



Effects of farmland heterogeneity on biodiversity are similar to—or even larger than—the effects of farming practices



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ABSTRACT

Pressure to increase food production to meet the demands of a growing human population can make conservation-motivated recommendations to limit agricultural expansion impractical. Therefore, we need to identify conservation actions that can support biodiversity without taking land out of production. Previous studies suggest this can be accomplished by increasing “farmland heterogeneity”—i.e. heterogeneity of the cropped portions of agricultural landscapes—by, for example, decreasing field sizes. However, it is not yet clear whether policies/guidelines that promote farmland heterogeneity will be as effective as those targeting farming practices. Here, we estimated the relative effects of six practices—annual/perennial crop, fertilizer use, herbicide use, insecticide use, tile drainage, and tillage—versus two aspects of farmland heterogeneity—field size and crop diversity—on the diversity of herbaceous plants, woody plants, butterflies, syrphid flies, bees, carabid beetles, spiders, and birds in rural eastern Ontario, Canada. The strength of effect of farming practices and farmland heterogeneity varied among taxonomic groups. Nevertheless, we found important effects of both farming practices and farmland heterogeneity on the combined (multi) diversity across these groups. In particular, we found greater multidiversity in untilled, perennial crop fields than tilled, annual crop fields, and greater multidiversity in agricultural landscapes with smaller crop fields and less diverse crops. The directions of effect of these variables were generally consistent across individual taxonomic groups. For example, richness was lower in landscapes with larger fields and more diverse crops than in landscapes with smaller fields and less diverse crops for all taxa except spiders. The negative effect of crop diversity on multidiversity and the richness of most of the studied taxa indicates that this aspect of farmland heterogeneity does not necessarily benefit wildlife species. Nevertheless, a compelling implication of this study is that it suggests that policies/guidelines aimed at reducing crop field sizes would be at least as effective for conservation of biodiversity within working agricultural landscapes as those designed to promote a wildlife-friendly farming practice.

1. Introduction

Pressure to increase food production to meet the demands of a growing human population (United Nations, 2017) poses a challenge for wildlife conservation. Biodiversity would likely benefit if we limited further agricultural expansion and removed land from production (e.g. Egan and Mortensen, 2012; Norris, 2008; Scharlemann et al., 2005); however, the need to feed people can make such conservation-

motivated recommendations impractical. A more practical approach would be to identify conservation actions that support biodiversity without taking land out of production.

Fahrig et al. (2011) hypothesized that biodiversity could be increased in agricultural landscapes—without taking land out of production—by increasing “farmland heterogeneity”, i.e. heterogeneity of the cropped portion of an agricultural landscape, including annual row crops, perennial forage crops, and managed pasture. Farmland

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heterogeneity can be increased by decreasing crop field sizes. Decreasing crop field sizes increases the length of edges between different crop types and between crop and natural/semi-natural land cover types. Farmland heterogeneity can also be increased by increasing crop diversity, i.e. planting more types of crops and having more even representation of the crop types in the landscape.

Empirical studies have found support for this hypothesis. More species and/or higher abundances are found in agricultural landscapes with smaller fields, when controlling for total farmland area. Such effects have been found in a range of taxa, including amphibians, mammals, birds, insects, spiders, and plants (Collins and Fahrig, 2017; Ekroos et al., 2019; Fahrig et al., 2015; Hass et al., 2018; Kirk et al., 2011; Monck-Whipp et al., 2018; Reynolds et al., 2018; Sirami et al., 2019; Zhou et al., 2018). Positive effects of crop diversity on wildlife have also been reported (Collins and Fahrig, 2017; Ekroos et al., 2019; Lee and Goodale, 2018; Monck-Whipp et al., 2018; Novotný et al., 2015; Palmu et al., 2014; Redlich et al., 2018a; Reynolds et al., 2018); however, these effects have been less consistent (and often weaker) than those of field size (Ekroos et al., 2019; Fahrig et al., 2015; Hass et al., 2018; Kirk and Freemark Lindsay, 2017; Redlich et al., 2018b; Wilson et al., 2017; Zhou et al., 2018). Taken together, these studies suggest that policies/guidelines that encourage farmers to increase farmland heterogeneity should benefit biodiversity in agricultural landscapes.

However, a key knowledge gap is whether such policies/guidelines will be as effective as those targeting other aspects of agricultural intensification, namely conventional farming practices such as the use of pesticides. In particular: what are the relative effects of farming practices versus farmland heterogeneity on wildlife found in the cropped portion of the landscape (i.e. farmland)? Many studies have documented negative effects of conventional farming practices on wildlife, including those in farmland (Tuck et al., 2014 and references therein). Some studies have evaluated the relative effects of practices versus landscape heterogeneity/complexity on wildlife in farmland (typically indexed as crop cover, or the amount/diversity of semi-natural habitats; e.g. Gagic et al., 2017; Roschewitz et al., 2005; Tamburini et al., 2016). However, few have evaluated the relative effects of farming practices versus farmland heterogeneity on wildlife in the cropped portion of the landscape. Additionally, the management implications of some previous studies are limited because they compared only the aggregated effect of many farming practices to the effects of individual farmland heterogeneity variables (Palmu et al., 2014; Sirami et al., 2019). Thus, one cannot use these study results to pinpoint which specific farming practices or aspects of farmland heterogeneity have the largest effects on biodiversity. Only a few studies have investigated the relative effects of individual farming practices versus field size on wildlife in farmland (Geiger et al., 2010) or individual farming practices versus crop diversity on wildlife in farmland (Chiron et al., 2014). These studies suggest that farmland heterogeneity is typically less important than fertilizer or pesticide use. However, there may be variability in responses among taxa. For example, Billeter et al. (2008) found that plant and bird richness in agricultural landscapes (including species found in crop fields, semi-natural patches, and linear features such as hedgerows) were significantly affected by a farming practice (fertilizer use) but not crop diversity; in contrast, arthropod richness in agricultural landscapes was significantly affected by crop diversity but not farming practices. To maximize biodiversity in working agricultural landscapes we want to identify the management actions that have the most benefit for species across taxa. Thus, there is a need for additional study of the relative effects of individual farming practice and farmland heterogeneity variables on farmland biodiversity, particularly to understand the relative importance of effects across taxonomic groups.

Here we address this knowledge gap, estimating the relative effects of individual farming practices, field size, and crop diversity on biodiversity in rural eastern Ontario, Canada, when controlling for the amount of farmland (i.e. crop cover). Specifically, we estimate the

relative effects of six farming practices—annual/perennial crop, fertilizer use, herbicide use, insecticide use, tile drainage, and tillage—versus field size and crop diversity on the combined (multi) diversity and species richness of herbaceous plants, woody plants, butterflies, syrphid flies, bees, carabid beetles, spiders, and birds in farmland. Given the results of previous comparisons of the effects of individual farming practices versus farmland heterogeneity on the richness of individual taxa, and the strong evidence of positive effects of wildlife-friendly practices on species richness, we expected farming practices to have larger effects on multidiversity than farmland heterogeneity.

2. Methods

2.1. Overview

This study builds on a previous study of the effects of farmland heterogeneity on biodiversity (Fahrig et al., 2015). That study sampled biodiversity in crop field edges and field interiors within 93, 1 × 1 km farmland-dominated sampling areas (hereafter shortened to “sampling areas”) in rural eastern Ontario, Canada (Appendix A). The dominant crop types in eastern Ontario are hay (30% of farmland), pasture (24%), corn (21%), and soybean (19%; OMAFRA, 2011). The sampling areas were primarily selected to represent the regional variation in two aspects of farmland heterogeneity: crop field size (measured as the mean size of crop fields) and crop diversity (Shannon diversity of crop types). Herbaceous plants, woody plants, butterflies, syrphid flies, bees, carabid beetles, spiders, and birds were surveyed in 4–8 sampling sites per area (depending on the taxonomic group). Half the sampling sites were at field edges and half in field interiors, except for woody plants and birds which were only sampled at field edges. The sampled taxa were selected to represent a range of potential responses to farmland heterogeneity, a range of ecosystem services, and for ease of sampling. The data from the bird surveys in field edges and herbaceous plant, butterfly, syrphid fly, bee, carabid beetle, and spider surveys in field interiors were previously used to evaluate the relative effects of field size and crop diversity on alpha, beta, and gamma diversity and on relative abundance per 1 × 1 km sampling area (Fahrig et al., 2015).

Here, we use data from a subset of the biodiversity surveys, in combination with additional data on farm management practices, from 112 sampling sites (57 field edge and 55 field interior sites) within 32 of the sampling areas (Appendix A). For each sampling site we calculated ‘multidiversity’ (Allan et al., 2014), i.e. the mean biodiversity across the studied taxa. In field edges multidiversity was based on herbaceous plants, woody plants, butterflies, syrphid flies, bees, carabid beetles, spiders, and birds. In field interiors multidiversity was based on herbaceous plants, butterflies, syrphid flies, bees, carabid beetles, and spiders. There are no publicly available data on farming practices in our study region at a resolution appropriate for our analyses. Instead, we collected data on farm management practices at biodiversity sampling sites using landowner interviews. We then estimated the relative effects of six farming practices—annual/perennial crop, fertilizer use, herbicide use, insecticide use, tile drainage, and tillage—and two measures of farmland heterogeneity—field size and crop diversity in the landscapes surrounding the sampling sites—on multidiversity using a mixed effects model. We also included two additional fixed effects: crop cover (the proportion of the landscape covered by crop fields), and the location of the sampling site within the field (field edge or field interior; hereafter referred to as the “sampling location”), to control for their effects on biodiversity. Sampling area was included as a random effect, to account for repeated sampling within each area. We repeated this analysis using species richness of each sampled taxon. Standardized model coefficients from the mixed effects models were used to estimate the effect sizes.



Fig. 1. (a) An example 1×1 km sampling area centered within the 3×3 km area included in the [Fahrig et al. \(2015\)](#) land cover maps. Crop cover type classifications were from the 40-cm-resolution land cover maps created by [Fahrig et al. \(2015\)](#) during the year of biodiversity sampling for each area. White represents non-farmland cover types (e.g. roads, urban development, forest, wetland). (b) Within the 1×1 km area we selected eight sampling sites—four at field edges (black dots) and four in field interiors (white dots)—within four fields (outlined in black). Landowners were surveyed for the farm management practices used on a subset of the sampled fields. (c) Mean field size, crop diversity, and crop cover were calculated within radii of 250 m, 500 m, 750 m, and 1000 m (landscape context) around each sampling site.

2.2. Selection of farmland-dominated sampling areas and sampling sites within sampling areas

[Fahrig et al. \(2015\)](#) selected a set of 93, 1×1 km sampling areas in rural eastern Ontario, Canada (Appendix A), according to criteria detailed in [Pasher et al. \(2013\)](#). The areas were selected to: (a) be representative of the variability in field size and crop diversity across eastern Ontario; (b) be spatially independent, i.e. non-overlapping with minimal spatial autocorrelation of field size and crop diversity across areas; (c) be dominated by agricultural land use (44–95% of the area used in crop production); and (d) have weak correlations between field size, crop diversity, and crop cover across the sampling areas. The 32 sampling areas used in the present study were similarly dominated by agricultural land use (51–92% of the landscape used in crop production); however, the correlations between field size, crop diversity, and crop cover were generally stronger than in the complete dataset (field size and crop diversity $r = -0.68$; field size and crop cover $r = 0.55$; crop diversity and crop cover $r = -0.35$).

For the full biodiversity dataset, eight sampling sites were selected within each sampling area ([Fig. 1a,b](#)), four at field edges and four in field interiors. To select these sites, all field edges within each 1×1 km area were delineated using 2008 aerial photographs ([Ontario Ministry of Natural Resources, 2010](#)) in ArcMap v10.0 (ESRI, Redlands, California). Four sampling sites at field edges were then randomly selected, under the following constraints. Sites were only selected if they were: (a) adjacent to another crop field; (b) ≥ 200 m from all other sites; (c) ≥ 50 m from non-agricultural land uses (e.g. houses, roads, forests); and

(d) ≥ 50 m from the edge of the 1×1 km area. Field edge sites were also selected to minimize tree cover in the adjacent non-crop vegetation. These conditions were confirmed by visual surveys of each site prior to the field season. If criteria were not met during visual surveys, or if landowner permission for surveys was denied, another random site was selected. Each of the four field edge sites was paired with a field interior sampling site in the same crop field, ~ 25 m from the field edge site.

2.3. Biodiversity surveys

Biodiversity surveys were conducted in each sampling area for each of eight taxonomic groups: herbaceous plants, woody plants, butterflies, syrphid flies, bees, carabid beetles, spiders, and birds (as described below). Each sampling area was sampled in one year (2011 or 2012), in random order. However, for logistical reasons, all sampling sites within a given sampling area were sampled on the same day. We identified individuals to the lowest taxonomic level possible (species, genus, or family). The majority of samples were identified to species; thus, to simplify, we hereafter refer to this as “species richness”. Species richness at a sampling site was the total number of species observed across all surveys at that site.

2.3.1. Herbaceous plants

Herbaceous plants were surveyed along a 50 m transect at each of the eight sampling sites per sampling area. Surveys were conducted twice per sampling site, first between May 24 and July 9 and again

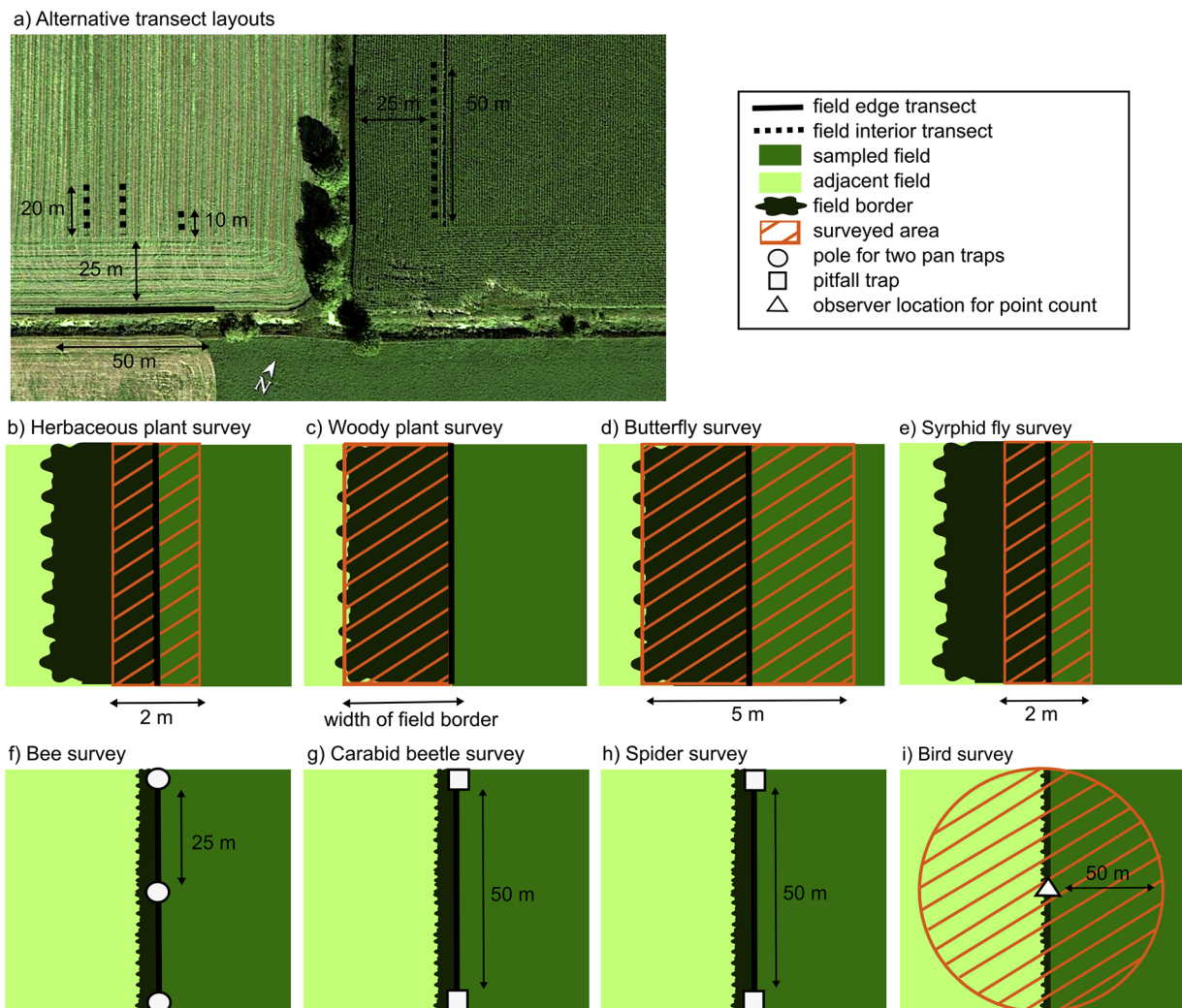


Fig. 2. (a) Examples of the alternative layouts of field edge and field interior transects used in biodiversity surveys. Field edge transects were at the very edge of the field and always aligned with the field edge. Where possible, the field interior transect was placed parallel to its field edge transect pair, at a distance of ~25 m into the field. Otherwise, we used a transect layout that preserved the approximate distance from the field edge transect and the total transect length (Fig. 2a). (b–i) Depiction of the sampling design for each taxonomic group. Note that in b, d, and e, half of the surveyed area was in the crop field and the other half was in the field border vegetation. Imagery taken from Google Earth Pro v. 7.3.0.3832.

between July 17 and August 30 in both sampling years. Field edge transects were aligned with the field edge (Fig. 2a). Where possible, the field interior transect was placed parallel to its paired field edge transect. However, it was not possible to survey in this manner in fields where crop rows ran perpendicular to the field edge: in these cases, we used a transect layout that preserved the approximate distance from the field edge transect and total transect length (Fig. 2a). The surveyor walked each transect once per survey and recorded all herbaceous plant species seen within 1 m of the transect. In field edge transects this meant that half the width of the transect was in the field and the other half was in the adjacent vegetation (Fig. 2b).

2.3.2. Woody plants

We surveyed for woody plants along the field edge transects used for herbaceous plants (see 2.3.1. Herbaceous plants). Woody plants were surveyed once per sampling site between July 17 and August 30 in both sampling years. The surveyor recorded the species of all woody individuals > 1 m tall found across the width of the border between the two crop fields (Fig. 2c).

2.3.3. Butterflies

We surveyed for butterflies along the same transects used for

herbaceous plants (see 2.3.1. Herbaceous plants) at three of the four paired sampling sites per area. Surveys were conducted twice per sampling site, first between June 27 and August 3 and again between August 4 and 31 in both sampling years. Surveys were conducted between 830 and 1730 on sunny days when winds were low (≤ 3 on the Beaufort scale) and temperatures were $> 15^\circ\text{C}$. The surveyor walked a transect once per survey at 5 m/min., and recorded all butterfly species seen within an imaginary 5 m^3 box in front of the observer, i.e. within 5 m from the ground, 2.5 m of either side of the transect, and 5 m in front of the observer. As for the herbaceous plant surveys, this meant that half the width of a field edge transect was in the field and the other half was in the adjacent vegetation (Fig. 2d).

2.3.4. Syrphid flies

Syrphid fly surveys were conducted immediately following the butterfly surveys, along the same transects (see 2.3.3. Butterflies). The surveyor walked a transect once per survey at 5 m/min., collecting all observed syrphids within an imaginary 2 m^3 box in front of the observer using a 38-cm diameter butterfly net (Fig. 2e). Collected syrphids were euthanized with ethyl acetate and frozen until they could be pinned and identified using Shannon (1923), Curran and Fluke (1926), Curran (1951), Telford (1970), Vockeroth and Thompson (1987), and

Vockeroth (1992).

2.3.5. Bees

We surveyed for bees using pan traps placed along the same six transects/sampling area used for butterfly and syrphid fly surveys (see Sections 2.3.3. Butterflies to 2.3.4. Syrphid flies). Bee surveys were conducted twice per sampling site, first between June 19 and July 31 and again between July 29 and August 31 in both sampling years. Different bee species are attracted by different pan trap colors (Geroff et al., 2014; Toler et al., 2005). Therefore we used multiple trap colors to sample for bees at each sampling site, i.e. two white pan traps, two blue pan traps, and two yellow pan traps per transect. Two pan traps of different colors were placed at the top of each of three poles per transect (for a total of six pan traps per sampling site). One pole was placed at each end of the transect and the third one in the centre of the transect (Fig. 2f). Pole height was set such that the trap openings were even with the top of the surrounding vegetation. Traps were filled 2/3-full with blue Dawn dish soap in water (10 drops/L water). Traps remained in the field for four days per survey. Collected bees were stored in 70% ethanol until they could be prepared for identification (dried, fluffed, and pinned). Specimens were identified by specialists at Agriculture and Agri-Food Canada, the American Museum of Natural History, and the Royal Saskatchewan Museum.

2.3.6. Carabid beetles

We surveyed for carabid beetles using pitfall traps placed along the same transects used for butterfly, syrphid fly, and bee surveys (see Sections 2.3.3. Butterflies to 2.3.5. Bees). Surveys were conducted twice per sampling site, first between June 15 and July 24 and again between July 25 and August 31 in both sampling years. We used two pitfall traps per transect, one at each end of the transect (Fig. 2g). Each trap was 15 cm high and 9 cm in diameter. We half-filled each trap with blue Dawn dish soap in water (10 drops/L water) and placed it such that its top edge was at ground level. A lid (~20 cm²) was placed ~3 cm above the trap to protect it from rain. Traps remained in the field for four days per survey. Collected carabid beetles were stored in 70% ethanol until they could be identified using Lindroth (1969, 1968, 1966, 1963, 1961).

2.3.7. Spiders

Spiders were collected in pitfall traps during the carabid beetle surveys (see 2.3.6. Carabid beetles; Fig. 2h). Collected spiders were stored in 70% ethanol until they could be identified using Ubick et al. (2005).

2.3.8. Birds

Birds were surveyed once at each of the four field edge sampling sites per sampling area between May 24 and July 9 in each year. We used a 10-minute point count, recording all birds seen or heard within three distances (0–50 m, 50–100 m, and > 100 m) from the point count location. Point counts were carried out between sunrise and four hours past sunrise, on mornings when winds were low (≤ 3 on the Beaufort scale) and there was no precipitation or fog. Species richness at a sampling site was the total number of species observed in the 0–50 m distance category (Fig. 2i). We did not include birds beyond 50 m because bird detectability declines with distance from the observer (Diefenbach et al., 2003).

2.4. Farm management practices surveys

We surveyed landowners of crop fields sampled in our biodiversity surveys between May 24 and August 31 in each year. We obtained farm management practices information for a subset of the sampled fields, as permitted by time and landowner availability/cooperation. Landowners were asked to describe the farm management practices used in their sampled field. The surveys were conducted by phone by J.

Girard, S. Collins, or S. Crowe, using contact information obtained while seeking permission to conduct biodiversity surveys on the properties. See Appendix B for a full transcript of the phone survey. Survey questions and methods were approved by the Carleton University Research Ethics Board (Project no. STPGP 381108 - 09).

Our intention was to use information obtained in these surveys to estimate values for a range of farming practices, including the amounts of nitrogen, phosphorous, and potassium applied per year, number of fertilizer/pesticide applications per year, and amounts of fertilizer/pesticide applied per year. However, we were unable to obtain such detailed information in many of our interviews, and if we limited analysis to only surveys that included detailed information for all farming practices then we would not have enough sites for an analysis. For example, farmers reported the amounts of nitrogen, phosphorous, and potassium applied per year for only eight of the 59 sites where chemical fertilizers were applied (Appendix B). Thus we instead used information obtained in these surveys to estimate six binary variables: whether the crop in the sampled field was annual (corn, soybean) or perennial (hay, alfalfa; hereafter simplified to “annual/perennial crop”), fertilizer use (yes/no), herbicide use (yes/no), insecticide use (yes/no), tile drainage (yes/no), and tillage (yes/no). This choice of farming practice variables primarily represents a balance between the number (and resolution) of farming practice variables and the sample size needed to test for their effects on multidiversity and the richness of individual taxa. Additionally, we note that some variables were excluded because there was little to no variation in values among sampling sites. For example, all landowners who reported applying fertilizers did so once per year (Appendix B).

2.5. Measurements of farmland landscape context

We calculated field size and crop diversity within radii of 250 m, 500 m, 750 m, and 1000 m around each sampling site (the “landscape context” of each sampling site; Fig. 1c). We also estimated the crop cover around each sampling site (as described above), so that we could control for the effects of this variable on multidiversity/species richness in our statistical analysis (see 2.6. Data analysis). This was necessary because there was substantial variation in crop cover across the sampling sites within sampling areas (Appendix C), despite our efforts to control for crop cover when selecting our sampling areas (see 2.2. Selection of farmland-dominated sampling areas and sampling sites within sampling areas). We note that we did not estimate the proportion of the landscape in semi-natural land cover types (i.e. semi-natural cover) because most of the non-crop area in our landscapes was semi-natural, resulting in strong, negative relationships between crop cover and semi-natural cover across our sampling sites (Appendix D).

These landscape measures were based on the fine-resolution (40 cm) land cover data sets created by Fahrig et al. (2015) using a combination of aerial photographs (40-cm resolution) commissioned by Fahrig et al. (2015) in the year of biodiversity sampling (2011 or 2012) and field observations. Individual crop fields were defined based on visible boundaries between crop and non-crop land cover types and/or a change in crop type. Thus areas of the same crop type separated by a non-crop land cover (e.g. field margin, road) were considered separate fields, and adjacent areas of different crop types (e.g. corn, soy) were considered separate fields. See Appendix D for a summary of the crop cover types and non-farmland cover types identified by Fahrig et al. (2015).

2.6. Data analysis

We included only the 112 sampling sites with complete biodiversity and farming practices survey data. To estimate overall biodiversity at each sampling site, we calculated an index of multidiversity. Multidiversity was calculated by first standardizing the species richness of each taxon across all sampling sites to a mean = 0 and SD = 1, and

Table 1

Total number of species across all sampling sites, and the mean, minimum, and maximum species richness per site for each taxonomic group. Multidiversity was calculated as the mean standardized species richness, averaged across all taxa sampled at a given sampling site.

Taxa	Species richness			
	Total	Mean	Minimum	Maximum
herbaceous plants	165	20.97	2	51
woody plants	41	3.12	0	12
butterflies	25	2.79	0	7
syrphid flies	29	2.17	0	10
bees	87	7.10	1	20
carabid beetles	45	3.76	0	11
spiders	60	3.83	0	12
birds	34	2.28	0	6
multidiversity	–	–0.05	–1.08	1.40

then averaging across the taxa for each site. Thus a positive value indicates higher than average multidiversity, and a negative value indicates lower than average multidiversity. Note that we did not simply add up the total number of species per site because this would result in a measure that was highly dependent on the most diverse taxon (herbaceous plants; see Table 1).

We included each of our three landscape context variables (field size, crop diversity, and crop cover) at its estimated scale of effect, i.e. the spatial extent within which the landscape variable has the strongest influence on multidiversity. We estimated the scale of effect for each landscape context variable while controlling for the effects of farming practices and the other landscape context variables, and allowed for selection of different spatial extents for different variables. To do so, we used linear mixed effects to model multidiversity as a function of the six farming practices and three landscape context variables 64 times. That is, we ran one model for each unique combination of the four spatial extents (250, 500, 750, and 1000 m) and the three landscape context variables (as, for example, in [Boscolo and Metzger, 2009](#)), i.e. all variables at 250 m, field size and crop diversity at 250 m and crop cover at 500 m, field size at 250 m and crop diversity and cover at 500 m, etc. (see Appendix E for the full list of models). We also included sampling location (field edge or field interior) as a fixed effect and sampling area as a random effect in each model. Each predictor variable was standardized to a mean = 0 and SD = 1 prior to analysis. We calculated the small-samples Akaike Information Criterion (AICc) for each model and retained the model with the smallest AICc for further analysis. Thus the scale of effect for each landscape context variable was the scale included in the most supported model.

We evaluated the relative effects of the six farming practices and two farmland heterogeneity variables (measured at their scales of effect) on multidiversity, using the following methods to minimize the potential impact of collinearity on our effect size estimates. First, we did this by including all predictors within the statistical model, because effect size estimates can be biased when an influential predictor is omitted from the model ([Smith et al., 2009](#)). Second, we used the standardized model coefficients from a regression-type model to estimate the relative effects of the variables. Although even low-moderate collinearity among predictors within a regression-type model increases uncertainty in the coefficient estimates for the correlated predictors (i.e. standard error of the estimate; [Graham, 2003](#)), it does not generally bias the size or direction of the model coefficient ([Smith et al., 2009](#)). An effect was considered strongly supported if it was significant at $\alpha = 0.05$ (i.e. the 95% confidence interval [CI] did not cross zero).

To determine which taxonomic groups drove effects of farming practices and farmland heterogeneity on multidiversity, we estimated the relative effects of farming practices and farmland heterogeneity on species richness for each individual taxonomic group. Each landscape context variable was measured at its scale of effect on multidiversity

(see above). We used a generalized linear mixed effects model with a negative binomial distribution and log link, including crop cover as a fixed effect and sampling area as a random effect in each model. We also included the sampling location as a fixed effect for all taxa except for woody plants and birds, because these taxa were sampled in field edges only. We then used these statistical models to predict how much species richness changed in response to a change in each farming practice and measure of farmland heterogeneity. However, to avoid implying that our predictions are of actual rather than relative species richness, we opted to express each change in richness as a percentage of the maximum species richness observed across all sampling sites (Table 1). For example, we calculated the increase in species richness when moving from an annual to perennial field as the (predicted richness in a perennial field – predicted richness in an annual field) / maximum observed richness at any sampling site \times 100%.

We also evaluated whether the effects of farming practices and farmland heterogeneity on multidiversity and the richness of individual taxa differed between field edges and interiors. To determine whether effects of annual/perennial crop on multidiversity differed between field edges and interiors, we used linear mixed effects to model multidiversity as a function of 10 fixed effects—six farming practices, two farmland heterogeneity variables, crop cover, and sampling location—plus an interaction between annual/perennial crop \times location. We also included a random effect of sampling area in the model. We then ran similar models to test for interaction effects between each of the remaining farming practice/farmland heterogeneity variables and sampling location. We did not include all interaction terms within a single model because of sample size limitations. We repeated the above analyses for species richness of all taxa sampled in field edges and interiors, with the exception that here we used generalized linear mixed effects with a negative binomial distribution and log link.

We tested for relationships among our 10 predictor variables. We used generalized linear mixed effects with a binomial distribution and logit link for pairwise comparisons of the binary farming practices variables, including sampling area as a random effect to account for non-independence and spatial autocorrelation of measurements within a sampling area. We used linear mixed effects for pairwise comparisons of continuous landscape context variables and for pairwise comparisons of farming practice to landscape variables, including sampling area as a random effect. We indexed the variance shared by two predictors as the r^2_{marginal} , i.e. the variance explained by fixed effects in a mixed effects model (calculated according to [Nakagawa and Schielzeth, 2013](#)).

We also tested for spatial autocorrelation of model residuals. We used a one-tailed Global Moran's I to test for positive spatial autocorrelation in model residuals, i.e. whether similarity in residual values declined with distance between sampling sites. We used a permutation approach (with 1000 permutations) to calculate the significance-level for each test and residuals were considered spatially autocorrelated at $p < 0.05$.

Analyses were conducted in R ([R Core Team, 2017](#)), using the lme4 ([Bates et al., 2015](#)), glmmADMB ([Fournier et al., 2012](#); [Skaug et al., 2015](#)), MuMIn ([Barton, 2016](#)), and ape ([Paradis et al., 2004](#)) packages.

3. Results

The total number of species identified per taxonomic group in the subset of 112 sampling sites used in our analyses ranged from 25 butterfly species to 165 herbaceous plant species (Table 1, Appendix F). Herbaceous plants had, on average, the most species per sampling site (mean = 20.97, range = 2–51 species) and syrphid flies the least (mean = 2.17, range = 0–10). Multidiversity ranged from –1.08 to 1.40 (mean = –0.05). See Appendix C for a summary of farming practice and landscape context variable values across our sampling sites.

The strength of effect of the landscape context variables varied with the spatial extent (Appendix E). We identified the scale of effect for

Table 2

Pairwise relationships among our 10 predictor variables. We used generalized linear mixed effects with a binomial distribution and logit link for pairwise comparisons of the binary farming practices variables and linear mixed effects for pairwise comparisons of continuous landscape context variables (at their scales of effect) and for pairwise comparisons of farming practice to landscape variables. Sampling area was included as a random effect to account for non-independence and spatial autocorrelation of measurements within a sampling area. We indexed the variance shared by two predictors as the r_{marginal}^2 , i.e. the variance explained by the fixed effect in a mixed effects model.

	fertilizer	herbicide	insecticide	tile drainage	tillage	field size	crop diversity	crop cover	sampling location
annual/perennial crop	< 0.01	0.01	0.07	0.04	0.00	< 0.01	0.12	0.01	< 0.01
fertilizer		< 0.01	0.12	– ^a	0.06	0.01	0.06	0.01	< 0.01
herbicide			0.07	0.01	0.16	< 0.01	0.01	0.02	< 0.01
insecticide				0.03	0.17	0.05	0.02	0.14	< 0.01
tile drainage					0.01	0.06	0.03	0.07	< 0.01
tillage						0.01	< 0.01	0.04	< 0.01
field size							0.01	0.24	< 0.01
crop diversity								0.03	< 0.01
crop cover									< 0.01

^a r_{marginal}^2 for the relationship between tile drainage and fertilizer use was omitted, because this model failed to converge.

each landscape context variable as the scale included in the most supported model (i.e. the model with $\Delta\text{AICc} = 0$), with effects of field size and crop cover on multidiversity within 500 m of the sampling site, and the effect of crop diversity within 250 m.

Although correlations between field size, crop diversity, and crop cover across our sampling areas were moderately strong (see 2.2. Selection of farmland-dominated sampling areas and sampling sites within sampling areas), the relationships between predictor variables across the sampling sites were generally weak (Table 2). The strongest relationship occurred between field size and crop cover ($r_{\text{marginal}}^2 = 0.24$), with more crop cover in landscapes with larger field sizes.

Inclusion of the sampling location (field edge or interior) and sampling area was sufficient to control for spatial autocorrelation in our model residuals. All Global Moran's I tests for spatial autocorrelation of model residuals were non-significant ($p \geq 0.08$; Appendix G).

Farming practices and farmland heterogeneity had similarly strong effects on farmland multidiversity (Fig. 3). For example, the effect of the most influential farming practice variable—annual/perennial crop—on multidiversity was only 1.4 times the effect of field size and 1.4 times the effect of crop diversity. Two farming practices variables—annual/perennial crop and tillage—and both farmland heterogeneity variables—field size and crop diversity—had significant effects on multidiversity (i.e. the 95% CI of each effect did not cross zero; Fig. 3). Thus this analysis indicates that farmland multidiversity is lower in farmlands with tilled, annual crops than untilled, perennial fields, and in landscapes with larger fields and more diverse crops.

The directions of effect of these strongly-supported farming practice and farmland heterogeneity variables on multidiversity were generally consistent across individual taxonomic groups. For example, annual/perennial crop—which had the strongest (negative) effect of any

variable on multidiversity—also had negative effects on species richness for 6 / 8 taxonomic groups (Fig. 4a). The strong negative effect of annual crops (relative to perennial ones) on multidiversity was largely driven by its negative effects on herbaceous plant, carabid beetle, and spider richness: annual/perennial crop had the largest effect of any farming practice/heterogeneity variable on richness of each of these taxa (Appendix H). It also had negative effects on syrphid fly, butterfly, and bird species richness. Our models predict that we can expect richness for these taxa to increase by 2–35% (relative to the maximum observed richness; Table 1) when moving from an annual to perennial field (Fig. 4a).

Field size and crop diversity also had consistently negative effects on the species richness of individual taxonomic groups. Richness was lower in landscapes with larger fields than in landscapes with smaller fields, and lower in landscapes with more diverse crops than in landscapes with less diverse crops, for all taxa except for spiders (Fig. 5). The negative effects of field size and crop diversity on species richness were particularly important for syrphid flies: field size and crop diversity had the largest and second-largest effects on fly richness, respectively (Appendix H). For taxa negatively affected by field size, our model predicts that we can expect richness to increase by 3–46% (relative to the maximum observed richness) when mean field sizes within a 500 m radius are reduced by ~12 ha (from 13 to 1 ha; Fig. 5a). For taxa negatively affected by crop diversity, our model predicts that we can expect richness to increase by 1–51% when the Shannon diversity of crop types within a 250 m radius is reduced from 1.58 to 0.00 (Fig. 5b).

Although tillage had a significant negative effect on multidiversity, its effect on the species richness of individual taxa was only negative for half of the taxonomic groups (Fig. 4b). However, when an effect of tillage on the richness of an individual taxonomic group was in the

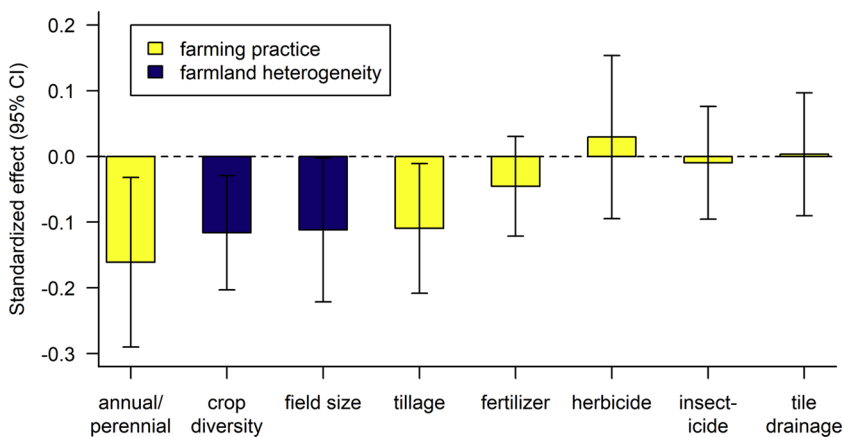


Fig. 3. Standardized effects (95% confidence interval; CI) of six farming practices (annual/perennial crop, fertilizer use, herbicide use, insecticide use, tile drainage, tillage) and two measures of farmland heterogeneity (field size, crop diversity) on farmland multidiversity. We modeled multidiversity as a function of these eight standardized predictor variables, crop cover, and sampling location (field edge or field interior), plus a random effect of sampling area, using a linear mixed effects model. Effects are ordered from the strongest (left) to weakest (right) effect. An effect is significant if its 95% CI does not cross zero.

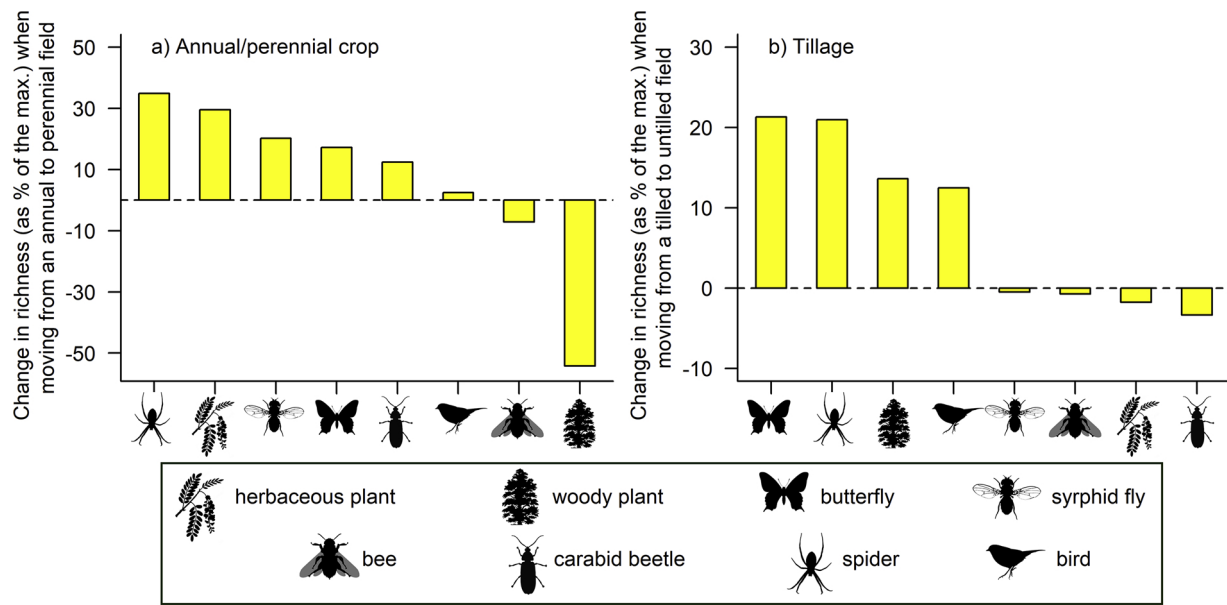


Fig. 4. (a) Predicted change in species richness (relative to the maximum observed richness) when moving from an annual to perennial crop field, calculated as the (predicted richness in a perennial field – predicted richness in an annual field) / maximum observed richness at any sampling site $\times 100\%$. (b) Predicted change in species richness (relative to the maximum observed richness) when moving from a tilled to untilled field, calculated as the (predicted richness in an untilled field – predicted richness in a tilled field) / maximum observed richness at any sampling site $\times 100\%$. For each taxon, we modeled species richness as a function of six farming practices (annual/perennial crop, fertilizer use, herbicide use, insecticide use, tile drainage, tillage) and two measures of farmland heterogeneity (field size, crop diversity) using generalized linear mixed effects with a negative binomial distribution and log link. We included a fixed effect of crop cover and a random effect of sampling area in all models. Sampling location (field edge or field interior) was included in all models except for models of woody plant and bird richness, because these taxa were sampled in field edges only. Silhouettes were taken from <http://phylopic.org/> (licensed for use under Public Domain licenses [<https://creativecommons.org/publicdomain/mark/1.0/>]), except for the bee and beetle silhouettes which were made available for use by M. Broussard under CC BY 3.0 licenses [<https://creativecommons.org/licenses/by/3.0/>]).

opposite direction (positive) it was weak. Tillage had the largest (negative) effect of any farming practice/heterogeneity variable on butterflies and birds, and the direction of effect of tillage was also negative for woody plants and spiders (Appendix H). Our model predicts that we can expect richness of these taxa to increase by 12–21% (relative to the maximum observed richness) when moving from a tilled to untilled field (Fig. 4b). In contrast, tillage had slightly positive effects on the richness of syrphid flies, bees, herbaceous plants, and beetles. For these taxa, we can expect richness to decline by 1–3% when moving from a tilled to untilled field (Fig. 4b).

Farming practices and farmland heterogeneity generally had similar effects on multidiversity and species richness in field interiors and edges. There were significantly different effects of annual/perennial crop ($X^2_{\text{annual/perennial crop} \times \text{sampling location}} = 9.83$, $p = 0.002$), crop diversity ($X^2_{\text{crop diversity} \times \text{sampling location}} = 5.99$, $p = 0.01$), and tillage ($X^2_{\text{tillage} \times \text{sampling location}} = 5.37$, $p = 0.02$) on multidiversity in field edges and interiors. However, the direction of effect for each of these variables was the same—i.e. negative—in field edges and interiors (Appendix I). Similarly, the directions of effect of these variables on the species richness of individual taxa were the same in field edges and interiors, with one exception: herbaceous plant richness decreased as crop diversity increased in field edges, but increased (slightly) as crop diversity increased in field interiors ($X^2_{\text{crop diversity} \times \text{sampling location}} = 9.78$, $p = 0.002$; Appendix I). Tile drainage had a negative effect on multidiversity in field interiors and a (slightly) positive effect on multidiversity in field edges ($X^2_{\text{tile drainage} \times \text{sampling location}} = 6.16$, $p = 0.01$). However, the effect of tile drainage on multidiversity was non-significant and smaller than the effects of annual/perennial crop, crop diversity, field size, and tillage whether we distinguished between field edges and interiors or not (Appendix I).

Finally, although the effects of sampling location and crop cover on multidiversity were not the focus of this study, we note that both had significant effects on farmland multidiversity (Appendix J).

Multidiversity was higher in field edges than field interiors, as was the richness of all individual taxa (except woody plants and birds, which were sampled in field edges only). Multidiversity was higher in landscapes with low crop cover than in landscapes with high crop cover. The richness of individual taxa was also typically higher in landscapes with less crop cover than in landscapes with more crop cover, except for butterflies and syrphid flies.

4. Discussion

We found that farmland heterogeneity can have similar—and sometimes even larger—effects on farmland biodiversity than the farm management practices used in individual crop fields. Although annual/perennial crop had the largest effect on biodiversity in our study, its effect was only 1.4 times the effect of field size and 1.4 times the effect of crop diversity. Additionally, we estimated that the effects of field size on multidiversity were larger than effects of using fertilizers ($2.5\times$), herbicides ($3.8\times$), insecticides ($11.4\times$), and tile drainage ($34.1\times$). The effects of crop diversity on multidiversity were $2.5\times$, $3.9\times$, $11.9\times$, and $35.3\times$ larger than effects of using fertilizers, herbicides, insecticides, and tile drainage, respectively.

This was surprising, given that previous comparisons of the effects of individual farming practices versus farmland heterogeneity on the richness of individual taxa have generally found the opposite (Billeter et al., 2008; Chiron et al., 2014; Geiger et al., 2010). However, these studies could have underestimated the effects of farmland heterogeneity relative to farming practices because they did not measure farmland heterogeneity at the spatial extent of its effects on the studied taxa. Previous studies have shown that the spatial extent at which landscape context variables are measured can strongly affect conclusions about the direction, relative importance, and estimated biological/statistical significance of an effect (e.g. Holland et al., 2004; Smith et al., 2011). To our knowledge, none of the previous studies of

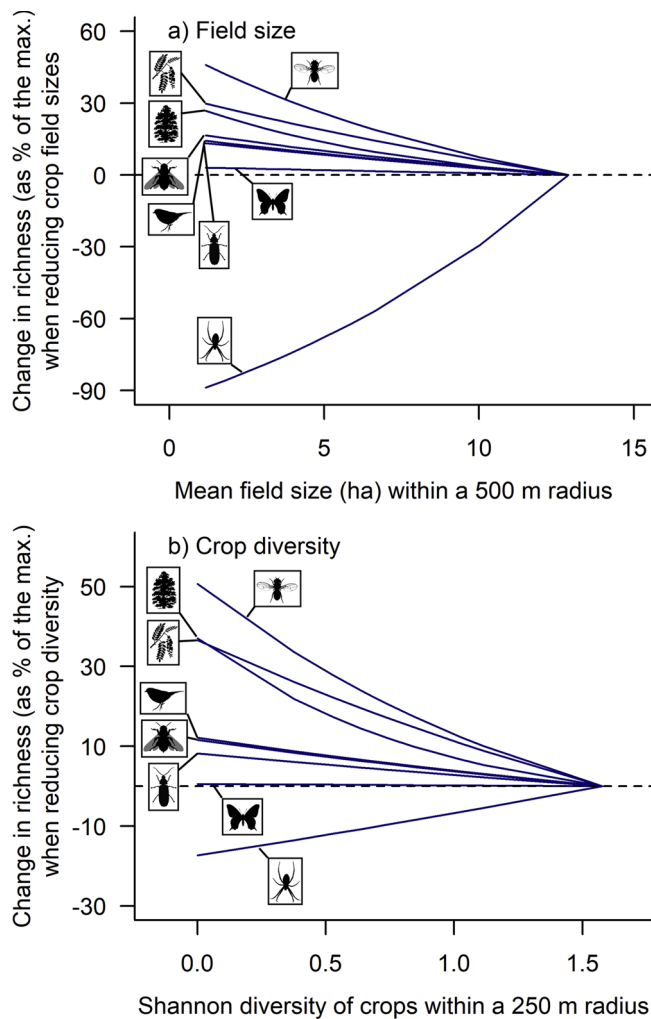


Fig. 5. (a) Predicted change in species richness (relative to the maximum observed richness) when mean field size within 500 m of the sampling site decreases, calculated as the (predicted richness at a given field size – predicted richness at the largest field size) / maximum observed richness at any sampling site (see Table 1) \times 100%. (b) Predicted change in species richness (relative to the maximum observed richness) when crop diversity within 250 m of the sampling site decreases, calculated as the (predicted richness at a given crop diversity – predicted richness at the highest crop diversity) / maximum observed richness at any sampling site \times 100%. See Fig. 4 for description of the analysis and figure legend.

the effects of individual farming practices versus farmland heterogeneity on biodiversity in farmland provide biological justification for their selected landscape size, nor did they empirically estimate the appropriate landscape size (as in the current study). Thus we may have found more similar magnitudes of effect of farming practices and farmland heterogeneity than previous studies because we ensured that farmland heterogeneity variables were measured at extents where they had the strongest effects on farmland biodiversity.

Alternatively, one might suggest that the relative effects of different farming practices and farmland heterogeneity on multidiversity and the richness of individual taxa in our study were biased by the relationships among those predictor variables. However, we argue that this is unlikely because of the steps we took to minimize the potential impact of these relationships on our relative effect size estimates (see 2.6. Data analysis). Additionally, our predictor variables were only weakly inter-related (all $r_{\text{marginal}}^2 \leq 0.24$; Table 2).

Another possibility is that the effects of farming practices were underestimated relative to the effects of farmland heterogeneity in our

study because we used simplified, binary farming practice variables but continuous measures of farmland heterogeneity. Although we cannot fully discount this explanation, supplementary analyses of the effects of the resolution of farming practice variables on estimates of their relative importance suggest this explanation is unlikely. For example, replacing our binary annual/perennial crop variable with crop identity in the sampled field did not change our conclusions. Although the analysis including crop identity did show that the negative effect of corn relative to hay fields on multidiversity was greater than the effect of annual/perennial crop, the effect of corn relative to hay on multidiversity was still only moderately greater than the effects of field size (1.9 \times) and crop diversity (1.8 \times ; Appendix K). Similarly, replacing the binary till/no-till variable with one that distinguished between conventional, conservation, and no-till did show that the negative effect of tillage on multidiversity was primarily driven by the negative effect of conventional tillage. However, the effect of tillage on multidiversity was similar in size to the effect of field size and the effect of crop diversity whether we distinguished between conventional and conservation tillage or not (Appendix K). Replacing fertilizer/no fertilizer with a variable distinguishing between use of chemical fertilizer, non-chemical fertilizer, and no fertilizer revealed that the effect of fertilizer on multidiversity was driven by the negative effect of chemical fertilizer. However, the effect of fertilizer on multidiversity was non-significant and was smaller than the effect of field size and the effect of crop diversity whether we distinguished between chemical and non-chemical fertilizers or not (Appendix K). Furthermore, we found that effect sizes were actually smaller in analyses including continuous measures of tillage intensity (number of tillage passes per year) and herbicide intensity (number of applications per year) than the binary versions of these variables (Appendix K). Nevertheless, we cannot discount the idea that other measures of the intensity of a farming practice, e.g. fertilizer or herbicide amounts, could yield stronger estimates of their effects on farmland biodiversity.

It is also possible that effects of some farming practices could be larger if we had estimated their effects at a landscape scale (e.g. proportion of fields treated with herbicides within 500 m of the sampled field) rather than field scale. For example, effects of fertilizers/pesticides may be greater at a landscape than field scale if occurrence of a species at a given site is not only affected by the within-field use of fertilizers/pesticides but also by use of fertilizers/pesticides within neighboring fields. Although studies have shown that chemicals associated with fertilizers/pesticides can be transported away from the site of application in a number of ways (Domagalski et al., 2008; Tang et al., 2012), to our knowledge the relative impact of landscape- versus field-scale measurements of fertilizers/pesticides on wildlife have not been studied. Thus this speculation needs to be tested in future studies.

Nevertheless, the observed effects of annual/perennial crop, tillage, and field size on multidiversity and the richness of individual taxa were consistent with previous studies. Most previous studies have found more species/greater abundances in landscapes with smaller fields than larger fields (Collins and Fahrig, 2017; Ekroos et al., 2019; Fahrig et al., 2015; Hass et al., 2018; Kirk et al., 2011; Monck-Whipp et al., 2018; Reynolds et al., 2018; Santana et al., 2017; Zhou et al., 2018; but see also Duro et al., 2014; Lee and Goodale, 2018), although the strength of effect varied from weak to strong across taxa and studies. Studies have similarly found more negative effects of annual than perennial crops on wildlife species (Glover et al., 2010; Robertson et al., 2011; Wilson et al., 2017), and that there are more species in untilled than tilled fields (Demjanova, 2004; Freemark and Kirk, 2001; Murphy et al., 2006; Sapkota et al., 2012; Sosnoskie et al., 2006; see Appendix L for supplementary discussion of these findings).

In contrast, the effect of crop diversity on multidiversity—and the richness of most studied taxa—was opposite to our prediction. A review of previous studies does suggest that effects of crop diversity on wildlife are inconsistent, with studies reporting positive (Collins and Fahrig, 2017; Ekroos et al., 2019; Lee and Goodale, 2018; Monck-Whipp et al.,

2018; Novotný et al., 2015; Palmu et al., 2014; Redlich et al., 2018a; Reynolds et al., 2018), negative (Hass et al., 2018), and mixed effects (Hiron et al., 2015; Kirk and Freemark Lindsay, 2017; Santana et al., 2017; Sirami et al., 2019; Wilson et al., 2017) of crop diversity on species richness/abundance. We note that these inconsistent findings may occur, at least in some cases, because the effect of crop diversity on biodiversity depends on the farmland amount: both Wilson et al. (2017) and Sirami et al. (2019) found evidence that crop diversity can have positive effects on biodiversity in landscapes with low crop cover, but negative effects on biodiversity in landscapes with high crop cover. However, we found no support for an interacting effect of crop diversity \times crop cover on multidiversity in our study (Appendix M).

Another possible explanation for our observed negative effect of crop diversity on farmland biodiversity is that this relationship is in fact driven by another, unmeasured landscape context variable that is correlated with crop diversity. We considered the possibility that the apparent negative effect of crop diversity on biodiversity was driven by the proportion of farmland in annual crops. In our study region there are more different annual crop types than perennial ones, and thus crop diversity may be higher in landscapes dominated by annual crops than in landscapes dominated by perennial crops. And, one would expect lower biodiversity in landscapes with more annual crops. However, the relationship between crop diversity and the proportion of farmland in annual crops was weak ($r_{\text{marginal}}^2 = 0.06$), and inclusion of the proportion of farmland in annual crops (at its scale of effect) in our statistical model did not change the direction of—or support for—a negative effect of crop diversity (Appendix M). We also considered the possibility that exclusion of semi-natural cover from our analyses could have led to an inaccurate estimate of the effect size of crop diversity. However, we found a very weak relationship between crop diversity and semi-natural cover ($r_{\text{marginal}}^2 < 0.01$), and our conclusions did not change when we included semi-natural cover in our statistical model (Appendix M). Therefore the negative effect of crop diversity on farmland biodiversity was not driven by its relationship with either the proportion of farmland in annual crops or semi-natural cover.

Our observed negative effect of crop diversity on biodiversity appears to contradict Fahrig et al. (2015), who found positive (though weak) effects of crop diversity on the richness/abundance of most taxa. This contradiction was particularly surprising because our biodiversity data included some of the data used by Fahrig et al. (2015). However, there are a number of differences between our study and Fahrig et al. (2015) that could potentially explain the opposite effects of crop diversity on farmland biodiversity observed in the two studies (as detailed in Appendix N). The most likely explanation is that crop diversity was measured within different spatial extents in the two studies. We measured crop diversity within a radius of 250 m around the sampling sites—selected empirically as this variable's scale of effect—whereas Fahrig et al. (2015) measured crop diversity within an arbitrary 1 \times 1 km landscape (approximately the same extent as our measurements within a 500-m radius). The effect of crop diversity on multidiversity in our study varied with the spatial extent, with strong negative effects when we measured crop diversity within a radius of 250 m and weak (non-significant) positive effects when we measured crop diversity at larger spatial extents (Appendix N). Thus our findings do not in fact contradict those of Fahrig et al. (2015).

Thus a key question to answer is: why does the negative effect of crop diversity on farmland biodiversity at a small spatial extent dissipate—and even become slightly positive—at larger spatial extents? We speculate that, if land cover within a 250 m extent indexes core habitat availability for species at the sampling site, then there may be fewer species when there is high versus low crop diversity because there is less area per crop type when crop diversity is high. Thus the area of a given crop type may be too small to support species that use it as habitat in landscapes with high crop diversity within 250 m. However, at larger extents the observed effect of crop diversity on multidiversity/species richness may become weakly positive if the benefits of crop

diversity for landscape complementation (Dunning et al., 1992) at the scale of movement among complementary resources (such as breeding and foraging habitats) are greater than its negative effect at the smaller spatial extent.

4.1. Management implications

The most compelling implication of this study is that it suggests that policies/guidelines aimed at reducing crop field sizes would be at least as effective for conservation of biodiversity within working agricultural landscapes as policies/guidelines designed to promote a wildlife-friendly farming practice, such as adoption of no-till or low-input (e.g. fertilizer, pesticide) farming practices. However, we caution against direct extrapolation of this conclusion to other agricultural regions. Such extrapolation would require that the range and distribution of predictor values in other regions is reasonably similar to those in our data set and region. Additionally, Dormann et al. (2013) demonstrated that collinearity among predictor variables can be problematic when extrapolating results to other sites with different relationships among those same variables (e.g. different degree of correlation between field size and crop cover). However, we note that Dormann et al. (2013) also found that regression-type models—like the ones used in this study—tended to produce reasonably accurate predictions so long as the correlations among predictors were not extreme (i.e. $|r|$ should be below ~ 0.70). Nevertheless, we recommend further research to determine whether our results apply in other agricultural regions, as well as to taxa not studied here. We also caution against extrapolation of the effects of farming practices versus farmland heterogeneity on biodiversity within the cropped portion of the landscape to wildlife found in other (e.g. semi-natural) land cover types. In this study we only sampled for biodiversity in crop fields and along crop field edges, and species found in other land cover types may respond differently to farming practices and the farmland landscape context.

We also stress that our findings confirm the conservation benefits of reducing, where possible, the amount of crop cover. In our study we found a significant negative effect of crop cover on farmland multidiversity even though we specifically selected sampling areas to reduce the range of variability in crop cover which, all else being equal, should reduce its estimated effect on farmland biodiversity. Thus we likely underestimated the effect of crop cover on biodiversity.

Nevertheless, recommendations to reduce crop cover in agricultural landscapes may not be practical, given the pressure to increase food production to meet the demands of a growing human population (United Nations, 2017). Indeed, projections based on current population and food consumption trends suggest land clearing for agriculture will continue (e.g. Alexandratos and Bruinsma, 2012; Wirsenius et al., 2010). Thus there is value in identifying conservation actions that can maintain or increase biodiversity in working agricultural landscapes without taking land out of production.

In addition to allowing for both biodiversity conservation and food production, biodiverse agricultural landscapes benefit people through provisioning of ecosystem services. For example, meta-analysis has shown that increases in plant diversity result in increases in provisioning of plant products, erosion control, invasion resistance, soil fertility, and regulation of pests and pathogens (Quijas et al., 2010). Pollination services may also be positively related to pollinator diversity (Klein et al., 2007).

For decision-makers, key next steps are to understand the potential socioeconomic impacts of reducing field size on yield and the likelihood that farmers would adopt policies/guidelines aimed at keeping field sizes small. Evidence suggests a preference for larger crop fields, with observations of increasing field sizes over time in some (but not all) crop types and regions (Daystar et al., 2017; Robinson and Sutherland, 2002; White and Roy, 2015). There are a number of factors that may motivate preference for larger fields, including increasing the amount of land in crops within a farm holding (by replacing field border

vegetation with crops), increasing efficiency of farm machinery, and the perception that plant productivity is lower in small than large fields, because small fields have higher edge:interior ratios, and productivity is lower at field edges. Both theoretical and empirical studies suggest that, although there are increases in machine efficiency with increasing field size, the marginal returns are declining (Deverell et al., 2009; Rodríguez and Wiegand, 2009; Xangsayasane et al., 2019). If there are no real gains in machine efficiency above a threshold field size, then reducing the size of fields to this threshold will have minimal impacts on efficiency. It is not yet clear whether there is a similar pattern for the relationship between field size and yield. Interestingly, there is a body of literature suggesting that productivity is actually greater in smaller fields than larger ones, although the validity of these findings is uncertain (Gourlay et al., 2017). Thus future work is needed to understand the effects of field size on yield.

Additionally, understanding the relative socioeconomic impacts of reducing the intensity of farming practices versus reducing field sizes can aid decision-making, allowing policymakers and farmers to identify the conservation action(s) with the lowest socioeconomic cost. If reducing field sizes has smaller effects on yield than adoption of wildlife-friendly practices, then reducing crop field sizes could be a promising strategy for conservation, allowing for conservation of biodiversity in working agricultural landscapes with minimal impact on agricultural production.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2019.106698>.

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