component of agricultural intensification in many regions, including eastern Ontario, is the shift from grazing lands and perennial forage crops to annual row crops, with associated increases in use of pesticides.

Objectives We predicted that bat abundance and diversity would be lower in sites surrounded by landscapes with more agriculture and where the agriculture was dominated by annual row crops rather than perennial forage crops.

Methods We assessed bat occurrence and relative bat abundance with acoustic bat recorders at the centres of 32 landscapes that varied in (1) the proportion of agriculture and (2) the proportion of

agriculture that is in annual row crops versus perennial forages (pasture and hay).

Results 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 in the surrounding landscape. Inconsistent with our second prediction, 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 in the surrounding landscape.

Conclusions Based on these results, 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 types. We speculate that farmlands with a diversity of crop types provide a more temporally stable supply of insect food for bats.

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Introduction

Agriculture intensification and expansion are occurring globally (Bruinsma 2009; Laurance et al. 2014).

Intensification generally involves (i) loss of grazing lands to annual crops and (ii) 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 receive very little inputs (e.g. herbicide), are disturbed infrequently and contain perennial plant species (Boutin and Jobin 1998). Conversely, annual row crops typically receive chemical inputs, are disturbed more frequently (e.g. tillage), and fields are actively managed to contain a single annual crop (Tscharntke et al. 2005; Boehmel et al. 2008). In contrast to agriculture intensification, agriculture expansion generally involves the loss of natural land covers and land features to agriculture (Matson et al. 1997). While some wildlife-friendly initiatives are carried out by farmers (Hobbs et al. 2008; Ward et al. 2018), these practices are limited globally (Prestele et al. 2018).

Insectivorous bats should be sensitive to agriculture intensification and expansion because of direct and indirect reductions in prey availability and roosting habitat. 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 applications (Stoate et al. 2001; Robinson and Sutherland 2002). Consistent with this, Put et al. (2018) found positive responses of bat abundance and diversity, and abundance of their insect prey, to organic farming. Less intensively managed agricultural land covers have a greater variety of vegetation, providing more varied habitats (Tews et al. 2004), and thus are expected to support higher diversity of insect prey (Knops et al. 1999; 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 and throughout a season, because different insect species can be active at different times during the night (Rydell et al. 1996) and at different times of the season (Davidai et al. 2015). Bats should also be sensitive to agriculture expansion, as natural land covers and features provide more roosting and foraging habitat (e.g. trees, edges, linear woody features) than agricultural land covers, particularly for bat species that do not roost in human-

made structures, such as houses (Henderson and Broders 2008; Jantzen and Fenton 2013).

Previous studies have found various responses of bats to surrounding landscape structure. Bats respond positively to the presence of woodland patches and waterbodies (Kalda et al. 2015), and to the diversity of crop types (Monck-Whipp et al. 2018) in the landscape. Bats also respond to landscape configuration, including positive responses to forest fragmentation per se (Ethier and Fahrig 2011), and higher bat abundance and diversity in landscapes with smaller crop fields (Monck-Whipp et al. 2018). However, as far as we are aware the effect of agricultural cover in annual row crops versus perennial forages on bats has not been studied.

From 2001 to 2016 in Ontario, Canada, high-intensity annual crops, primarily corn and soybeans, 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 once every 3 years, and the fields receive no pesticide inputs (Farm & 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 & Food Care Ontario 2015). These changes in agricultural practices through time, combined with recent precipitous population declines in North American bat species (Frick et al. 2010; Hammerson et al. 2017), highlight the need to identify landscape patterns that support remaining bat populations.

Our objective was to measure relative bat abundance and diversity in a set of sample sites centred in landscapes that were selected such that the proportion of the landscape in agriculture and the proportion of agricultural lands in annual crops (versus perennial forage crops) varied independently. As described above, forest cover provides roosting and foraging 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 sample sites with more agricultural land cover in the surrounding landscapes. 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. Consistent with this, previous studies have shown higher bat activity in perennial forages than in annual row crops (Lentini et al. 2012; Millon et al. 2015; but see Wolcott and Vulinec 2012). As a result, we expected more bats in sites surrounded by landscapes where the agriculture is dominated by perennial forages relative to landscapes where the agriculture is dominated by annual crops. Thus we predicted that bat species richness, abundance and individual species presence would be highest in sites surrounded by landscapes where (1) the proportion of agricultural land cover was low and (2) agricultural land cover was dominated by perennial forages.

Materials and methods

Overview

To test our predictions we used acoustic recordings to estimate relative bat species richness, total bat abundance and individual bat species abundance or presence in 32 sites for which the surrounding landscapes varied in (1) the proportion of agriculture and (2) the proportion of agriculture that was in annual row crops versus 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, given that in our region most non-annual crop cover is perennial forage. For a given landscape, a high value for the proportion of agriculture that was in annual row crops indicated that the landscape was dominated by annual row crops, while a low value indicated that the landscape was dominated by perennial forage. Total bat activity was used as an index of total bat abundance. We then performed generalized linear mixed modeling (GLMM) with bat species richness, total bat activity and species-specific activity or presence as response variables and the proportion of the surrounding landscape in agriculture and the proportion of agriculture in annual crops as predictor variables.

Study region

We conducted our study in eastern Ontario, to the southwest of Ottawa, Canada. During the eighteen and nineteen 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. Corn and soybeans were first grown in the area in the 1970s, and now agricultural land in annual row crop production exceeds the area in perennial forages. In 2016, the agricultural land in eastern Ontario was composed of 43.1% (370,919 ha) annual row crops and 34.6% (297,661 ha) perennial forage land (pasture: 131,739 ha, hay: 165,922 ha; OMA-FRA 2017).

Landscape selection

Thirty-two bat sample sites were selected in eastern Ontario. The sample sites were surrounded by landscapes 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 the sampling site where bats were recorded (Figs. 1, 2). The sampling site at the centre 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 were calculated in ArcGIS 10.3.1 (ESRI, Redlands, California, USA) using the 2013 Annual Crop Inventory (AAFC 2013) data layer.

To select the sample sites we began with 313 candidate 1-km radius circular landscapes that were at least two km apart edge to edge and centred on potential sampling sites along country roads within 100 km of the city of Ottawa. To narrow down our set of 313 candidate sites to a number that we could feasibly survey for bats, we first selected sites whose surrounding landscapes had at least 35% agriculture. From these we then sub-selected sites to reduce variation in the proportions of the surrounding landscapes in water/wetland and developed area, to control for the effects that these land cover types have on bat activity. Bat activity is known to be positively associated with water (Korine et al. 2016; Torrent et al. 2018) and negatively associated with development (Geggie and Fenton 1985; Walters et al. 2007). Our remaining 87 sites had < 0.25 water/wetland and < 0.2 developed area within their 1-km radius surrounding landscapes. We sub-selected from these sites to limit any correlation between our two landscape variables of interest, i.e. the proportion of the surrounding landscape in agriculture and the proportion of agriculture in annual crops

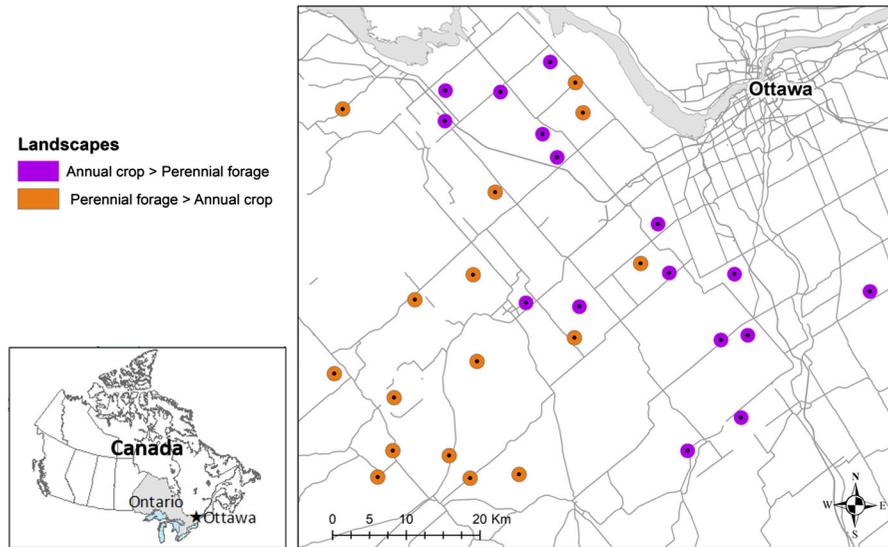


Fig. 1 Locations of 32 sample sites in eastern Ontario within 100 km of Ottawa, where bat surveys were conducted using bat recorders. Bat recorders were placed at the centres (black dots) of the landscapes (dark and light circles). Landscapes that had

more of their agricultural cover in annual crops than perennial forages are indicated in dark 1-km radius circles, and those that had more agriculture in forages than annual crops are indicated in light 1-km radius circles

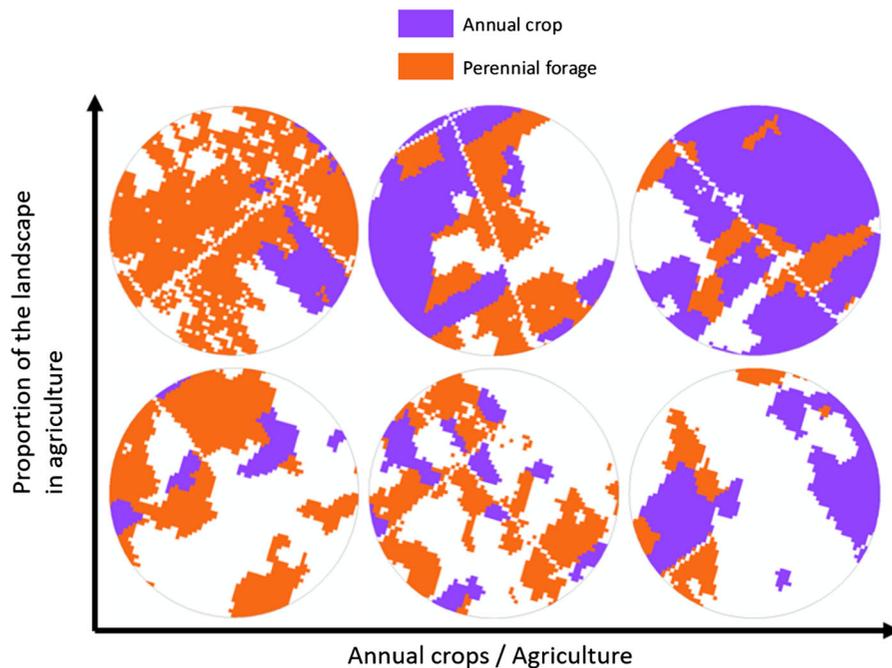


Fig. 2 Example landscapes with a 1 km radius extent depicting the variation in the proportion of the landscape in agriculture [dark shaded (annual crops) plus light shaded (perennial forage) areas] and the proportion of agriculture that is annual crops (dark shaded areas divided by dark shaded plus light shaded areas). In all, bats were sampled at the centres of 32 agricultural

landscapes, to determine how bat species richness, total bat activity and individual bat species activity or presence are related to (1) the proportion of the surrounding landscape in agriculture and (2) the proportion of agriculture in the surrounding landscape that is annual crops. Non-agriculture (white) areas in the landscapes are mainly forested

($r = -0.03$, Spearman's rank correlation). This resulted in 32 sites (Figs. 1, 2). The bat sampling sites (at the centres of the landscapes) were on average 6.4 km (range 3.7–17.6 km) apart. Some sampling sites were shifted slightly when in situ verification revealed that the originally-selected sampling site lacked a nearby tree or shrub, which was necessary for installing bat recording equipment (below). The landscapes surrounding our final 32 sampling sites had an average of 0.04 water/wetland (range 0.001–0.201) and 0.04 developed area (range 0.017–0.098) within a 1-km radius of the sample sites.

Field data: echolocation recordings

From June 13th to July 29th 2016, one bat recorder (SM2 + BAT, Wildlife Acoustics, Maynard, Massachusetts, USA) was deployed at each of the 32 sampling sites, for two deployment periods. Each deployment period was three or four sampling nights long. From each deployment period, recordings from two 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 resulted in lower recorded bat activity (Erickson and West 2002) which could reflect an actual reduction in bat activity or reduced microphone sensitivity. Therefore, the total number of acoustic surveys analyzed was 128, i.e. 32 landscapes \times 2 deployments \times 2 survey nights per deployment. The time between the first and second deployment periods at each landscape was on average 20 days, and the minimum time between successive sampling at the same site was 7 days (range 7–27 days). We had eight individual recorders, and we sampled two to six sites simultaneously that were on average 19.6 km apart (range 4.1–57.6 km). We also ensured that the order in which we visited the sample sites was independent of our two main predictor variables; the proportion of the surrounding 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 deter tampering. The microphones we used (SMX-US, Wildlife Acoustics) were omni-directional, so this would have had little effect on the number of bat recordings based on microphone orientation.

The bat recorders were programed to passively record full-spectrum echolocation passes from sunset ($\sim 20:30$ to $21:00$) to sunrise ($\sim 5:15$ to $5:45$). The recorders were triggered to record automatically when sound above 12 dB and between 1 and 96 kHz was detected. The unit was set to record for a minimum of 2 s and up to a maximum of 20 s if sound continued to be detected. The recorder would stop recording prior to 20 s if there was silence for 2 s. We recorded for a maximum of 20 s per recording segment, to reduce instances where the same individual bat triggered the recorder multiple times on the same flight (pass) by the microphone. Note these settings were nearly identical to settings in previous studies in our study area (Ethier and Fahrig 2011; Monck-Whipp et al. 2018), ensuring that bat activity estimates could be compared.

Bat species identification

Each 2–20 s recording is called a bat “pass”. A bat pass is made up of a quick succession of repetitive calls. Within a pass there can be three types of calls: search-phase, approach-phase and feeding buzzes (Gillam 2007; Harvey et al. 2011). Search-phase calls are made when a bat is commuting and searching for prey. If a bat finds a prey item, the calls will increase in repetition (approach-phase calls), and just prior to prey capture the bat will vocalize a “feeding buzz” (Schnitzler and Kalko 2001). A feeding buzz occurs when the calls are so rapid that they are not easily distinguishable from each other (Gillam 2007). Search-phase calls are consistently different for different bat species in our region (Ethier and Fahrig 2011; Adams 2013), whereas approach-phase calls and feeding buzzes are not.

Search-phase calls are typically used to identify bat passes to species (Fenton and Bell 1981). We identified bat species based on the following acoustic parameters of search-phase calls: call duration, inter-pulse interval, maximum frequency, minimum frequency, dominant frequency, slope and curvature. The program Spek 0.8.2 (General Public Licence) 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 calls (false-positives: 10.9% of recordings). We included only search-phase passes containing at least two calls above 16 dB, with a duration of 0.99–30 ms and a minimum frequency range of 15–60 kHz, to remove weak and fragmented calls (Adams 2013).

We measured the acoustic parameters of the calls in the retained search-phase passes using Scan'R 1.6.0 (Binary Acoustic Technology). We then entered these parameters in a quadratic discriminate function analysis model (QDFA) created by Ethier and Fahrig (2011) specifically for identifying bat passes of species in our region. This model was created using 269 reference search-phase calls, of known species identity, that had been previously recorded by researchers in the Fenton laboratory at The University of Western Ontario, Ontario, Canada (Hooton 2010; Adams 2013), and that were provided by them to Ethier and Fahrig (2011) for construction of their QDFA model. The reference calls belonged 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 QDFA gives a posterior probability of the parameters of the call being attributed to each species in our region (0–1). Using the reference bat passes, the model has an overall species identification rate of 88.8% (see supplementary material in Ethier and Fahrig 2011 for more detail). Note that the species identification rate of our QDFA model is based on the 269 reference search-phase calls and not the search-phase calls we collected. From each bat pass, we used the call with the highest signal-to-noise ratio in the QDFA. Following Ethier and Fahrig (2011), 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 call with the second highest signal-to-noise ratio. If the posterior probability of the second call was > 0.5 for the same species as the first call, we assigned the pass to that species; otherwise, we classified the pass as “Unknown”. If the posterior probability of the call with the highest signal-to-noise ratio was < 0.5 for all species, we also classified the pass as “Unknown”. Four percent of all

passes were categorized as “Unknown”. We ran the QDFA model in R 3.2.4 (R Core Team 2017) using the `qda()` function from the *MASS* (Venables and Ripley 2002) package.

We were concerned that the accuracy levels of the QDFA model might have been over-estimated because Ethier and Fahrig (2011) had derived them using a randomization procedure with the same data from which the QDFA model had been built. To account for this potential issue, we also tested our predictions for groups of species whose search-phase calls are similar (Online Resource Fig. 3 and Table 7). We created two groups of calls; the first group contained calls of little brown bat, northern long-eared bat and tri-colored bat, and the second group contained calls of hoary bat and silver-haired bat. We did not include big-brown bat or eastern-red bats in the grouped analyses because these species have distinct search-phase call characteristics (Gehrt and Chelsvig 2004; Silvis et al. 2016).

Landscape predictor variables

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

As described above, for site selection we used landscape variables measured within 1-km radius landscapes around the sample sites. 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 measured the landscape predictor variables within a range of 15 nested spatial extents, from 0.125 to 6 km radius around each sampling site (Fig. 3; Online Resource Table 1). Land cover data were taken from the 2016 Annual Crop Inventory (AAFC 2017).

Potential confounding variables

As described above, we selected sample sites to minimize the variation across landscapes with respect to the amount of water/wetland and the amount of

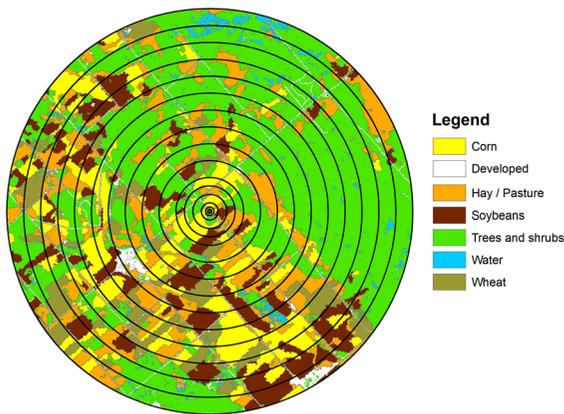


Fig. 3 Example of land cover in one of the 32 sample agricultural landscapes. Bat surveys were conducted at the centre focal point of the landscape. The land cover is mapped within each of 15 circular landscapes (0.125, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5 and 6 km radius), to estimate 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)

urban development in the surrounding landscapes. This was done to minimize the likelihood that these variables, which are known to affect bat activity (Geggie and Fenton 1985; Walters et al. 2007; Korine et al. 2016; Torrent et al. 2018), would mask effects of our variables of interest. We also minimized variability in bat recordings due to temperature (Erickson and West 2002) by selecting the two warmest nights from each deployment period. Nevertheless there was still variation across sample sites in temperature and date of sampling. We expected bat activity to increase with date of sampling due to overall population growth during the breeding season.

To verify that temperature and date of sampling would not affect the interpretation of our results, we performed Spearman's correlations between these variables and our landscape predictor variables of interest. The correlations were generally low, ranging between -0.08 and 0.42 (Online Resource Table 2). However, some of the correlations were significant, and we included in our final GLMMs any variables that were significantly ($p < 0.05$) correlated with either of the landscape predictor variables of interest. We also conducted analyses excluding these potentially confounding variables, regardless of their correlations with our predictor variables of interest, which did not alter our conclusions (Online Resource Table 6). Note that potentially confounding variables

were treated as covariates instead of random effects in our analyses (below) because they were on continuous scales and we had a priori expectations of linear relationships.

Statistical analysis

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

Before testing our predictions we first estimated the appropriate spatial extent for measuring the landscape predictors (their scales of effect), for each bat response. To do this we conducted GLMMs in two stages. First, for each response variable (bat species richness, total bat activity and species-specific activity or presence/absence) and each landscape predictor (proportion of the surrounding landscape in agriculture and proportion of agriculture in annual crops) we did a series of 15 models, one model for each of the 15 nested spatial extents, with the landscape predictor measured at that spatial extent, and including site ID and recorder ID as random effects. The 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, we tested our predictions by conducting a GLMM for each response variable using the landscape predictors at their scales of effect for that response. Although correlations between the landscape predictor variables and all potential confounding variables were low (Online Resource Table 2), as described above, we included in the models any potentially confounding variables that were significantly correlated to either of the landscape predictors at its scale of effect. We also included landscape ID and recorder ID as random effects. Recorder ID (a unique identifier for each of the eight recorders used) was included to account for differences in sensitivity among the recorders. Note 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 the GLMMs for the species richness of bats we used a Poisson distribution, appropriate for count data.

For the GLMMs for total bat activity and the activity of the three most common bat species (big brown bat, hoary bat, little brown bat) we used a negative binomial distribution to account for overdispersion tested for with `dispersiontest()` from the *AER* package (Kleiber and Zeileis 2008). Binomial distributions were used on presence/absence data for the four least common bat species (eastern red bat, northern long-eared bat, silver-haired bat, tri-colored bat). 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()` function from *glmmADMB* (Skaug et al. 2016), the `glmer()` function from *lme4* (Bates et al. 2015) and the `AICc()` function from *MuMIn* (Barton 2014) packages. The data set used in our analysis is available through Mendeley Data (Put et al. 2017). Our first prediction would be supported if the proportion of the surrounding landscape in agriculture had a negative relationship with the bat response variables at the sample sites. Our second prediction would be supported if the surrounding proportion of agriculture in annual crops had a negative relationship with the bat response variables. We interpreted p values ≤ 0.05 as showing moderate or strong evidence of an effect and p values > 0.05 and ≤ 0.10 as being suggestive of an effect (Murtaugh 2014).

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 hump-shaped pattern. For these response variables we tested whether adding a quadratic term for the proportion of agriculture in annual crops to the model would better predict the responses we observed. Last, 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. We counted the number of feeding buzzes manually when visually inspecting the bat passes.

Results

Over all 128 acoustic surveys at the 32 sites, we recorded 13,245 bat passes. We detected all seven species which should be found in our study area, 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 all the 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 , $p > 0.10$; Online Resource Table 3). There was a strong positive correlation across acoustic surveys ($r = 0.85$) between total bat activity and total feeding buzzes (Online Resource Fig. 2), indicating that in locations with greater bat activity, bats are foraging more.

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 to 4.5 km for the proportion of the landscape in agriculture and from 0.25 to 6 km for the proportion of agriculture in annual crops, depending on the response variable (Fig. 4). 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 (Online Resource Table 2). Correlations between our landscape predictors and the potentially confounding variables were generally low (range -0.08 to 0.42 ; Online Resource Table 2), but some of the correlations involving average temperature and ordinal date were statistically significant.

Consistent with our first prediction, bat species richness, total bat activity and activity levels or presence of four bat species had significant ($p < 0.05$) or near significant ($p < 0.1$) negative responses to the proportion of the surrounding landscape in agriculture, and the direction of the effect was negative for all the other species except silver-haired bats (Fig. 5, Table 1, Online Resource Table 5).

Contrary to our second prediction, the activity levels or presence of bats was not highest at sites surrounded by landscapes with agriculture dominated by perennial forage crops. Bat species richness, total bat activity and presence of three bat species had significant ($p < 0.05$) or near significant ($p < 0.1$) quadratic responses to the proportion of agriculture

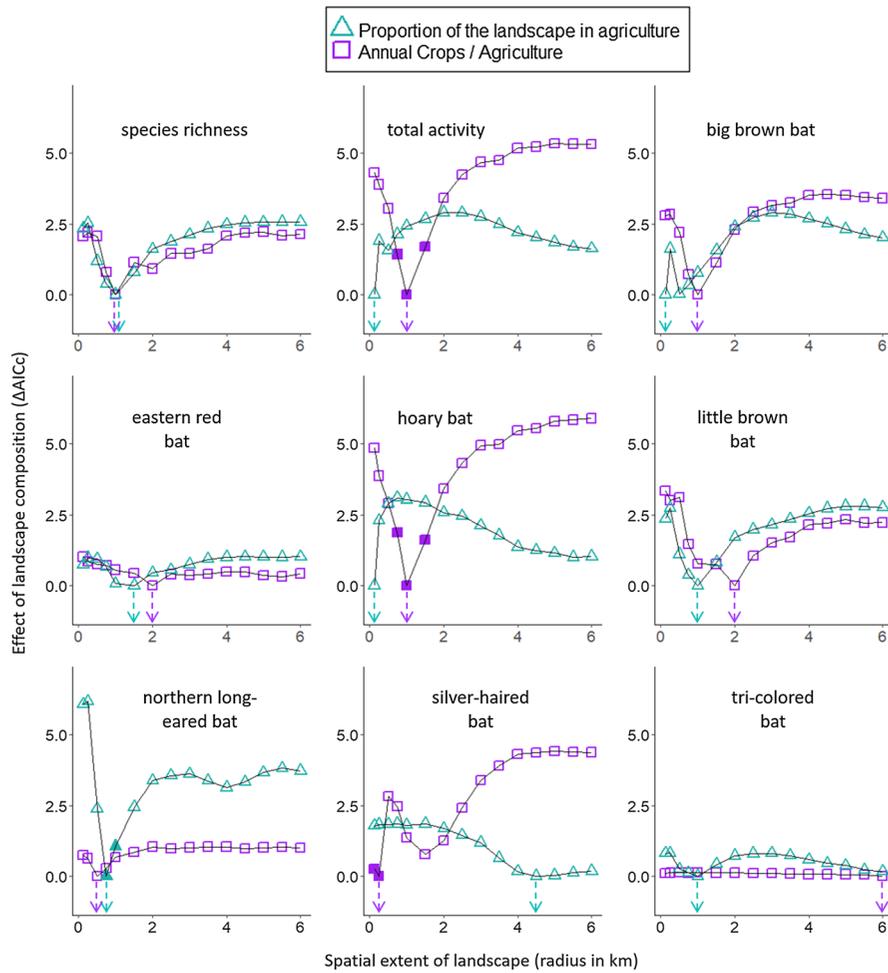


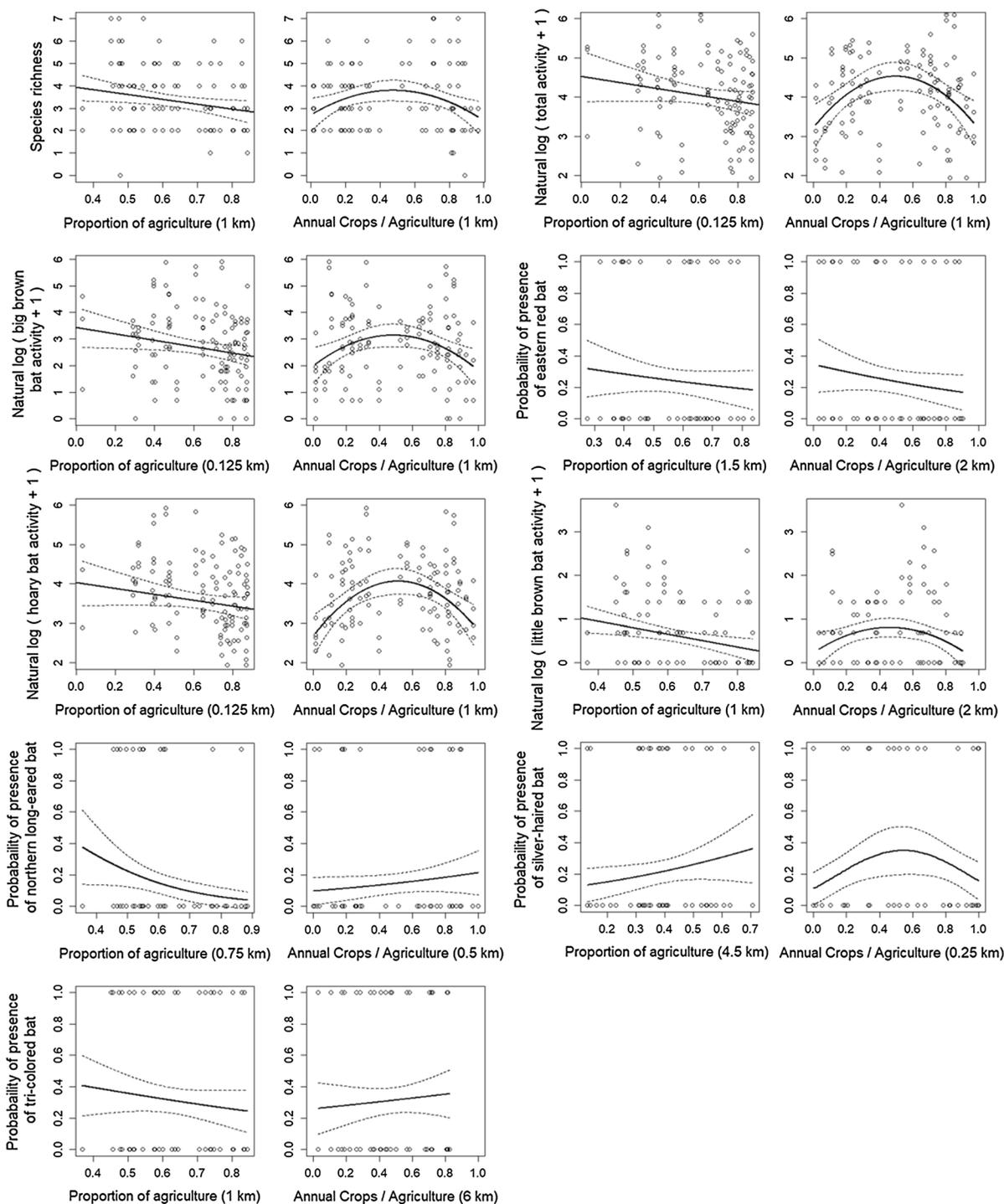
Fig. 4 Estimation of the scale of effect of each of two landscape variables—the proportion of the surrounding landscape in agriculture (triangles) and the proportion of agriculture in annual crops (squares)—on bat richness and abundance

response variables measured at the centre points of each of 32 landscapes. The 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 where the $\Delta AICc$ value equals 0 (vertical arrows). Filled-in symbols indicate statistical significance at the 0.05 level

that is annual crops in the surrounding landscape, where activity was greatest where the proportion of agriculture in annual crops was about 0.46 to 0.51 (Fig. 5, Table 1, Online Resource Table 5). The amount of variance explained by the species richness, total activity, big brown bat, eastern red bat, hoary bat, little brown bat and tri-colored bat (Conditional $R^2 = 0.64, 0.42, 0.51, 0.49, 0.64, 0.56$ and 0.62 , respectively) models was relatively high. However, the amount of variance explained for the northern long-eared bat and silver-haired bat (Conditional $R^2 = 0.08$ and 0.19 , respectively) models was relatively low.

Discussion

We found support for our prediction that bat abundance and richness would be lower at sites surrounded by landscapes containing more agriculture. 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 of northern long-eared bats in sites surrounded by landscapes with lower proportions of agriculture. Consistent with these findings, studies have found higher bat abundances in landscapes with more forest cover (Ethier and Fahrig 2011; Heim et al. 2015;



Rodríguez-San Pedro and Simonetti 2015), higher bat abundances closer to vegetated strips in agricultural landscapes (Estrada et al. 1993; Verboom and

Huitema 1997; Boughey et al. 2011), and have also found that agricultural landscapes with more hedgerows and woodlots have higher bat abundance

◀ **Fig. 5** 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 (Fig. 4). There was a single bat sampling site at the centre of each landscape. In the plots, there are four data points per sampling site—one from each sampling night. Bat species richness is the number of different bat species recorded at a site during a sampling night. Total bat activity is the summed number of bat passes recorded at a site during a sampling night. The scale of effect for each landscape predictor variable on a given response variable (Fig. 4) is indicated in brackets on the x-axis. Log-transformations were performed to facilitate interpretation of the plots, but data were not log-transformed in the analyses. Dashed lines represent the 95% confidence intervals

(Verboom and Huitema 1997). These studies are consistent with our result because (i) landscapes with higher proportions of agriculture typically have larger fields (Roschewitz et al. 2005; 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 the 6-km radius).

Table 1 Standardized model estimates and standard errors (in brackets) from GLMMs predicting the effect of the proportion of the surrounding 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 at sampling sites at the centres of the landscapes (* p value < 0.05, † p value < 0.10)

Although the relationships between agricultural cover and the presence of eastern red bats and tri-colored bats were not significant, the direction of response for these species was consistent with the negative responses observed for the other species. The relationship was positive for silver-haired bats, but also not significant. The non-significant relationships for these three species with agricultural cover were unexpected because all of them depend on natural roosting sites (Campbell et al. 1996; Limpert et al. 2007; Poissant et al. 2010), the availability of which should be reduced in landscapes containing more agriculture or alternatively, less forest. We infer from this that availability of roosting habitat may not be as important a factor limiting bat populations in our study area as we had assumed.

We note, however, that our results for effects of agricultural cover on individual species should be interpreted with caution, as they are not entirely consistent with other studies. For example, in the same study region Ethier and Fahrig (2011) found no significant effects of forest cover (approximately the inverse of agricultural cover) on the four species for

Response variable	Landscape predictor variables			Potential confounding variables	
	Proportion of agriculture	Annual crops/agriculture	Annual crops/agriculture ²	Ordinal date	Average temperature
Species richness	- 0.10 (0.06) [†]	0.48 (0.25) [†]	- 0.48 (0.25) [†]		- 0.01 (0.05)
Total bat activity	- 0.24 (0.14) [†]	1.49 (0.64)*	- 1.55 (0.64)*		
Big brown bat activity	- 0.33 (0.19) [†]	1.58 (0.90) [†]	- 1.70 (0.90) [†]		
Eastern red bat presence	- 0.11 (0.43)	- 0.29 (0.44)			- 0.41 (0.29)
Hoary bat activity	- 0.21 (0.12) [†]	1.41 (0.55)*	- 1.44 (0.54)*		
Little brown bat activity	- 0.50 (0.27) [†]	2.28 (1.09)*	- 2.33 (1.11)*		- 0.09 (0.15)
Northern long-eared bat presence	- 0.72 (0.31)*	0.32 (0.27)			
Silver-haired bat presence	0.09 (0.31)	1.80 (1.24)	- 1.84 (1.15)	0.28 (0.24)	
Tri-colored bat presence	- 0.45 (0.47)	0.10 (0.44)		1.09 (0.37)*	- 0.54 (0.33)

The scale of effect used in each GLMM for the landscape predictors is in Figs. 4 and 5. 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 the corresponding GLMMs (see Online Resource Table 4). If the GLMM with the quadratic term had a lower AICc value than the one without, then we included the quadratic term in our final GLMM for that response variable. We included potentially confounding variables in our final GLMMs that were significantly ($p < 0.05$) correlated with either of the landscape predictor variables of interest based on the Spearman’s correlation coefficient

which we did find significant or near significant effects of agriculture cover. Also, they found significant effects of forest cover on the three species for which we did not find significant or near significant effects of agricultural cover. Nevertheless, the direction of some of the effects they found was consistent with some of our results: they found a significant positive effect of forest cover (i.e. a negative effect of agriculture cover) on eastern red bats and a significant negative effect of forest cover (i.e. a positive effect of agriculture) on silver-haired bats, both of which are consistent in direction with our results. However, Ethier and Fahrig (2011) also found a significant negative effect of forest cover on tri-coloured bats, which is not consistent with our result. Like Ethier and Fahrig (2011), we also found that the direction of the relationships often shifted with the spatial extent within which agricultural cover was measured (Online Resource Fig. 1).

Some of the differences in the effects of agricultural cover for different species between the results of Ethier and Fahrig (2011) and our study may be statistical artefacts of the relatively small sample sizes of both studies (22 and 32 sampling sites, respectively). Multi-landscape studies are often plagued with small sample sizes for logistical reasons. This can be mitigated to some extent by using a structured site selection procedure, as we did, in which sites are selected to minimize correlations among variables of interest and among potential confounding variables (Pasher et al. 2013). However, it is not possible to control for all potentially confounding variables in site selection. Thus, another potential reason for the different responses to agricultural cover observed between our study and that of Ethier and Fahrig (2011) is that the two studies selected sample landscapes along different gradients. Ethier and Fahrig (2011) selected their sample landscapes over gradients of forest cover and forest fragmentation per se, i.e. fragmentation independent of forest cover. As we did not control for habitat fragmentation per se and they did not control for the proportion of agriculture in annual row crops, it is possible that these variables contributed to the differences in results for agricultural cover between the two studies. Microhabitat characteristics have been found to have strong effects on bat activity in some studies (Charbonnier et al. 2016) and so microhabitat differences could also have contributed to the differences in species responses to

agricultural cover between our study and Ethier and Fahrig (2011).

We did not find support for our prediction that bat sample sites surrounded by landscapes where the agriculture is dominated by perennial forages would have greater bat diversity and abundances than bat sample sites surrounded by landscapes where the agriculture is dominated by annual row crops. This finding is in contrast to evidence that, at a local scale, bat species richness and activity are higher at pastures containing native perennial plant species than at annual crop fields (Lentini et al. 2012). Our results suggest that we cannot extrapolate this local-scale association between bat activity and pasture to infer a negative response to the proportion of agriculture in annual row crops within the landscape surrounding bat sample sites. Such inconsistencies between the effects of locally-measured variables and the same variables measured over the landscape are common (e.g. Fahrig et al. 2019), underlining the need to evaluate effects of landscape context by measuring them directly rather than by inferring them from local-scale effects.

It is possible that the lack of a consistent negative effect of the proportion of agriculture in annual row crops on bats is because the perennial forages in our landscapes consisted of more hay land than pasture. Similar to annual row crop fields, hay land is often planted with one crop species (e.g. alfalfa), 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. Greater insect diversity would be expected to provide a more stable level of prey availability for bats 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). 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 negative response of bats to the proportion of agriculture in annual row crops in the surrounding 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 due to constraints in interpretation of remotely-sensed imagery used to assign land covers.

On the other hand, we did find a peaked relationship between the proportion of agriculture in annual row crops in the surrounding landscape and species

richness, total bat abundance and the abundance 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, insect 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 the United States (Davidai et al. 2015). With higher insect diversity in perennial forage fields (Nicholls and Altieri 2013; 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 as indexed by total feeding buzzes (Online Resource Fig. 2), which is opposite to what we would have seen if bat activity were elevated in low-prey sites. Bats are thought to forage efficiently (Fujioka et al. 2016), and would be expected to move on quickly if they encountered a low-prey area.

Conclusions

Given our findings, we suggest that overall bat abundances can be increased in agricultural landscapes by reducing the conversion of natural areas to agriculture and by 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 throughout the season and short-term insect pest outbreaks at annual row crops, which together would provide consistently high availability of prey for bats in these landscapes.

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