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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

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landscape heterogeneity (including all land cover types, e.g., Bolívar-Cimé et al., 2013) or semi-natural habitat heterogeneity (e.g., Billeter 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 (Boughey et al., 2011; Frey-Ehrenbold et al., 2013; Lentini et al., 2012; Limpens et al., 1989; Verboom and Huitema, 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 km^2 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-b1eb-d058803f80f9). 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