Agriculture, Ecosystems and Environment 319 (2021) 107567

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

More milkweed in farmlands containing small, annual crop fields and many hedgerows

Amanda E. Martin [a,b,*], Greg W. Mitchell [a,b], Judith M. Girard [c], Lenore Fahrig [d]

[a] Environment and Climate Change Canada, National Wildlife Research Centre, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada
[b] Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada
[c] Environment and Climate Change Canada, Canadian Wildlife Service, 335 River Road, Ottawa, ON K1V 1C7, Canada
[d] Geomatics and Landscape Ecology Laboratory, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

ARTICLE INFO

Keywords:
Asclepias
Danaus plexippus
Agricultural intensification
Farmland heterogeneity
Farming practices
Monarch butterfly

ABSTRACT

Milkweed has declined substantially, with over 80% declines in some agricultural regions. This threatens monarch butterfly (*Danaus plexippus*) persistence, because monarch larvae feed solely on milkweed. Thus conservation actions are needed to enhance the availability of milkweed, particularly in agricultural landscapes. Conservation actions to date have largely focused on reducing intensive agricultural practices, mainly use of herbicides. However, research suggests that landscape-scale alteration of the cropped portion of an agricultural landscape (the "farmland"), for example, to reduce crop field sizes, can benefit herbaceous plants such as milkweed. Here we collected data on milkweed occurrence and cover in agricultural landscapes in Ontario, Canada, capturing variability in milkweed from field edge to interior by sampling in the interior and along the edges of 68 crop fields. We used these data to evaluate the relative effects of farming practices within the sampled field (e.g. herbicide, fertilizer use) on milkweed versus the effects of mean field size, crop diversity, hedgerow cover, and the proportion of farmland in annual crops in the surrounding landscape. Additionally, we evaluated the effects of these variables on the cover of other herbaceous plants, to identify which—if any—could benefit milkweed without increasing overall weed cover. We found more milkweed at sites surrounded by landscapes with smaller crop fields, lower crop diversity, and higher cover of annual crops. Milkweed was more likely to occur at sites surrounded by landscapes with more hedgerows. These landscape-scale effects on milkweed were often larger than those of within-field farming practices. Importantly, we found that most variables had opposite effects on milkweed relative to other plants. Thus, altering the landscape to benefit milkweed does not imply an increase in weed cover.

1. Introduction

Monarch butterfly (*Danaus plexippus*) is a migratory species of conservation concern in North America. It is subdivided into two populations: the eastern population, which breeds east of the Rocky Mountains and primarily migrates to, and overwinters in, central Mexico, and the western population that breeds west of the Rocky Mountains and primarily migrates to, and overwinters on, the Pacific coast of California, USA. Both populations have declined precipitously over the last few decades. The size of the eastern population on its overwintering grounds declined 84% from its maximum recorded size in 1996–1997 to 2019–2020 (Rendón-Salinas et al., 2021). The western population has declined by >99% since the 1980s, with a single year drop of 86% between 2018 and 2019 (Pelton et al., 2019).

Loss of milkweed (plants in the subfamily Asclepiadoideae, including *Asclepias* spp.) within the monarch breeding range is tantamount to loss of monarch breeding habitat, because monarch larvae feed solely on milkweed. Although the importance of this threat relative to others (e.g. loss of overwintering habitat) is still debated (Flockhart et al., 2015; Inamine et al., 2016; Pleasants et al., 2017), loss of breeding habitat is consistently recognized as a threat to monarch persistence in both the academic literature (Belsky and Joshi, 2018; Crone et al., 2019; Malcolm, 2018; Thogmartin et al., 2017b) and in species at risk threat assessments and recovery planning documents (COSEWIC, 2016;

---

* Corresponding author.
E-mail addresses: Amanda.Martin@ec.gc.ca (A.E. Martin), Gregory.Mitchell@ec.gc.ca (G.W. Mitchell), Judith.Girard@ec.gc.ca (J.M. Girard), lenore_fahrig@carleton.ca (L. Fahrig).

https://doi.org/10.1016/j.agee.2021.107567
Received 29 August 2020; Received in revised form 3 July 2021; Accepted 6 July 2021
Available online 22 July 2021
0167-8809/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

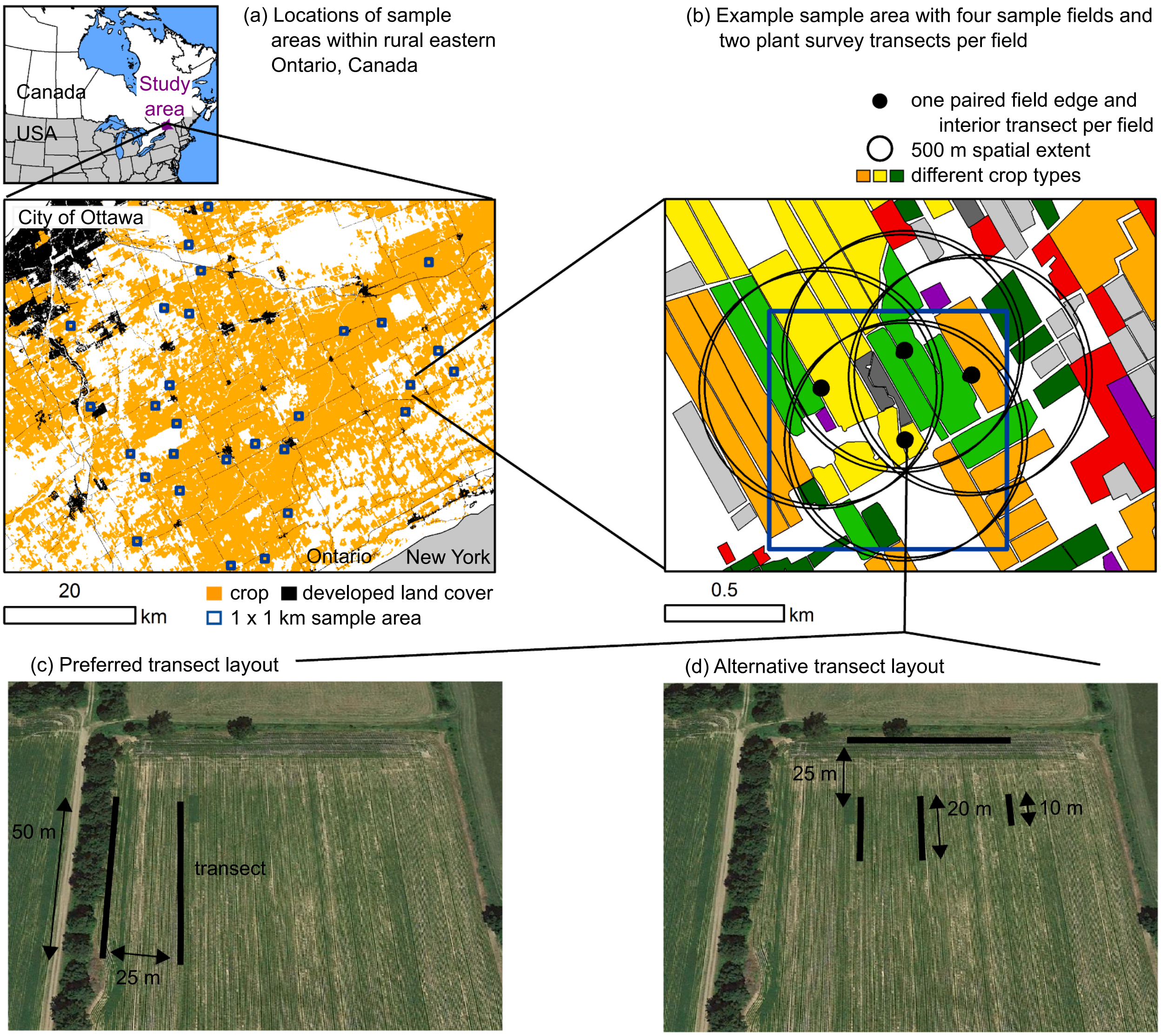

Fig. 1. Depiction of the study design. (a) Locations of the 29, 1 × 1 km sample areas in rural eastern Ontario, Canada. (b) An example sample area with four sample fields. Circles illustrate one spatial extent within which we estimated the mean field size, crop diversity, hedgerow cover, proportion of farmland in annual crops, and total crop cover for each transect. These variables were measured within radii of 250, 500, 750, and 1000 m of the center of each transect. Each field had one 50 × 2 m field edge transect and one 50 × 2 m field interior transect for surveying milkweed and other herbaceous plants. These two transects are represented by a single point in the figure, as they were ~25 m apart. (c–d) Example layouts of a field edge transect and field interior transect within a sample field. A field edge transect was at the very edge of the field and aligned with the field edge, with half of the surveyed area in the crop field and the other half in the field border. Where possible, the field interior transect was placed parallel to its paired field edge transect, ~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. Land cover was from (a) Agriculture and Agri-Foods Canada's (2012) annual crop inventory and (b) the 40-cm-resolution land cover maps created for Fahrig et al. (2015). Imagery in (c–d) was from Google Earth Pro v. 7.3.0.3832.

Environment and Climate Change Canada, 2016).

Enhancing the availability of milkweed within agricultural landscapes may be vital for monarch conservation in North America (Thogmartin et al., 2017a). Agriculture is a dominant land use within the monarch breeding range, covering a large area of the potential breeding habitat. Additionally, a given amount of milkweed can produce more monarchs in agricultural than non-agricultural land cover types. For example, Pleasants and Oberhauser (2013) and Pitman et al. (2018) found that the average density of monarch eggs on milkweed was 3.5× to 3.9× higher in agricultural than non-agricultural areas, including natural and restored meadows, abandoned fields, roadsides, and private lawns and gardens.

There have been substantial declines in the availability of milkweed in agricultural areas over time, and these declines can exceed what is observed in non-agricultural areas. For example, Pleasants and Oberhauser (2013) estimated that milkweed abundance in agricultural fields declined by 81% from 1999 to 2010 in Iowa, whereas its decline in non-agricultural land cover types was only 31%. Hartzler (2010) estimated a 90% decline in the area of crop fields occupied by common milkweed in Iowa, compared to no change in milkweed cover along roads. It is estimated that milkweed numbers in the dominant Midwestern USA crop types (corn and soybean) dropped from 856.3 million to 6 million stems between 1999 and 2014 (Pleasants, 2017).

Adoption of herbicide-resistant crops—and the resulting increase in herbicide use (e.g. Brookes, 2014; Kniss, 2017)—has largely been identified as the cause of milkweed declines in agricultural areas (e.g. Hartzler, 2010; Pleasants and Oberhauser, 2013; but see Boyle et al., 2019). Studies have also found that declines in monarch abundance coincide with increases in herbicide use in the breeding range (Crone et al., 2019; Stenoien et al., 2015; Thogmartin et al., 2017b), further supporting the idea that use of herbicides has indirectly contributed to monarch butterfly declines.

Other farming practices associated with agricultural intensification may also contribute to milkweed declines. For example, Boyle et al. (2019) found some evidence that milkweed abundance declines with increasing fertilizer use. Tillage can also have negative impacts on milkweed, in part because tillage buries milkweed seeds deep enough to impede germination and establishment (Yenish et al., 1996). Thus, we expect milkweed to be more available for monarchs in crop fields with less intensive farming practices.

However, there may be other options to promote milkweed occurrence and abundance in agricultural landscapes. In particular, research suggests that altering the composition and pattern of the cropped portion of a landscape (the "farmland context") can benefit non-crop herbaceous plants at a site, most likely because those changes result in larger populations in the surrounding landscape that in turn can immigrate to the local site. Studies have found more plant species in farmlands with smaller crop fields than in farmlands with larger fields, and more species in farmlands with a greater diversity of crop types than in farmlands with less diverse crops (Alignier et al., 2020; Fahrig et al., 2015; Zhou et al., 2018). Herbaceous plants can also benefit from having more and wider wooded hedgerows in the landscape (Graham et al., 2018). The types of crops within the farmland context can also affect herbaceous plants. There can be more plant species in farmlands with less annual crop cover, i.e. crops that need to be replanted every year (e.g. corn), and with more perennial crop, i.e. crops that are not replanted each year (e.g. hay; unpublished analysis associated with Martin et al., 2020). Thus, we expect milkweed to be more likely to occur and more abundant in farmlands with smaller crop fields, more diverse crops, more hedgerows, and lower proportion of the farmland in annual than perennial crops.

When resources (e.g. money) for conservation action are limited, it is useful to understand not only which options could achieve a conservation objective—such as increasing milkweed availability for monarchs—but the relative effects of these options. This allows resources to be focused on the most effective options. It is not clear whether we should expect within-field farming practices to have larger effects on milkweed at a site than the farmland context of the site. For example, Billeter et al. (2008) found that the negative effect of fertilizer use on herbaceous plant richness was stronger than the effect of crop diversity. In contrast, Martin et al. (2020) found that mean crop field size and crop diversity had stronger effects on herbaceous plant species in fields and field edges than a number of within-field farming practices, including use of herbicides and fertilizers.

It is also not clear which (if any) of the proposed options could effectively meet the objective of increasing milkweed without causing substantial negative impacts on farmers' livelihoods. There are different ways in which a given conservation action could ultimately impact agricultural production. For example, actions designed to benefit one group of herbaceous plant species—milkweed—could benefit other plants, leading to an overall increase in the cover of other non-crop herbaceous plants.

Here we use data on the occurrence and abundance of milkweed and other non-crop herbaceous plants in and along the edges of crop fields, farming practices in the crop fields, and the farmland context to address the following:

1. Are milkweed more likely to occur and more abundant in farmlands with smaller crop fields, more diverse crops, more hedgerows, and a lower proportion of annual crop cover?
2. Are effects of within-field farming practices on milkweed stronger than effects of the farmland context?
3. Do within-field farming practices and the farmland context have similar effects on milkweed cover and the cover of other herbaceous plants?

Specifically, we considered six farming practices: the use of herbicide, chemical fertilizer, non-chemical fertilizer, tile drainage, and tillage, and whether the sampled field was an annual crop rather than a perennial crop. We also considered four aspects of the surrounding farmland that could potentially be managed to benefit milkweed: mean field size, crop diversity, the proportion of the landscape in hedgerows ("hedgerow cover"), and the proportion of cropped area in annual rather than perennial crops ("proportion annual crops").

2. Methods

2.1. Data collection

2.1.1. Selection of sample areas, fields, and transects

We had 29 1 × 1 km "sample areas" within the breeding range of the eastern monarch population, in rural eastern Ontario, Canada (Fig. 1a). These sample areas were the subset of the 93 sample areas used in Fahrig et al. (2015) for which we could obtain farming practices information for at least one sample field (see Section 2.1.2, below). Sample areas were selected based on criteria detailed in Pasher et al. (2013). In summary, the areas were selected to: (a) represent the variability in mean field size and crop diversity across eastern Ontario; (b) be spatially independent, i.e., with minimal spatial autocorrelation of mean field size and crop diversity across sample areas and at least 6 km from the center of all other sample areas; (c) be dominated by agricultural land use; and (d) minimize, to the degree possible, the correlations between mean field size, crop diversity, and crop cover across the sample areas.

Up to four sample fields were randomly selected within each sample area, and a site along the edge of each field was selected for a 50 m × 2 m field edge transect (Fig. 1b). The transect locations were randomly selected, under the constraints that they had to be (a) between two adjacent crop fields; (b) ≥200 m from all other transects; (c) ≥50 m from non-agricultural land uses; and (d) ≥50 m from the edge of the 1 × 1 km sample area. Transects were located at sites with low tree cover between the two adjacent crop fields, resulting in few transects directly adjacent to a hedgerow (11 of 68 field edge transects) and very weak relationships between hedgerow adjacency of the transects and hedgerow cover in the surrounding landscapes ($r^2 < 0.01$). Visual surveys were conducted to confirm that these constraints were met prior to the field season. If they were not met, or if landowner permission to access fields for surveys was not obtained, another random field was selected within the sample area. Transects were aligned with the field edge, such that half the width of the transect (1 m) was in the field and the other half was in the adjacent vegetation. We expected milkweed to also occur within crop fields, and wanted to capture that in our study. To do so we paired each field edge transect with a 50 m × 2 m field interior transect in the field, ~25 m from the field edge transect. Where possible, the field interior transect was parallel to its paired field edge transect (Fig. 1c). However, where crop rows ran perpendicular to the field edge, we used a layout that preserved the approximate distance from the field edge transect and the total 50 m transect length (Fig. 1d). This was done to avoid potential damage to crop plants when surveyors moved along the field interior transect during plant sampling (see Section 2.1.3).

2.1.2. Measurements of farming practices

The owners of sample fields were surveyed by phone between May 24 and August 31 in each year, to obtain farming practice information for as many sample fields as possible, given time and land owner availability/cooperation. Survey questions and methods were approved by the Carleton University Research Ethics Board (Project no. STPGP 381108-09). We used information obtained in these surveys to estimate: herbicide use (yes/no), non-chemical fertilizer use (yes/no), chemical fertilizer use (yes/no), tile drainage (yes/no), and tillage (yes/no), and whether the sampled field was an annual crop or perennial one. We sampled for herbaceous plants in hay, legume, corn, soybean, cereal, and fallow crop fields. A crop was classified as perennial if it was hay and annual if it was legume, corn, soybean, or cereal. We also classified fallow fields as annual, because fields in our study were typically left fallow for short (often one-year) periods (JMG, pers. obs.). For full survey details see Martin et al. (2020). In total, we obtained farming practices data for 136 transects in 68 fields (68 field edge and 68 field interior transects), with 2–8 transects per sample area.

2.1.3. Estimates of occurrence and cover of milkweed and other herbaceous plants

Herbaceous plants were surveyed along each transect once in either 2011 or 2012, sampling all transects within a given sample area in the same day and year. All surveys were conducted between July 17 and August 30, during the approximate period when monarchs are most abundant in the study region (Crewe et al., 2019; Davis and Howard, 2005). The surveyor walked each transect once per survey and estimated the proportional cover of each non-crop herbaceous species, i.e. the area in m^2 covered by the species/100 m^2 survey area.

2.1.4. Measurements of farmland context variables and total crop cover

We estimated the farmland context variables surrounding each transect using the 40-cm resolution land cover data set created for Fahrig et al. (2015) for the year of sampling (2011 or 2012). This land cover data set covers a 3 × 3 km area centered on each 1 × 1 km sample area. Each crop field was defined by the 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 type—such as a hedgerow—were defined as separate fields, as were adjacent areas of different crop types. The mean field size, crop diversity, hedgerow cover, and proportion annual crops were estimated within four different landscape extents, i.e. circular buffers with radii of 250 m, 500 m, 750 m, and 1000 m, centered on the midpoint of each transect (Fig. 1b). Across our landscape extents we sampled a greater diversity of crop types then were represented in our sampled fields. We defined a crop as annual if it was canola, cereal, corn, fallow, legume, mixed vegetable, pea, sod, soybean, strawberry, or sunflower. A crop was defined as perennial if it was hay, pasture, or apple. We also estimated the total crop cover, i.e. the proportional cover of annual + perennial fields, within the four landscape extents, as described above. Despite efforts to minimize variation in crop cover during site selection (see Section 2.1.1, above), there was substantial variation in crop cover around transects, e.g. 42–89% crop cover within a 1000-m radius. Given that crop cover may affect the occurrence/abundance of milkweed, as found for other herbaceous plant species (Martin et al., 2020; Zhou et al., 2018), we included crop cover in our analyses to control for its effects (see Section 2.2, below).

Note that we focus here on the comparison between effects of within-field farming practices and landscape-scale farmland composition and pattern on milkweed. Farming practices within the surrounding landscape might also indirectly affect milkweed in our transects. However, we could not assess this as there are no publicly-available data on farming practices in our study region at an appropriate resolution, and it was not feasible to survey landowners of all 1618 individual crop fields in the landscapes surrounding our transects. In any case, we expect that the direct effects of farming practices within a sample field, e.g. herbicide or ploughing directly killing plants and seeds, represent the dominant effects of farming practices on milkweed in our transects.

2.2. Data analysis

We tested our predictions for effects of farmland context variables on milkweed (research question 1, see Section 1) and evaluated the relative importance of within-field farming practices versus farmland context (research question 2) simultaneously. We did this by estimating the standardized effects of the six farming practice variables (herbicide use, non-chemical fertilizer use, chemical fertilizer use, tile drainage, tillage, and crop type in the sample field) and four farmland context variables (mean field size, crop diversity, hedgerow cover, and proportion annual crops) on milkweed occurrence and cover using a zero-inflated beta mixed effects model. This approach is appropriate for modeling a proportional response variable such as ours, where there is an excess of zeros (see Section 3). It accommodates the excess zeros by having one part of the model estimate effects of predictor variables on the probability of occurrence and a second part that estimates the effects of predictor variables on milkweed cover for sites where milkweed occurs. In addition to the farming practice and farmland context variables, we included total crop cover, Julian date of sampling, and transect location (field edge or field interior), to control for their effects on milkweed. We also included a random effect of sample area, to account for non-independence of data collected on transects within a sample area, including that all transects within a sample area were sampled on the same day by the same surveyor(s). We took a Bayesian (rather than frequentist) approach to statistical modeling (as detailed in Appendix A), primarily because Bayesian approaches are more conducive to complex model fitting and produce unbiased inferences regardless of the sample size (see Ellison, 1996; Kéry, 2010 for further discussion).

We included each farmland context variable and crop cover at the scale where its relationship to the biological responses (milkweed occurrence and cover) was strongest, often referred to as a variable's "scale of effect". This was necessary because the strength and direction of relationship between a biological response and a landscape-scale variable can depend on the spatial extent within which that landscape variable is measured (e.g. Ethier and Fahrig, 2011; Martin and Fahrig, 2012); thus arbitrary selection of a spatial extent could very well lead to underestimation of the effects of the farmland context relative to farming practices. Evidence suggests little support for a priori selection of an appropriate extent (Jackson and Fahrig, 2015; Miguet et al., 2016). Instead we used an empirical approach to identify the scale of effect for each farmland context variable and for crop cover, which involves fitting models between the biological response and a landscape-scale variable at multiple spatial extents. As we increase the spatial extent considered we include more landscape information relevant to the response, improving model fit, until a point where the extent becomes larger than that affecting the response and the fit starts to decline. We then use this analysis to identify the extent with the strongest model fit. In this case we also used an approach that (a) controlled for effects of other landscape variables and within-field farming practices on milkweed occurrence and cover, and (b) allowed for selection of different spatial extents for different landscape variables (as in Martin et al., 2020). We evaluated a set of 1024 candidate models which were identical with the exception that each included a unique combination of the four spatial extents (250, 500, 750, and 1000 m) for each of five variables: mean field size, crop diversity, hedgerow cover, proportion annual crops, and crop cover. Candidate model 1 included all variables at 250 m; candidate model 2 included mean field size, crop diversity, hedgerow cover, and proportion annual crops at 250 m and crop cover at 500 m; candidate model 3 included mean field size, crop diversity, and hedgerow cover at 250 m and proportion annual crops and crop cover at 500 m; and so on (see Appendix B). We used the Deviance Information Criterion (DIC; calculated according to M. Plummer, p. 620 in Spiegelhalter et al., 2002) to evaluate relative support for each candidate model, and the scale of effect for each farmland context variable and for crop cover was the scale included in the most supported model.

This most supported model was then used to address our research questions. We evaluated the relative effects of within-field farming practices and farmland context variables (at their scales of effect) on milkweed occurrence and cover using the median standardized coefficient value from the posterior distribution to estimate the importance of each variable. Each effect estimate represents the effect of a variable on milkweed occurrence (or cover) when controlling for the effects of all other variables on occurrence (cover). And we evaluated support for predicted effects of farmland context variables on milkweed occurrence and cover using the 90% credible (or highest posterior density) interval,

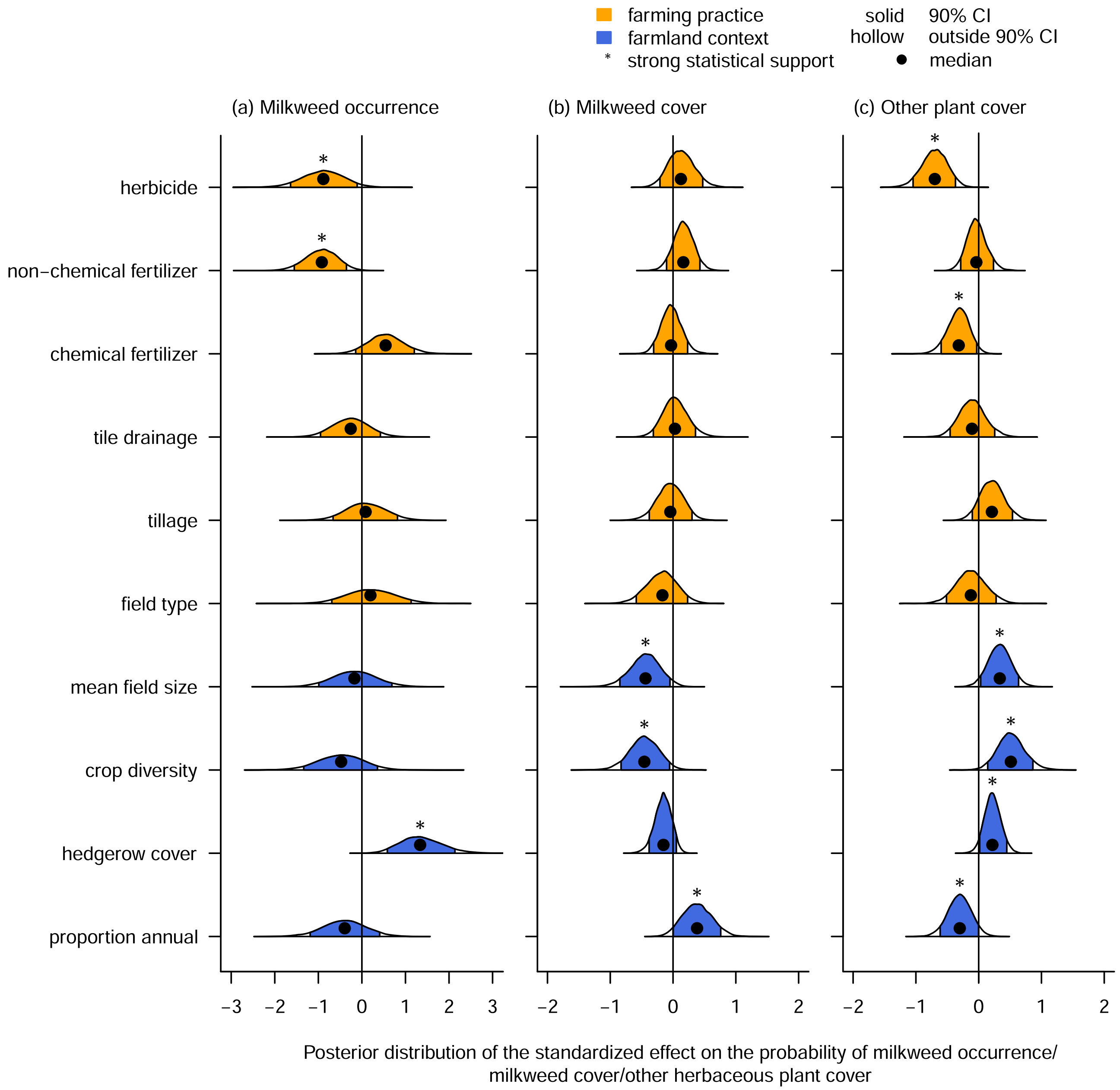

Fig. 2. Standardized effects of the within-field farming practices and farmland context variables on the (a) probability of milkweed occurrence, (b) milkweed cover, and (c) cover of other (non-milkweed, non-crop) herbaceous plants in rural eastern Ontario, Canada (n = 136 transects). Farmland context variables were estimated at the landscape extent showing the strongest effects on milkweed: 250 m for proportion annual crops, 500 m for hedgerow cover, 750 m for mean field size, and 1000 m for crop diversity. Shown are the estimated posterior distribution (as a probability density function), 90% credible interval (CI), and median effect for each variable. An effect was considered strongly supported if its 90% CI did not cross zero.

hereafter referred to as the 90% CI. An effect was considered strongly supported if its 90% CI did not cross zero. We used the 90% CI, not the frequently-used 95% CI, because estimates of the 90% CI are more stable than estimates of the 95% CI (Kruschke, 2015).

We also estimated the expected changes in the probability of milkweed occurrence and milkweed cover in response to changes in each predictor variable, using the median effect sizes from the most supported zero-inflated beta mixed effects model. Predicted changes in occurrence/cover in response to changes in a single farming practice, farmland context variable, etc. depend on values for all other predictors. To capture this variability, we estimated the change in occurrence/cover in response to changes in each variable 4096 times, once for each unique combination of two states for each predictor: (1) herbicide: yes, no; (2) non-chemical fertilizer: yes, no; (3) chemical fertilizer: yes, no; (4) tile drainage: yes, no; (5) tillage: yes, no; (6) crop type in the sampled field: annual, perennial; (7) mean field size: 6007 m^2, 28,119 m^2; (8) Shannon diversity of crop types: 0.00, 1.86; (9) proportion of the landscape in hedgerows: 0.00, 0.16; (10) proportion of cropped area of the landscape in annual crops: 0.12, 1.00; (11) proportion of the landscape in crops (annual + perennial): 0.50, 0.95; (12) Julian date of sampling: 199, 241; and (13) transect location: field edge, interior. For continuous predictors, the values are the minimum and maximum values observed in our dataset.

To determine whether within-field farming practices and the farmland context have similar effects on milkweed and the cover of other herbaceous plants (research question 3, see Section 1), we modeled the relative effects of the six farming practices and four farmland context variables on other herbaceous plants, using the methods described

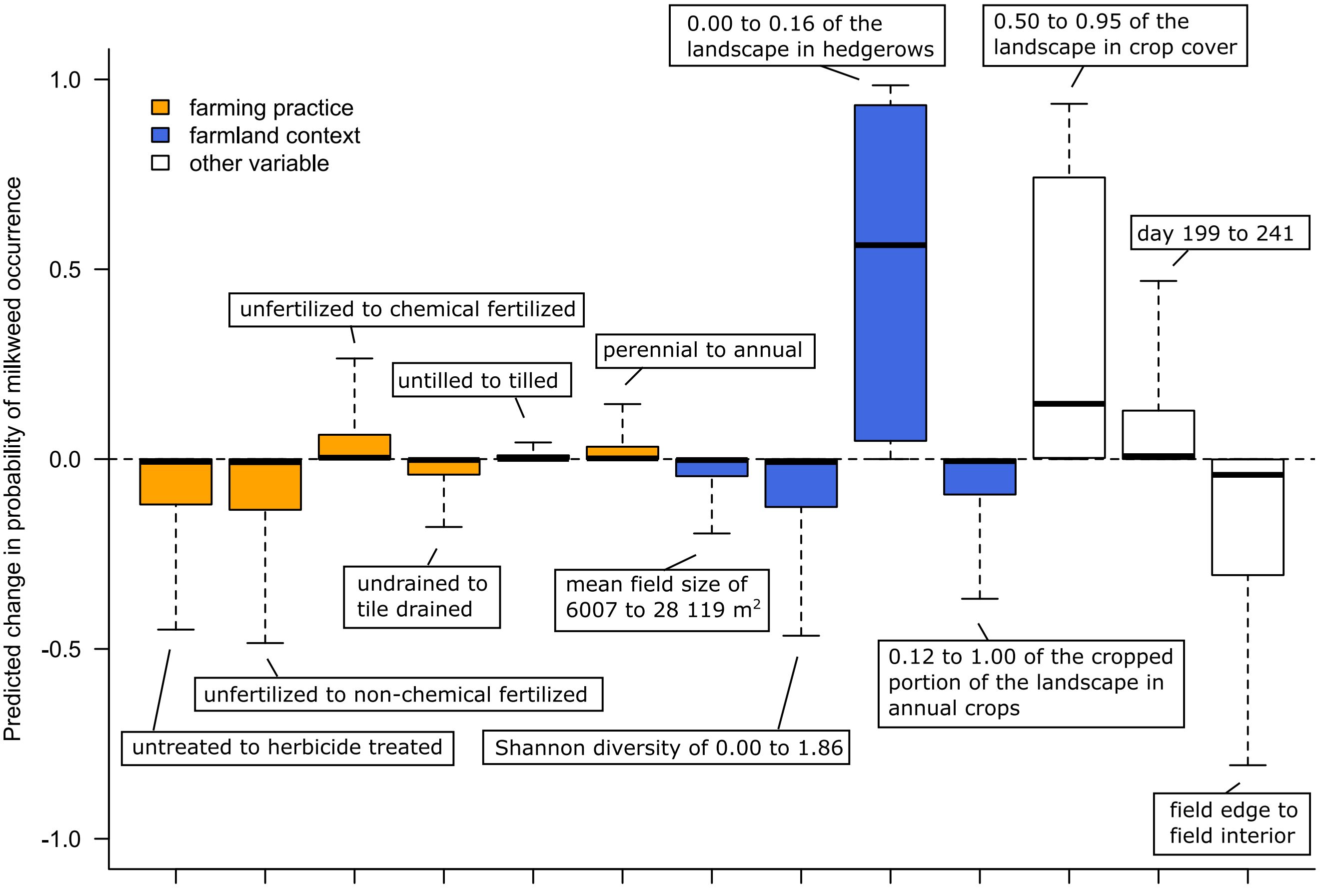

Fig. 3. Predicted changes in the probability of milkweed occurrence in response to changes in farming practices, farmland context, total crop cover, date of sampling, and transect location. Predictions are from our zero-inflated beta mixed effects model, modeling milkweed occurrence and cover as functions of these 13 variables plus a random effect of sample area. Farmland context variables were estimated at the landscape extent showing the strongest effects on milkweed: 250 m for proportion annual crops, 500 m for hedgerow cover, 750 m for mean field size, and 1000 m for crop diversity. Crop cover was estimated at the 500 m extent. Predicted changes in occurrence in response to changes in a single farming practice, farmland context variable, etc. depend on values for all other predictors. To capture this variability, we estimated the change in occurrence in response to changes in each variable 4096 times, representing a range of possible values for the other 12 predictor variables (see Section 2.2 for details). Line = median, box = interquartile range, whiskers = extreme values.

above (and in Appendix A), with the following three exceptions. First, we used a zero- and one-inflated beta mixed effects model to estimate the effects of variables on the proportional cover of other herbaceous plants rather than a zero-inflated beta mixed effects model, because there were transects with proportional cover estimates of zero and one. Second, we modeled the effects of farming practices and farmland context on cover only, rather than both occurrence and cover. There were not enough transects with zero cover (1% of transects) to estimate effects of predictors on the probability of occurrence of other herbaceous plants. Third, we modeled the farmland context variables at the scales of effect for milkweed, not at the scales of effect for other herbaceous plants, because we were primarily interested in determining the effects of the farmland context on other plants within the landscape context relevant to milkweed. However, we note that results were very similar when farmland context variables were included at the scales of effect for other herbaceous plants (Appendix C).

We also tested for collinearity among the farming practice variables, farmland context variables at their scales of effect, and crop cover at its scale of effect. We used generalized linear models with a binomial distribution and logit link for comparisons of farming practices, and indexed the strength of relationship using Nagelkerke's r^2. For all other comparisons we used linear regression, and indexed the strength of relationship using r^2.

We checked for positive spatial autocorrelation of model residuals for each of the 15,000 MCMC samples from the model of milkweed occurrence and cover, and the model of other herbaceous plant cover, with the farmland context variables and crop cover at their scales of effect on milkweed. We used a one-tailed Global Moran's I to test for positive spatial autocorrelation in model residuals from each MCMC sample, i.e. whether similarity in residual values declined with distance between transects, using a permutation approach with 5000 permutations to calculate the significance level.

Analyses were conducted in R version 3.6.3 (R Core Team, 2020) using the 'zoib' (Liu and Kong, 2015, 2018), 'rjags' (Plummer, 2018), 'HDInterval' (Meredith and Kruschke, 2018), 'lme4' (Bates et al., 2015), 'MuMIn' (Barton, 2016), and 'ape' (Paradis et al., 2004) packages. Bayesian models were run in JAGS version 4.3.0 (Plummer, 2003). Data and R scripts are available on figshare (Martin et al., 2021).

3. Results

Milkweed was observed at 85% of the 68 sample fields and 55% of the 136 transects. Milkweed was typically observed at only one of the two transects within a sample field; this was the case for 71% of the 58 fields with milkweed. If milkweed was observed at only one of two transects, the observation was almost always at the field edge (98% of 41 fields). When milkweed was observed on a transect, its proportional cover ranged from 0.001 to 0.104 (median = 0.005). Ninety-eight percent of milkweed cover was common milkweed (*Asclepias syriaca*) and the remaining 2% was identified as another *Asclepias* species. Other

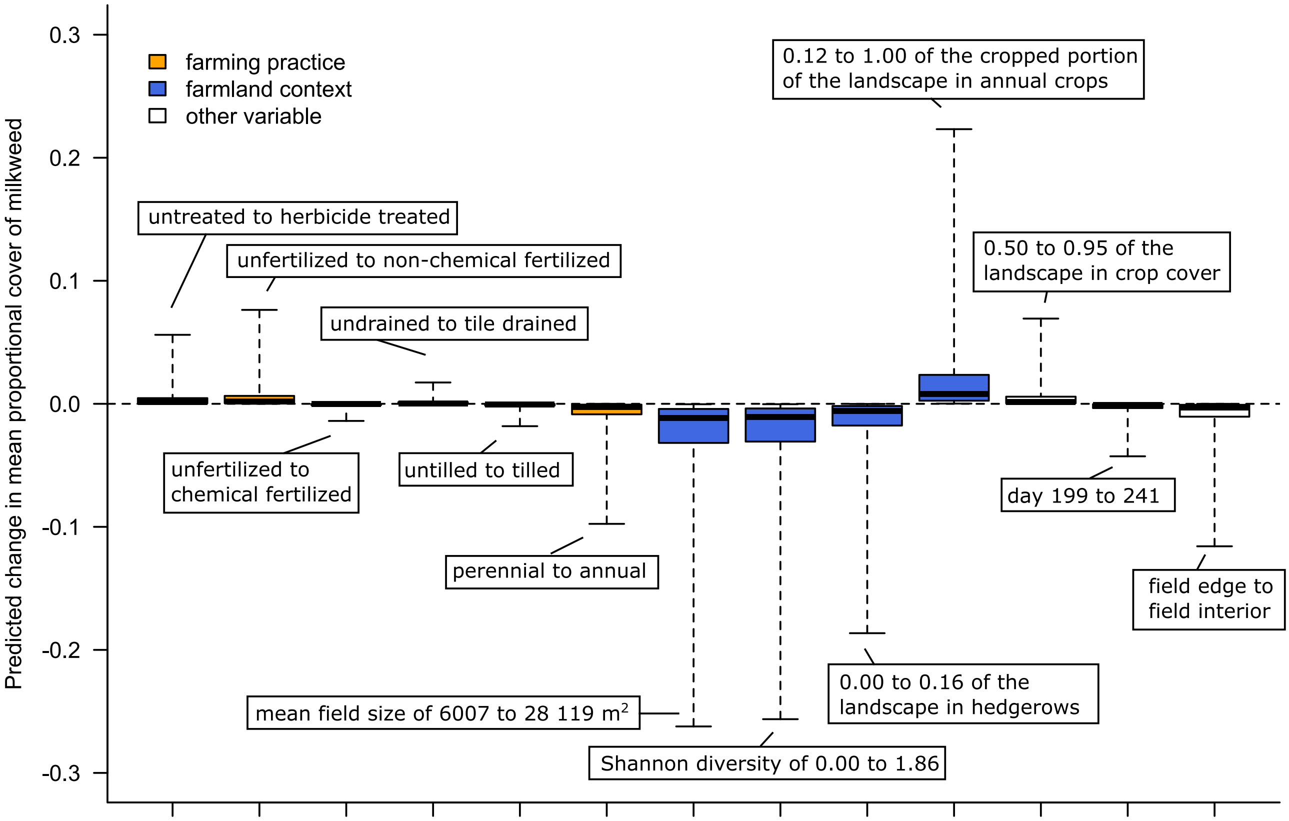

Fig. 4. Predicted changes in the mean proportional cover of milkweed in response to changes in farming practices, farmland context, crop cover, date of sampling, and transect location. Predictions are from our zero-inflated beta mixed effects model, modeling milkweed occurrence and cover as functions of these 13 variables plus a random effect of sample area. Farmland context variables were estimated at the landscape extent showing the strongest effects: 250 m for proportion annual crops, 500 m for hedgerow cover, 750 m for mean field size, and 1000 m for crop diversity. Crop cover was estimated at the 500 m extent. Predicted changes in cover in response to changes in a single farming practice, farmland context variable, etc. depend on values for all other predictors. To capture this variability, we estimated the change in cover in response to changes in each variable 4096 times, representing a range of possible values for the other 12 predictor variables (see Section 2.2 for details). Line = median, box = interquartile range, whiskers = extreme values.

herbaceous plants were observed at 99% of transects (see Appendix D for the species list). When other plants were observed, the cover ranged from 0.001 to 1.000 (median = 0.416).

Different landscape-scale variables had different scales of effect (Appendix B). The scale of effect was 250 m for proportion annual crops, 500 m for hedgerow cover and crop cover, 750 m for mean field size, and 1000 m for crop diversity.

We found strong support, i.e. a 90% CI that did not cross zero, for effects of hedgerow cover in the surrounding landscape on the probability of milkweed occurrence, and for effects of mean field size, crop diversity, and proportion annual crops on milkweed cover (Fig. 2a and b). The positive effect of hedgerow cover on the probability of milkweed occurrence was consistent with our prediction (Fig. 3). We also, as expected, found greater cover of milkweed in sites surrounded by agricultural landscapes with smaller fields than larger fields (Fig. 4). In contrast, effects of crop diversity and proportion annual crops on the cover of milkweed were opposite to our expectations (Fig. 4). That is, we found more milkweed in sites surrounded by landscapes with less diverse crops than more diverse crops, and there was more milkweed in landscapes with more annual than perennial crop cover.

The median effects of farmland context variables on milkweed occurrence and cover were often larger than the effects of within-field farming practices (Figs. 2a–b, 3 and 4). This was particularly apparent for milkweed cover. Crop diversity, mean field size, and proportion annual crops had median effects on milkweed cover that were 2.25× to 15.90× larger than the effect of any farming practice. The median effect of hedgerow cover on the probability of occurrence was 1.45× to 15.44× larger than the effect of any practice. Effects of farming practices on milkweed occurrence and cover were weakly supported (with 90% CI that crossed zero), with two exceptions. Milkweed were less likely to occur in fields treated with herbicides and in fields treated with non-chemical fertilizers (Fig. 2a).

Surprisingly, we found that within-field farming practices and farmland context often had opposite effects on the occurrence/cover of milkweed relative to the cover of other herbaceous plants. Chemical fertilizer, field type (annual/perennial), mean field size in the landscape, and crop diversity in the landscape had opposite effects on the probability of milkweed occurrence relative to the cover of other herbaceous plants (Figs. 2 and 5). Median effects on milkweed cover and the cover of other herbaceous plants were in the opposite direction for herbicide, non-chemical fertilizer, tile drainage, tillage, mean field size, crop diversity, hedgerow cover, and proportion annual crops in the landscape (Figs. 2 and 5).

Pairwise relationships between our predictor variables were generally weak (Appendix E). The strongest relationships were between herbicide use and crop type in the sample field (Nagelkerke $r^2 = 0.54$) and between proportion annual crops in the landscape and crop type in the sample field ($r^2 = 0.52$).

Tests for spatial autocorrelation of model residuals suggested that inclusion of transect location (field edge vs. interior) and sampling area in models were generally sufficient to control for positive spatial autocorrelation. Global Moran's I tests found support for positive spatial autocorrelation in only 5% of our MCMC runs for milkweed and 5% for other herbaceous plants. Our conclusions were the same whether or not we included these MCMC runs in our estimates of the median effect sizes and 90% CI (Appendix F).

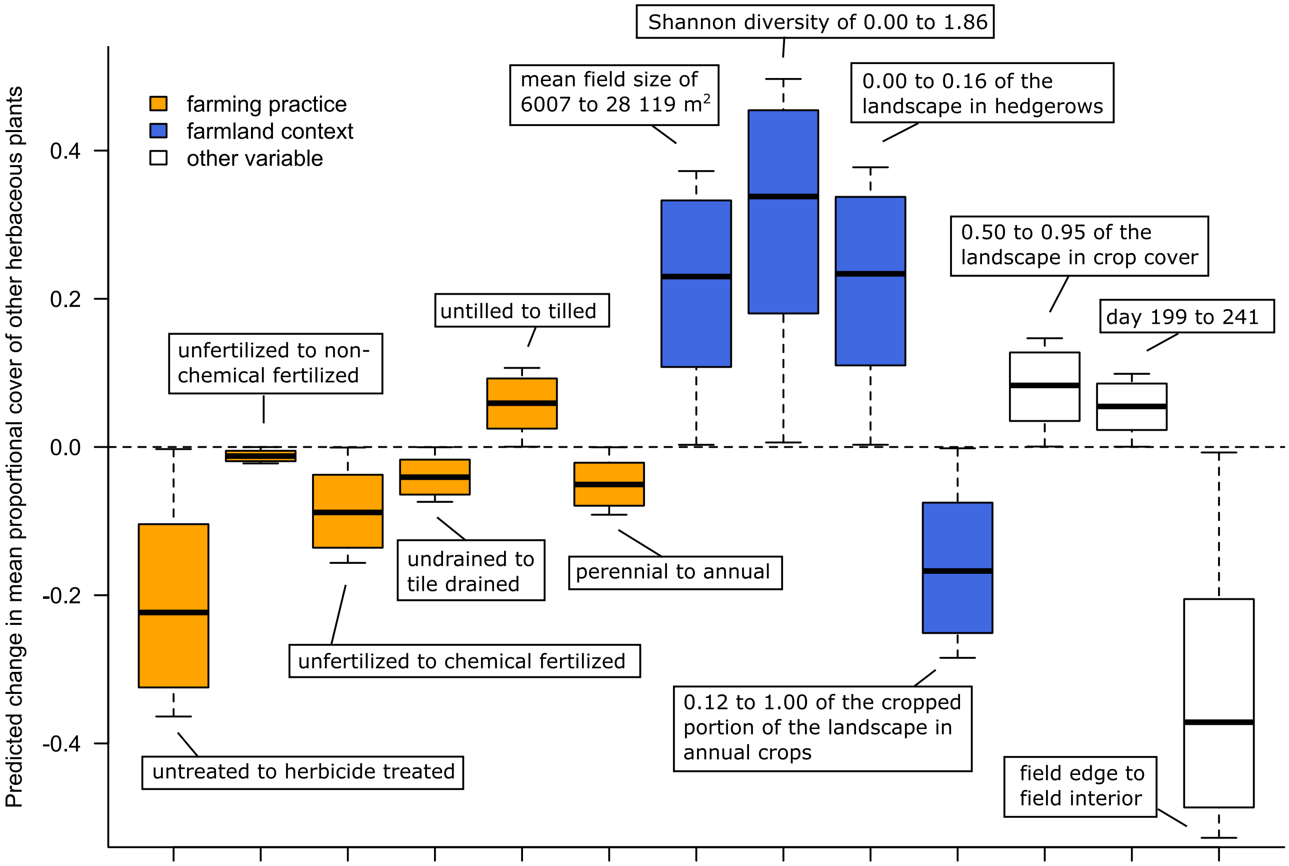

Fig. 5. Predicted changes in the mean proportional cover of other (non-milkweed, non-crop) herbaceous plants in response to changes in farming practices, farmland context, total crop cover, date of sampling, and transect location. Predictions are from our zero- and one-inflated beta mixed effects model, modeling cover of other plants as a function of these 13 variables plus a random effect of sample area. Farmland context variables were estimated at the 250 m extent for proportion annual crops, 500 m for hedgerow cover, 750 m for mean field size, and 1000 m for crop diversity. Crop cover was estimated at the 500 m extent. Predicted changes in cover in response to changes in a single farming practice, farmland context variable, etc. depend on values for all other predictors. To capture this variability, we estimated the change in cover in response to changes in each variable 4096 times, representing a range of possible values for the other 12 predictor variables (see Section 2.2 for details). Line = median, box = interquartile range, whiskers = extreme values.

Finally, although effects of crop cover in the landscape, date of sampling, and transect location were not the focus of the study, we did find strongly supported effects of these variables. We found that milkweed was more likely to occur in sites surrounded by landscapes with more crop cover than less crop cover (median [90% CI] = 1.58 [0.86 to 2.33]; Fig. 3). We were more likely to detect milkweed later in the sampling period (0.62 [0.08 to 1.19]; Fig. 3). Milkweed was also more likely to occur (−2.24 [−2.85 to −1.65]; Fig. 3) and was more abundant (−0.31 [−0.53 to −0.09]; Fig. 4) in field edges than interiors. Similarly, other plants were more abundant in field edges than interiors (−1.18 [−1.33 to −1.01]; Fig. 5).

4. Discussion

We found that effects of the farmland context on milkweed occurrence and cover were often larger than the effects of farming practices used within a crop field, including herbicide application. Crop diversity, mean field size, and proportion annual crops in the surrounding landscape had median effects on milkweed cover that were 2.25× to 15.90× larger than the effects of any farming practice, and the effect of hedgerow cover on the probability of occurrence was 1.45× to 15.44× larger than the effect of any farming practice. This is consistent with Martin et al. (2020), who found that farmland context variables (specifically, mean crop field size and crop diversity) can have stronger effects on the diversity of wildlife and plant species than within-field farming practices. Other studies comparing the relative effects of farming practices on plant diversity/abundance versus landscape-scale variables (e.g. percent of the landscape in intensive land use) also showed that landscape-scale variables can have larger effects than farming practices in some (but not all) cases (e.g. Armengot et al., 2011; José-María et al., 2010; Petit et al., 2016).

It is not likely that our estimates of the relative importance of farming practices and farmland context were biased by relationships among these variables, or underestimated because we used simplified, binary farming practice variables but continuous measures of the farmland context. There were generally weak relationships between predictors in our study (see Appendix E). Additionally, we used a regression-type model to estimate effects of all variables simultaneously, which allows for generally unbiased estimates of size and direction of an effect even when relationships among predictors are strong (Morrissey and Ruxton, 2018; Smith et al., 2009). And, although we cannot fully discount this possibility, supplementary analyses suggest that differences in the resolution of farming practice variables are unlikely to explain why effects of the farmland context on milkweed were strong relative to effects of within-field farming practices (Appendix G).

Although the magnitude of effect of farmland context variables varied among candidate models and spatial extents, our conclusion regarding the relative importance of farmland context versus farming practices was not strongly dependent on the selected extents of measurement. Farmland context was important for milkweed across the set of candidate models. A farmland context variable had the largest median effect on milkweed occurrence or abundance in 93% of candidate models and, in the remaining 7% of models, a farmland context variable always had the second or third largest effect. We also compared the median effect sizes for each pair of farmland context and farming practice variables across the set of 1024 candidate models, and calculated the proportion of models in which the farmland context variable had a larger effect on milkweed occurrence/cover than the farming practice (Table B2). These proportions suggest that, if we selected a random set of spatial extents for measurement of landscape-scale variables we would expect each farmland context variable in that model to have a larger effect on milkweed occurrence than 33–100% of the farming practice variables. We would also expect to find that each farmland context variable has a larger effect on milkweed cover than 50–100% of the farming practice variables.

Nevertheless, it is possible that effects of annual crop cover and crop diversity on milkweed were underestimated in our analyses, because the identified scales of effect for these variables were at the smallest and largest extents we tested, respectively. Ideally, we would have tested extents smaller than 250 m and larger than 1000 m, to ensure that we found the extents at which these farmland context variables had their strongest effects (Jackson and Fahrig, 2015). However, analyses at smaller extents were not feasible due to low variance in some variables at smaller spatial extents. Even at the 250-m extent, the number of fields within the landscape was limited (median [range] = 5 [2–12] fields). Analyses at larger extents were also not possible, because of the limited extent of our high-resolution land cover map (see Section 2.1.4). Thus it is possible that the difference in effects of annual crop cover/crop diversity in the landscape and within-field farming practices on milkweed are even larger than indicated by our analysis.

It is also possible that effects of some farming practices could have been larger than effects of farmland context had we estimated their effects at a landscape scale rather than in the sample fields. However, we speculate that the direct effects of farming practices within a sample field, e.g. herbicide application or ploughing that directly kill plants and seeds in a sample site, represent the dominant effects of farming practices on our transects. If so, then our results should not change much if farming practices are estimated within the surrounding landscape rather than in the sampled field. Future study is needed to test this speculation.

As expected, we found more milkweed in sites surrounded by landscapes with smaller fields than larger fields, and more milkweed in sites surrounded by landscapes with more hedgerows; however, the effect of crop diversity on the cover of milkweed was opposite to our prediction. Some previous studies have found that the effect of crop diversity on wildlife species richness and abundance can depend on the total amount of crop cover in the landscape, with positive effects of crop diversity in landscapes with low crop cover, but negative effects in landscapes with high crop cover (Sirami et al., 2019; Wilson et al., 2017). We, however, found no support for an interacting effect of crop diversity × crop cover on milkweed occurrence or abundance (Appendix H). One may also suggest that the negative effect of crop diversity on milkweed cover could be driven by a relationship between crop diversity and milkweed habitat, i.e. that lower crop diversity benefits milkweed because the land cover types milkweed use as habitat may be more available in landscapes with less diverse crops. We also found no support for this explanation. In our study region, common milkweed—the dominant milkweed species in our landscapes—primarily uses farmland (including managed pastures and annual row crops), roadsides, and natural grassland (OMAFRA, 2016). Relationships between crop diversity and farmland habitats cannot explain the effect of crop diversity on milkweed, because we controlled for the relationship between farmland habitat (i.e. crop cover) and milkweed in our analysis. In addition, natural grasslands did not drive relationships between milkweed and crop diversity, because there were no natural grasslands within our study landscapes. Last, road density, as a surrogate for roadside habitat amount (data from Statistics Canada, 2011), has a weakly positive relationship with crop diversity across all spatial extents ($r = 0.02$–0.26); thus, if anything, we could expect a slight increase in roadside habitat availability with increasing crop diversity. Therefore, the negative effect of crop diversity on milkweed cover does not appear to be driven by a relationship between crop diversity and milkweed habitat.

We instead speculate that the negative effect of crop diversity on milkweed occurs because crop diversity benefits other herbaceous plant species, and milkweed do better in places with less competition from other plants. This is consistent with the observed opposite effect of crop diversity on milkweed and the cover of other herbaceous plants (Fig. 2), and is supported by Evetts and Burnside (1975), who found that both the reproductive success and growth of common milkweed were significantly impeded by competition with other herbaceous species. Thus, the reduced abundance of other herbaceous plants in landscapes with less diverse crops could reduce competition for resources and allow for increased reproduction and growth of milkweed.

This speculation may also help to explain the effects of the other farmland context variables on milkweed, because mean field size, hedgerow cover, and proportion annual crops in the landscape surrounding our sampling sites also had opposite effects on the cover of milkweed and other herbaceous plants. Interestingly, the positive effect of mean field size on herbaceous cover was opposite to our prediction and to observed negative effects of mean field size on plant species richness (Alignier et al., 2020; Gaba et al., 2010; Zhou et al., 2018; but see also Appendix I). Thus, sites surrounded by large fields may have low plant species richness but high abundances of a few species, which do not include milkweed. Smaller field sizes may also benefit milkweed because, all else being equal, a landscape with smaller fields has more field edge. We found that milkweed was much more likely to occur and was more abundant in field edges than field interiors. Thus, smaller fields may result in larger populations of milkweed in the surrounding landscape that in turn can increase immigration to the local milkweed population.

As expected, we found that herbicide use had a strong negative effect on the occurrence of milkweed. This is consistent with previous studies that found strong declines in milkweed and monarch populations over time with increasing intensity of glyphosate use, the dominant herbicide in our region (see Appendix J; Crone et al., 2019; Stenoien et al., 2015; Thogmartin et al., 2017b). Thus the observed 26% increase in the extent of herbicide application in our study region from 1996 to 2016 (Statistics Canada, 2021) may very well have contributed to declines in milkweed in this region.

Finally, we found that non-chemical fertilizer use reduced milkweed occurrence. Interspecific competition does not appear to explain this relationship, because the relationship between non-chemical fertilizer use and the cover of other plants was very weak (Fig. 2c). It is possible that high concentrations of fertilizers could directly impact milkweed. Effects of fertilizer on milkweed are poorly understood (Borders and Lee-Mäder, 2014). However, Darby et al. (2019) did report a weak, negative effect of increasing nitrogen fertilization rates on milkweed seed pod production.

4.1. Management implications

A compelling implication of this study is that it suggests altering agricultural landscapes to benefit milkweed does not need to result in more weed cover that could reduce crop yields. This is because we found effects of variables on milkweed occurrence and cover that were opposite to their effects on other plant cover. In particular, our results suggest that reducing mean field sizes and crop diversity could result in increased occurrence and cover of milkweed for monarchs in agricultural landscapes without increasing the abundance of other herbaceous plants. However, future research is needed to determine whether benefits of reducing mean field sizes and crop diversity for milkweed translate into positive effects on monarchs.

Given the current biodiversity crisis (IPBES, 2019), management actions that can simultaneously benefit many wildlife and plant species

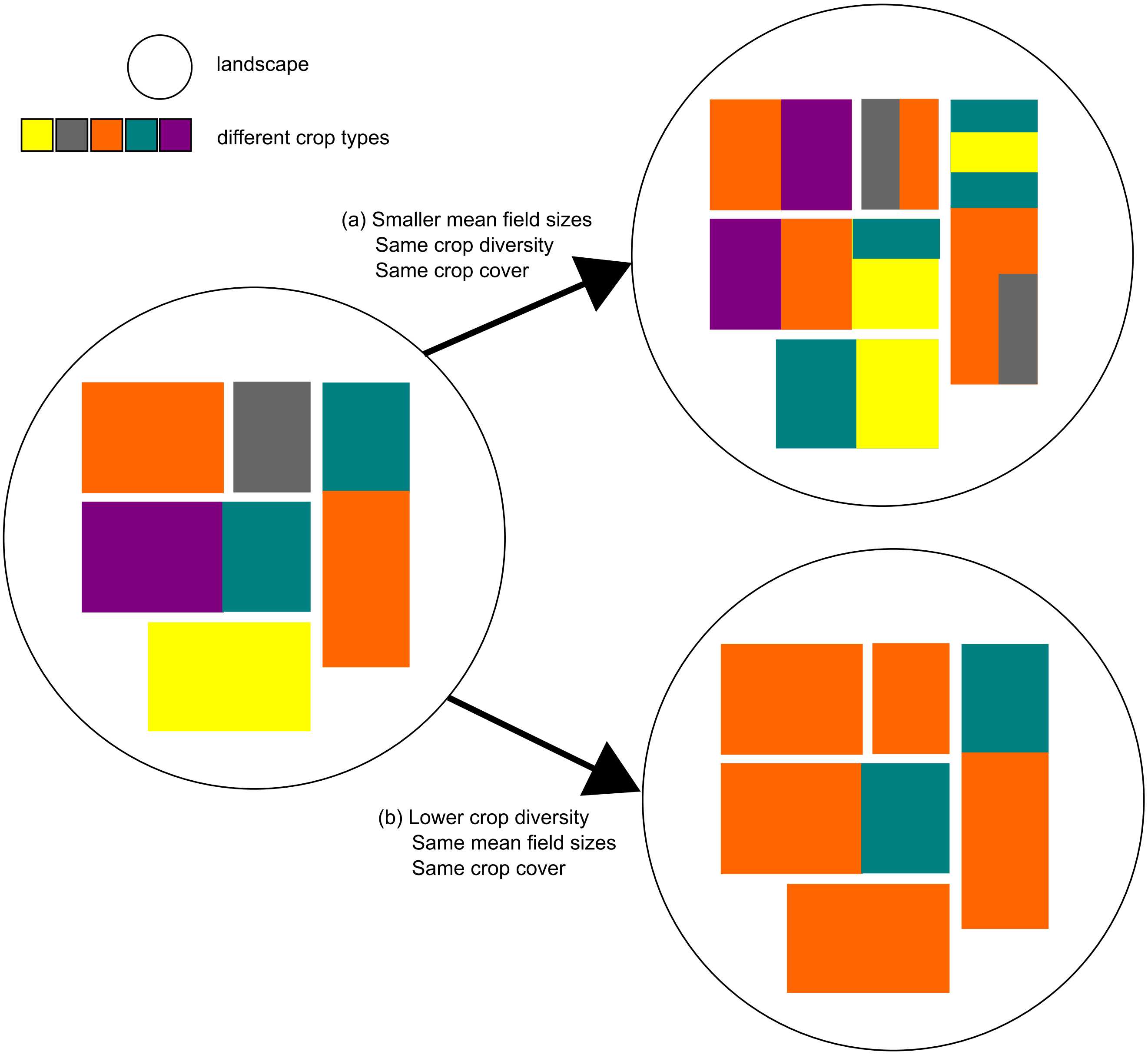

Fig. 6. Although we typically observe a negative relationship between mean field size and crop diversity across agriculture-dominated landscapes, it is possible (a) to modify the cropped portion of an agricultural landscape to decrease mean field size without changing the crop diversity and (b) to modify the cropped portion of an agricultural landscape to decrease crop diversity without changing the mean field size. Note that the total area of the landscape in crop cover is identical across the three example landscapes.

are urgently needed. Thus, we can ask: which of the two management options to benefit milkweed—reducing field sizes or reducing crop diversity—would be most likely to also benefit other wildlife species in agricultural landscapes? Despite a typically negative relationship between mean field size and crop diversity (Appendix E), it is possible to modify the cropped portion of an agricultural landscape to reduce field sizes without affecting crop diversity, and vice versa (Fig. 6). Previous studies consistently show higher biodiversity in landscapes with smaller fields (Collins and Fahrig, 2017; Ekroos et al., 2019; Fahrig et al., 2015; Hass et al., 2018; Martin et al., 2020; Monck-Whipp et al., 2018; Reynolds et al., 2018; Sirami et al., 2019; Zhou et al., 2018). For crop diversity the results are more mixed, but there are a number of studies showing benefits of increasing crop diversity for wildlife (e.g. Lee and Goodale, 2018; Monck-Whipp et al., 2018; Novotný et al., 2015; Palmu et al., 2014). Thus, guidelines/policies aimed at reducing field sizes are more likely to benefit milkweed and biodiversity than guidelines/policies to reduce crop diversity.

Key next steps for decision-makers are to understand the economic impacts of reducing field sizes and the likelihood of farmers adopting policies/guidelines aimed at reducing the sizes of crop fields. Our results suggest reducing field sizes would increase milkweed without increasing weed cover. However, reducing field sizes might affect crop yields in other ways, for example, by changing pest insect abundances or machine efficiency. If smaller fields can benefit milkweed and biodiversity without substantial negative impacts on farmers, then this could be a particularly promising strategy for monarch conservation in agricultural landscapes.

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.

Acknowledgments

We thank the team of postdoctoral fellows, graduate students, and research assistants who assisted with data collection and species identification. We also acknowledge the landowners and farmers, who permitted access to their properties for biodiversity surveys and provided us with information on farming practices in the sampled fields. The data were collected as part of a much larger Strategic Project funded by the Natural Sciences and Engineering Research Council of Canada. Additional financial support was provided to AEM by the Government of Canada through the Federal Department of Environment and Climate Change. Finally, we thank the two anonymous reviewers for their comments, which substantially improved the quality of our manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107567.

References

Agriculture and Agri-Foods Canada, 2012. 2012 Annual crop inventory. Government of Canada Open Data. https://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9.

Alignier, A., Solé-Senan, X.O., Robleño, I., Baraibar, B., Fahrig, L., et al., 2020. Configurational crop heterogeneity increases within-field plant diversity. J. Appl. Ecol. 57, 654–663. https://doi.org/10.1111/1365-2664.13585.

Armengot, L., José-María, L., Blanco-Moreno, J.M., Romero-Puente, A., Sans, F.X., 2011. Landscape and land-use effects on weed flora in Mediterranean cereal fields. Agric. Ecosyst. Environ. 142, 311–317. https://doi.org/10.1016/j.agee.2011.06.001.

Barton, K., 2016. MuMIn: multi-model inference. R package version 1.43.17.

Bates, D., Mäechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Belsky, J., Joshi, N.K., 2018. Assessing role of major drivers in recent decline of monarch butterfly population in North America. Front. Environ. Sci. 6, 86. https://doi.org/10.3389/fenvs.2018.00086.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., et al., 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. J. Appl. Ecol. 45, 141–150. https://doi.org/10.1111/j.1365-2664.2007.01393.x.

Borders, B., Lee-Mäder, E., 2014. Milkweeds: A Conservation Practitioner's Guide. The Xerces Society for Invertebrate Conservation, Portland.

Boyle, J.H., Dalgleish, H.J., Puzey, J.R., 2019. Monarch butterfly and milkweed declines substantially predate the use of genetically modified crops. Proc. Natl. Acad. Sci. 116, 3006–3011. https://doi.org/10.1073/pnas.1811437116.

Brookes, G., 2014. Weed control changes and genetically modified herbicide tolerant crops in the USA 1996–2012. GM Crops Food 5, 321–332. https://doi.org/10.4161/21645698.2014.958930.

Collins, S.J., Fahrig, L., 2017. Responses of anurans to composition and configuration of agricultural landscapes. Agric. Ecosyst. Environ. 239, 399–409. https://doi.org/10.1016/j.agee.2016.12.038.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC), 2016. COSEWIC assessment and status report on the Monarch *Danaus plexippus* in Canada. Ottawa.

Crewe, T.L., Mitchell, G.W., Larrivée, M., 2019. Size of the Canadian breeding population of monarch butterflies is driven by factors acting during spring migration and recolonization. Front. Ecol. Evol. 7, 308. https://doi.org/10.3389/fevo.2019.00308.

Crone, E.E., Pelton, E.M., Brown, L.M., Thomas, C.C., Schultz, C.B., 2019. Why are monarch butterflies declining in the West? Understanding the importance of multiple correlated drivers. Ecol. Appl. 29, e01975 https://doi.org/10.1002/eap.1975.

Darby, H., Ziegler, S., Bruce, J., Gupta, A., Ruhl, L., et al., 2019. 2018 Milkweed Production Trials – Combined Report. University of Vermont Extension, Vermont.

Davis, A.K., Howard, E., 2005. Spring recolonization rate of monarch butterflies in eastern North America: new estimates from citizen-science data. J. Lepid. Soc. 59, 1–5.

Ekroos, J., Tiainen, J., Seimola, T., Herzon, I., 2019. Weak effects of farming practices corresponding to agricultural greening measures on farmland bird diversity in boreal landscapes. Landsc. Ecol. 34, 389–402. https://doi.org/10.1007/s10980-019-00779-x.

Ellison, A.M., 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. Ecol. Appl. 6, 1036–1046. https://doi.org/10.2307/2269588.

Environment and Climate Change Canada, 2016. Management Plan for the Monarch (*Danaus plexippus*) in Canada. Species at Risk Act Management Plan Series, Ottawa.

Ethier, K., Fahrig, L., 2011. Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. Landsc. Ecol. 26, 865–876. https://doi.org/10.1007/s10980-011-9614-2.

Evetts, L.L., Burnside, O.C., 1975. Effect of early competition on growth of common milkweed. Weed Sci. 23, 1–3.

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., et al., 2015. Farmlands with smaller crop fields have higher within-field biodiversity. Agric. Ecosyst. Environ. 200, 219–234. https://doi.org/10.1016/j.agee.2014.11.018.

Flockhart, D.T.T., Pichancourt, J.-B., Norris, D.R., Martin, T.G., 2015. Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. J. Anim. Ecol. 84, 155–165. https://doi.org/10.1111/1365-2656.12253.

Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V., Petit, S., 2010. Weed species richness in winter wheat increases with landscape heterogeneity. Agric. Ecosyst. Environ. 138, 318–323. https://doi.org/10.1016/j.agee.2010.06.005.

Graham, L., Gaulton, R., Gerard, F., Staley, J.T., 2018. The influence of hedgerow structural condition on wildlife habitat provision in farmed landscapes. Biol. Conserv. 220, 122–131. https://doi.org/10.1016/j.biocon.2018.02.017.

Hartzler, R.G., 2010. Reduction in common milkweed (*Asclepias syriaca*) occurrence in Iowa cropland from 1999 to 2009. Crop Prot. 29, 1542–1544. https://doi.org/10.1016/j.cropro.2010.07.018.

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Bosem Baillod, A., et al., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc. R. Soc. B Biol. Sci. 285, 20172242 https://doi.org/10.1098/rspb.2017.2242.

Inamine, H., Ellner, S.P., Springer, J.P., Agrawal, A.A., 2016. Linking the continental migratory cycle of the monarch butterfly to understand its population decline. Oikos 125, 1081–1091. https://doi.org/10.1111/oik.03196.

IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn. https://doi.org/10.5281/zenodo.3553579.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. https://doi.org/10.1111/geb.12233.

José-María, L., Armengot, L., Blanco-Moreno, J.M., Bassa, M., Sans, F.X., 2010. Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal fields. J. Appl. Ecol. 47, 832–840. https://doi.org/10.1111/j.1365-2664.2010.01822.x.

Kéry, M., 2010K. Advantages of the Bayesian approach to statistics. Introduction to WinBUGS for Ecologists: A Bayesian Approach to Regression, Anova, Mixed Models, and Related Analyses. Academic Press, Burlington, pp. 2–4.

Kniss, A.R., 2017. Long-term trends in the intensity and relative toxicity of herbicide use. Nat. Commun. 8, 14865. https://doi.org/10.1038/ncomms14865.

Kruschke, J.K., 2015. Markov Chain Monte Carlo. In: Doing Bayesian Data Analysis: A Tutorial with R, JAGS, and STAN. Academic Press, London, pp. 143–191.

Lee, M.-B., Goodale, E., 2018. Crop heterogeneity and non-crop vegetation can enhance avian diversity in a tropical agricultural landscape in southern China. Agric. Ecosyst. Environ. 265, 254–263. https://doi.org/10.1016/j.agee.2018.06.016.

Liu, F., Kong, Y., 2015. zoib: an R package for Bayesian inference for beta regression and zero/one inflated beta regression. R J. 7, 34–51. https://doi.org/10.32614/rj-2015-019.

Liu, F., Kong, Y., 2018. zoib: Bayesian inference for beta regression and zero-or-one inflated beta regression. R package version 1.5.4.

Malcolm, S.B., 2018. Anthropogenic impacts on mortality and population viability of the monarch butterfly. Annu. Rev. Entomol. 63, 277–302. https://doi.org/10.1146/annurev-ento-020117-043241.

Martin, A.E., Collins, S.J., Crowe, S., Girard, J., Naujokaitis-Lewis, I., et al., 2020. Effects of farmland heterogeneity on biodiversity are similar to—or even larger than—the effects of farming practices. Agric. Ecosyst. Environ. 288, 106698 https://doi.org/10.1016/j.agee.2019.106698.

Martin, A.E., Fahrig, L., 2012. Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecol. Appl. 22, 2277–2292. https://doi.org/10.1890/11-2224.1.

Martin, A., Mitchell, G., Girard, J., Fahrig, L., 2021. Data from: More milkweed in farmlands containing small, annual crop fields and many hedgerows. Figshare. https://doi.org/10.6084/m9.figshare.14839479.

Meredith, A.M., Kruschke, J., Meredith, M.M., 2018. Package "HDInterval". R package version 0.2.0.

Miguet, P., Jackson, H.B., Jackson, N.D., Martin, A.E., Fahrig, L., 2016. What determines the spatial extent of landscape effects on species? Landsc. Ecol. 31, 1177–1194. https://doi.org/10.1007/s10980-015-0314-1.

Monck-Whipp, L., Martin, A.E., Francis, C.M., Fahrig, L., 2018. Farmland heterogeneity benefits bats in agricultural landscapes. Agric. Ecosyst. Environ. 253, 131–139. https://doi.org/10.1016/j.agee.2017.11.001.

Morrissey, M.B., Ruxton, G.D., 2018. Multiple regression is not multiple regressions: the meaning of multiple regression and the non-problem of collinearity. Philos. Theory Pract. Biol. 10, 3. https://doi.org/10.3998/ptpbio.16039257.0010.003.

Novotný, D., Zapletal, M., Kepka, P., Beneš, J., Konvička, M., 2015. Large moths captures by a pest monitoring system depend on farmland heterogeneity. J. Appl. Entomol. 139, 390–400. https://doi.org/10.1111/jen.12185.

Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA), 2016. Ontario weeds: common milkweed. Excerpt from Publ. 505, Ontario Weeds. http://www.omafra.gov.on.ca/english/crops/facts/ontweeds/common_milkweed.htm (Accessed 23 February 2021).

Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G., Hedlund, K., 2014. Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. Basic Appl. Ecol. 15, 241–249. https://doi.org/10.1016/j.baae.2014.03.001.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290. https://doi.org/10.1093/bioinformatics/btg412.

Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C., et al., 2013. Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. Landsc. Ecol. 28, 371–383. https://doi.org/10.1007/s10980-013-9852-6.

Pelton, E.M., Schultz, C.B., Jepsen, S.J., Black, S.H., Crone, E.E., 2019. Western monarch population plummets: status, probable causes, and recommended conservation actions. Front. Ecol. Evol. 7, 258. https://doi.org/10.3389/fevo.2019.00258.

Petit, S., Gaba, S., Grison, A.-L., Meiss, H., Simmoneau, B., et al., 2016. Landscape scale management affects weed richness but not weed abundance in winter wheat fields. Agric. Ecosyst. Environ. 223, 41–47. https://doi.org/10.1016/j.agee.2016.02.031.

Pitman, G.M., Flockhart, D.T.T., Norris, D.R., 2018. Patterns and causes of oviposition in monarch butterflies: implications for milkweed restoration. Biol. Conserv. 217, 54–65. https://doi.org/10.1016/j.biocon.2017.10.019.

Pleasants, J., 2017. Milkweed restoration in the Midwest for monarch butterfly recovery: estimates of milkweeds lost, milkweeds remaining and milkweeds that must be added to increase the monarch population. Insect Conserv. Divers. 10, 42–53. https://doi.org/10.1111/icad.12198.

Pleasants, J.M., Oberhauser, K.S., 2013. Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. Insect Conserv. Divers. 6, 135–144. https://doi.org/10.1111/j.1752-4598.2012.00196.x.

Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik, K., Leisch, F., Zeileis, A. (Eds.), 3rd International Workshop on Distributed Statistical Computing. TU Wien, Vienna.

Plummer, M., 2018. rjags: Bayesian graphical models using MCMC. R package version 4-8.

R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reynolds, C., Fletcher Jr., R.J., Carneiro, C.M., Jennings, N., Ke, A., et al., 2018. Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: a multi-scale and multi-taxon investigation. Landsc. Ecol. 33, 241–255. https://doi.org/10.1007/s10980-017-0595-7.

Sirami, C., Gross, N., Bosem Baillod, A., Bertrand, C., Carrié, R., et al., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc. Natl. Acad. Sci. 116, 16442–16447. https://doi.org/10.1073/pnas.1906419116.

Smith, A.C., Koper, N., Francis, C.M., Fahrig, L., 2009. Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. Landsc. Ecol. 24, 1271–1285. https://doi.org/10.1007/s10980-009-9383-3.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., van der Linde, A., 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. B 64, 583–639. https://doi.org/10.1111/1467-9868.00353.

Statistics Canada, 2021. Selected land management practices and tillage practices used to prepare land for seeding, historical data. https://doi.org/10.25318/3210016201-eng.

Statistics Canada, 2011. 2011 Census road network. https://www12.statcan.gc.ca/census-recensement/2011/geo/RNF-FRR/index-2011-eng.cfm?year=11 (Accessed 23 February 2021).

Rendón-Salinas, E., Martínez-Meza, F., Mendoza-Pérez, M.A., Cruz-Piña, M., Mondragon-Contreras, G., et al., 2021. Area of forest occupied by the colonies of monarch butterflies in Mexico during the hibernation season of 2019-2020 (English translation). https://monarchjointventure.org/images/uploads/documents/2019-2020_Survey_-_Monarch_Butterfly.pdf (Accessed 20 January 2021).

Stenoien, C., Nail, K.R., Oberhauser, K.S., 2015. Habitat productivity and temporal patterns of monarch butterfly egg densities in the eastern United States. Ann. Entomol. Soc. Am. 108, 670–679. https://doi.org/10.1093/aesa/sav054.

Thogmartin, W.E., López-Hoffman, L., Rohweder, J., Diffendorfer, J., Drum, R., et al., 2017a. Restoring monarch butterfly habitat in the Midwestern US: "all hands on deck". Environ. Res. Lett. 12, 074005 https://doi.org/10.1088/1748-9326/aa7637.

Thogmartin, W.E., Wiederholt, R., Oberhauser, K., Drum, R.G., Diffendorfer, J.E., et al., 2017b. Monarch butterfly population decline in North America: identifying the threatening processes. R. Soc. Open Sci. 4, 170760 https://doi.org/10.1098/rsos.170760.

Wilson, S., Mitchell, G.W., Pasher, J., McGovern, M., Hudson, M.-A.R., et al., 2017. Influence of crop type, heterogeneity and woody structure on avian biodiversity in agricultural landscapes. Ecol. Indic. 83, 218–226. https://doi.org/10.1016/j.ecolind.2017.07.059.

Yenish, J.P., Fry, T.A., Durgan, B.R., Wyse, D.L., 1996. Tillage effects on seed distribution and common milkweed (*Asclepias syriaca*) establishment. Weed Sci. 44, 815–820.

Zhou, W., Lee, M.-B., Goodale, E., 2018. The relationship between the diversity of herbaceous plants and the extent and heterogeneity of croplands in noncrop vegetation in an agricultural landscape of south China. Glob. Ecol. Conserv. 14, e00399 https://doi.org/10.1016/j.gecco.2018.e00399.