

## ARTICLE

# Support for an area–heterogeneity tradeoff for biodiversity in croplands

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## Abstract

Rapid expansion of the human population poses a challenge for wildlife conservation in agricultural landscapes. One proposal for addressing this challenge is to increase biodiversity in such landscapes by increasing crop diversity. However, studies report both positive and negative effects of crop diversity on biodiversity. One possible explanation, derived from the “area–heterogeneity tradeoff hypothesis,” is that the effect of crop diversity on biodiversity depends on a tradeoff between increasing the number of crop types in a landscape and decreasing the amount of each single crop type. This should cause positive effects of increasing crop diversity at low to intermediate crop diversity and negative effects at intermediate to high crop diversity. We also propose two factors that could change the point at which the effect of increasing crop diversity shifts from positive to negative. First, we predicted that this shift would occur at a lower crop diversity when the surrounding landscape contains less semi-natural habitat and at a higher crop diversity when the landscape contains more semi-natural habitat. This should increase the likelihood of detecting negative effects of crop diversity when semi-natural cover is low and positive effects when it is high. Second, we predicted that the shift from a positive to negative effect would occur at a lower crop diversity when it is measured locally than when it is measured at greater distances from the site, making detection of negative crop diversity effects more likely when measurements are at local extents. We tested these predictions using data on the biodiversity of herbaceous plants, butterflies, syrphid flies, woody plants, bees, carabid beetles, spiders, and birds at 221 crop field edges in Eastern Ontario, Canada. We found support for an area–crop diversity tradeoff. Semi-natural cover and measurement extent influenced the biodiversity–crop diversity relationship, with positive effects when semi-natural cover was high and negative effects when semi-natural cover was low and when crop diversity was measured at local extents. The results suggest that policies/guidelines designed to increase crop diversity will not benefit biodiversity in the landscapes where conservation action is

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most urgently needed, that is, in landscapes with high agricultural use and low semi-natural cover.

#### KEYWORDS

agricultural intensification, agricultural policy, area–heterogeneity tradeoff, crop mosaic, field size, habitat heterogeneity, intermediate heterogeneity hypothesis, landscape composition, landscape configuration, scale of effect, spatial scale

## INTRODUCTION

Rapid expansion of the human population poses a challenge for wildlife conservation in agricultural landscapes, requiring conservation actions that can support biodiversity without compromising our ability to feed people (Fróna et al., 2019). Fahrig et al. (2011) hypothesized that crop fields could be managed to benefit biodiversity—without removing land from crop production—by increasing the heterogeneity of “farmland,” that is, the cropped portions of a landscape, including annual row crops, perennial forage crops, and managed pastures. Farmland heterogeneity can be increased by increasing crop diversity, resulting in more types of crops and more even representation of crop types, or by reducing crop field sizes and increasing the length of edges between crop fields or the length of edges between crop and natural/semi-natural land-cover types.

The positive effects of small crop fields on biodiversity are well supported in the empirical literature. Researchers typically find more species and higher species diversity in agricultural landscapes with smaller fields, when controlling for total farmland area. Such effects have been found in a range of taxa, including plants, invertebrates, and vertebrates (Alignier et al., 2020; Ekroos et al., 2019; Fahrig et al., 2015; Hass et al., 2018; Martin et al., 2020; Sirami et al., 2019; Zhou et al., 2018).

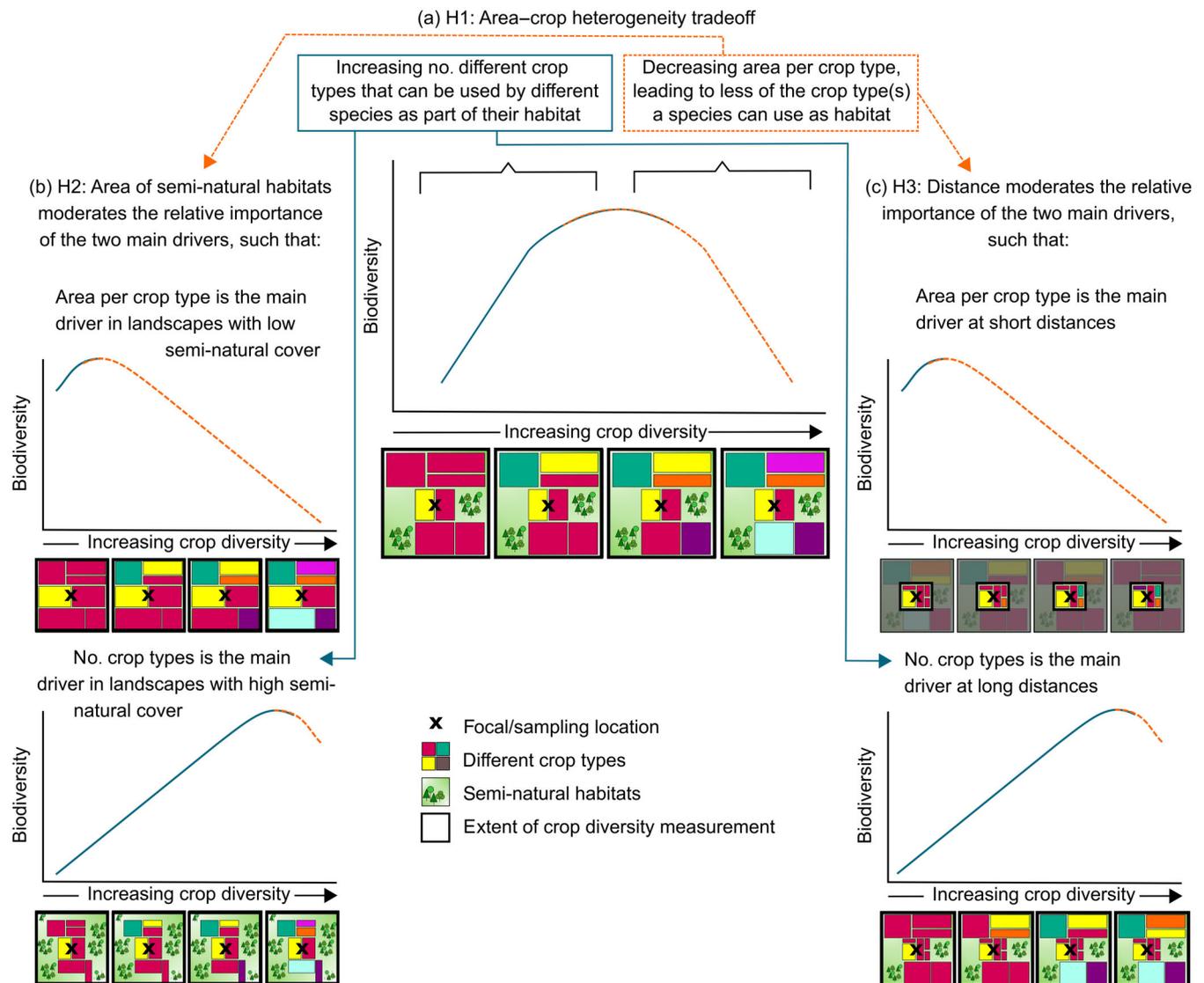
In contrast, the effects of crop diversity on biodiversity are inconsistent and often weaker than the effects of field size. Some studies have found positive effects of crop diversity on species richness and diversity (Lee & Goodale, 2018; Novotný et al., 2015; Palmu et al., 2014; Redlich et al., 2018). However, others have found the opposite (Hass et al., 2018; Martin et al., 2020) or a combination of positive and negative effects (Reynolds et al., 2018; Wilson et al., 2017). A number of studies have also failed to detect significant effects of crop diversity on biodiversity (e.g., Ekroos et al., 2019; Fahrig et al., 2015).

This leads to the question: Why are the effects of crop diversity on biodiversity positive in some cases but negative in others? One possible explanation is derived from the “area–heterogeneity tradeoff hypothesis,” which posits that increasing a landscape’s habitat

heterogeneity—often indexed as an increase in the number of land-cover types—will increase biodiversity up to some threshold, above which further increases in habitat heterogeneity will reduce biodiversity (Duelli, 1997; Kadmon & Allouche, 2007). This results in maximum biodiversity at an intermediate level of habitat heterogeneity. Increasing habitat heterogeneity is expected to benefit biodiversity because different species use different land-cover types as habitat, and increasing the number of different land-cover types should provide habitat for more species. However, over a given area of land, increasing the number of land-cover types also results in a smaller area of each land-cover type and, thus, less habitat for species that use a particular land-cover type as habitat. As habitat area decreases, the probability of local extinction/extirpation increases. Thus, at some point, increasing habitat heterogeneity will result in too little of a given land-cover type to support species that use that type as habitat, resulting in loss of species and a negative effect of habitat heterogeneity on biodiversity.

Fahrig et al. (2011) proposed a similar relationship between farmland heterogeneity and biodiversity, that is, for a given area of land in crops, biodiversity should be highest at an intermediate crop diversity level (Figure 1a). This proposed relationship relies on an expected tradeoff between increasing the number of crop types in a landscape and decreasing the amount of each single crop type within the cropped portion of the landscape. When crop diversity increases from low to intermediate levels, the increase in the number of crop types benefits biodiversity by providing habitat for more species that can use crops as part of their habitat. However, above some threshold, further increases in crop diversity result in too little of each given crop type to support species that use that crop type as part of their habitat, resulting in maximum predicted biodiversity at an intermediate level of crop diversity.

Here we test and extend this hypothesis, suggesting factors that could affect the relative importance of the two drivers of the area–crop diversity tradeoff and, in turn, whether the effect of crop diversity on biodiversity is predominately positive or negative across a range of crop diversity values. In particular, we hypothesize that



**FIGURE 1** Illustration of the three hypotheses tested in this study. (a) The area–crop diversity tradeoff hypothesis posits that biodiversity is highest at an intermediate crop diversity. From low to intermediate crop diversity, the increase in the number of crop types benefits biodiversity by providing habitat for more species. However, above some threshold, further increases in crop diversity result in too little of each crop type to support species that can use specific crop types (e.g., corn, soybean, pasture) as part of their habitat. (b) The amount of semi-natural habitat in an agricultural landscape is expected to move the point at which the effect of increasing crop diversity shifts from positive to negative. We expect species’ tolerances for reduced area per crop type are low in landscapes with low semi-natural cover, because in these landscapes wildlife must depend strongly on resources in the crops they can use for foraging, breeding, and so forth. This should cause the peak in the relationship between biodiversity and crop diversity to shift to the left in landscapes with low semi-natural cover, increasing the likelihood of detecting negative effects of crop diversity on biodiversity in these landscapes. In contrast, when there is sufficient semi-natural habitat in the surrounding landscape, species should be less sensitive to the area per crop type because they can obtain necessary resources from semi-natural habitats. This should cause the peak in the relationship between biodiversity and crop diversity to shift to the right in landscapes with very high semi-natural cover, increasing the likelihood of detecting positive effects of crop diversity on biodiversity in these landscapes. (c) The spatial extent of measurement of crop diversity is expected to moderate the relative importance of increasing the number of crop types versus area per crop type for biodiversity. At small extents, species should be highly sensitive to reductions in the area of crop types they can use as habitat, because if there is too little of that crop type, then it will not support a population of the species. The effect of crop diversity would then shift from positive to negative in landscapes with low crop diversity when measuring crop diversity close to the sampling location. In contrast, at larger extents, encompassing the scale of species movements (e.g., dispersal), the benefits of crop diversity could outweigh the negative effects of having less area of a given crop type at the local extent, because there would be more species to immigrate into the local site. The effect of crop diversity on biodiversity would then shift from positive to negative in landscapes with high crop diversity when measuring crop diversity far from the sampling location.

the cover of semi-natural habitats within an agricultural landscape moderates the relative importance of these two drivers, changing the point at which the effect of crop diversity shifts from positive to negative (Figure 1b). In a high-intensity agricultural landscape containing little semi-natural cover, wildlife species will be highly dependent on resources within the particular crop types they can use for foraging, breeding, and so forth, and thus they will be highly sensitive to reductions in the area of these crop types. Thus, we expect that, when there is little semi-natural cover, the effect of crop diversity on biodiversity will shift from positive to negative at a low crop diversity, increasing the likelihood of detecting negative effects of crop diversity on biodiversity. In contrast, when there are sufficient semi-natural habitats in the surrounding landscapes, species should be less sensitive to the amount of a crop type because they can obtain necessary resources from semi-natural habitats. This expectation is based on the assumption that semi-natural habitats can provide resources needed to support populations of many species that occur in the cropped portion of an agricultural landscape. In landscapes with sufficient semi-natural habitats, we expect species to have high tolerances for reduced area per crop type. Thus, the benefits of increasing the number of different crop types that can be used by different species to supplement resources obtained in semi-natural habitat (e.g., providing additional foraging opportunities; Puckett et al., 2009) will create a positive effect of crop diversity even at high crop diversity levels and increase the likelihood of detecting the positive effects of crop diversity on biodiversity.

We also hypothesize that the relative importance of increasing the number of crop types versus decreasing the amount of each crop type varies with spatial extent. As stated previously, we expect that changing the relative importance of the two drivers will move the point at which the effect of crop diversity on biodiversity shifts from positive to negative (Figure 1c). Different ecological processes likely dominate species' responses to their environment at the scale of local population habitat use versus the scale of species movements (e.g., dispersal). At small extents, we expect species to be highly sensitive to reductions in the area of crop types they can use as habitat. This is because if there is too little of a crop type at the scale of a local population, then that crop type will not support the persistence of the population. Thus, when we measure crop diversity close to the sampling site, we expect to find that the effect of crop diversity on biodiversity will shift from positive to negative in landscapes with low crop diversity. This could translate into an increased likelihood of detecting the negative effects of crop diversity on biodiversity with decreasing extent, because the response would be negative across most of

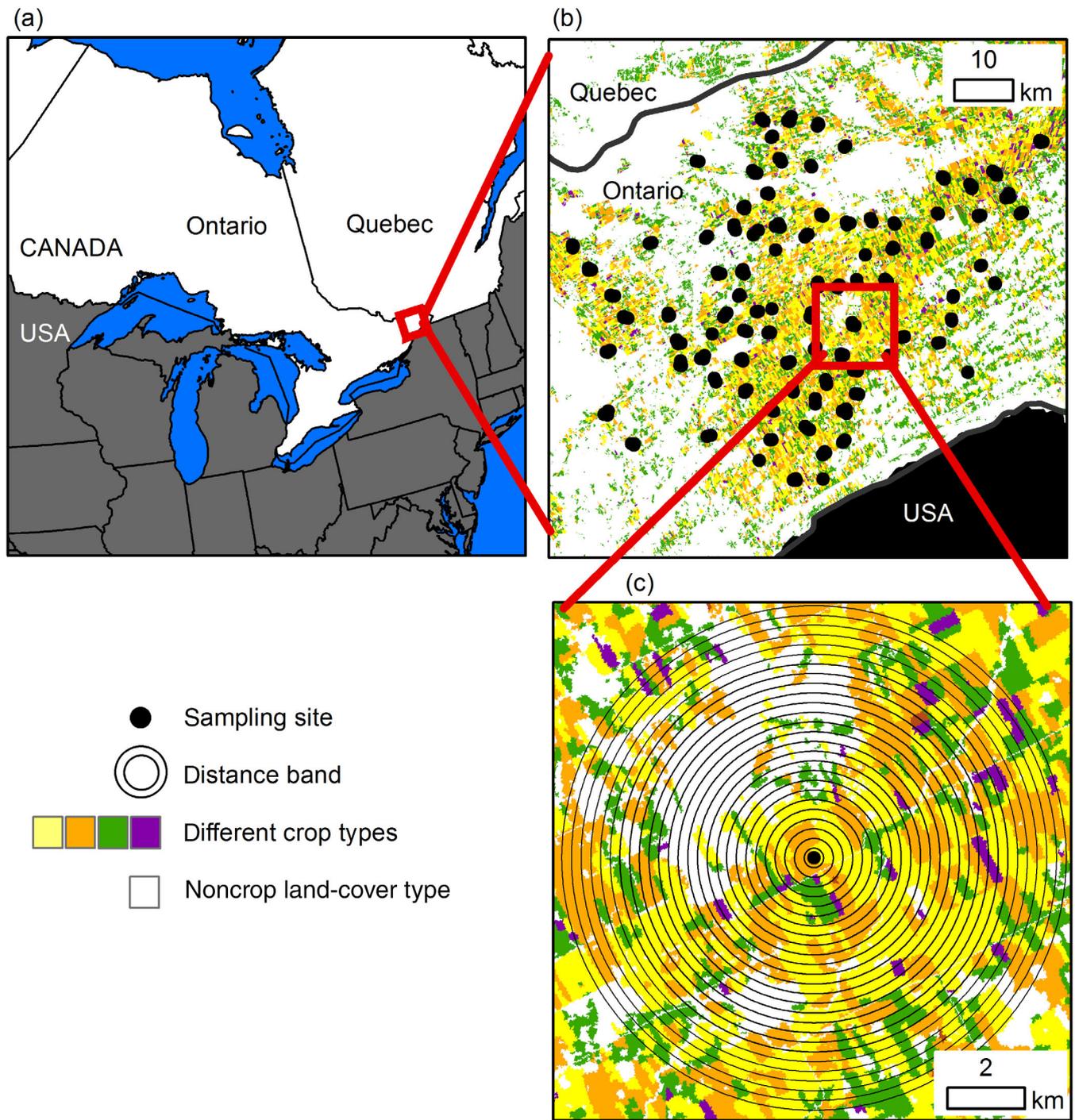
the range of crop diversity values. However, the benefits of crop diversity for biodiversity at larger extents—encompassing the scales of species movements—could outweigh the negative effects of having less of a given crop type at the local extent by supporting more different species in the surrounding landscape that could immigrate to the local site. Crop diversity at larger extents could also benefit individual species that could use different crop types for complementary resources (such as breeding and foraging habitats, or summer and winter grounds) through landscape complementation (Dunning et al., 1992). Thus, when crop diversity is measured far from sampling sites, we expect to find that the effect of crop diversity on biodiversity shifts from positive to negative in landscapes with relatively high crop diversity and that we will be more likely to detect the positive effects of crop diversity on biodiversity.

We tested these expectations using the Agriculture and Agri-Food Canada Annual Crop Inventory (Agriculture and Agri-Food Canada, 2013) and data on biodiversity within the cropped portion of agricultural landscapes, sampling herbaceous plants, butterflies, syrphid flies, woody plants, bees, carabid beetles, spiders, and birds at the edges of 221 crop fields in rural Eastern Ontario, Canada. Biodiversity was indexed as the standardized mean number of species across the eight taxonomic groups at each site (hereafter “multidiversity”; see Allan et al., 2014). We chose this synthetic metric, rather than repeating analyses for each taxonomic group, because our goal was to look at the effects of crop diversity on biodiversity in agricultural landscapes; thus, a measure of diversity across taxa is more relevant to this goal. These taxa were selected because they are relatively easy to survey and, together, provide a broad representation of biodiversity and a range of different expected sensitivities to landscape variables, including crop diversity. We recognize that our results for this set of taxa may be different than results if we, for example, selected taxa that were all expected to respond strongly to crop diversity. However, capturing the variability in responses of different taxa/species to crop diversity in our study is more relevant to our goal.

## METHODS

### Biodiversity surveys

Data on biodiversity were taken from a large-scale project, covering ~10,000 km<sup>2</sup> of the Lake Simcoe-Rideau ecoregion in Eastern Ontario, Canada (Figure 2a; Ontario Ministry of Natural Resources, 2018), to evaluate the effects of farmland heterogeneity and farm management practices on biodiversity. The climate in this region



**FIGURE 2** Locations of (a) the study region in Eastern Ontario, Canada, where we sampled for biodiversity at (b) 221 sites, clustered within 88, 1 × 1-km sample areas. (c) We measured Shannon diversity of crop types (e.g., corn, soybean, pasture), proportional cover of semi-natural habitats, number of semi-natural habitat types, and mean field size within 26 distance bands centered on each sampling site, where upper and lower distance thresholds for each band were defined as radii from 0.25 to 6.50 km in increments of 0.25 km. Land cover is from the Agriculture and Agri-Food Canada Annual Crop Inventory (Agriculture and Agri-Food Canada, 2013).

has been described as mild (mean annual temperature: 4.9–7.8°C) and moist (mean annual precipitation: 759–1087 mm; Crins et al., 2009). Forests are the dominant natural land cover, with tree species including sugar maple, silver maple, red maple, American beech, white

ash, black ash, green ash, eastern hemlock, yellow birch, eastern white cedar, and balsam fir (Crins et al., 2009). Agriculture is the primary human land use in eastern Ontario, dominated by hay (30% of agricultural land), pasture (24%), corn (21%), and soybean (19%; OMAFRA, 2011).

Full details of the site selection and biodiversity sampling are in Fahrig et al. (2015) and Martin et al. (2020). In summary, this project collected data on eight taxonomic groups—herbaceous plants, butterflies, syrphid flies, woody plants, bees, carabid beetles, spiders, and birds—in 93 1 × 1-km sample areas, with a random subset of 46 of the sample areas surveyed in 2011 and the remaining 47 in 2012. Sample areas were selected to (1) represent variability in crop diversity and mean field size across the study region; (2) be spatially independent; (3) be dominated by agricultural land uses; and (4) minimize correlations between crop diversity, mean field size, and crop cover across the sample areas (see Pasher et al., 2013 for details). All selected sampling sites were adjacent to another crop field,  $\geq 200$  m from all other sites,  $\geq 50$  m from nonagricultural land uses (e.g., roads), and  $\geq 50$  m from the edge of the 1 × 1-km sample area. The number of sampling sites within a sample area varied among taxa, ranging from four to eight sampling sites per sample area. Woody plants were only sampled in the field margin, and birds were sampled within a circular area (50-m radius), centered on the field edge. All other taxa were sampled at field edges and within crop fields. Survey methods varied among taxa: visual surveys along transects for herbaceous plants, woody plants, and butterflies; net collection along transects for syrphid flies; pan traps for bees; pitfall traps for carabid beetles and spiders; and visual and auditory point counts for birds (Appendix S1: Figure S1). The timing of sampling also varied among taxa (Appendix S1: Table S1). It took ~1 to 1.5 months to sample a taxon across all 46 (or 47) sites. The order of sampling was randomized within each survey period, to avoid potentially confounding relationships between sampling date and our landscape variables. We note that there were no overall differences in landscape variable measurements between sites sampled in 2011 and 2012.

We used data from the subset of field edge sampling sites with “complete” biodiversity surveys, that is, data from two replicate surveys for all taxa except for woody plants and birds, which were sampled once per site. This resulted in a total of 221 sites within 88 sample areas (Figure 2b).

## Landscape variables

We measured crop diversity as the Shannon diversity of crop types within 26 circular distance bands, centered on each sampling site, where upper and lower thresholds for each band were defined as radii from 0.25 to 6.50 km in increments of 0.25 km (Figure 2c), using the Agriculture and Agri-Food Canada Annual Crop Inventory (Agriculture and Agri-Food Canada, 2013) for the year of biodiversity sampling (either 2011 or 2012). Previous

research showed that analyses of the effects of landscape variables on biological responses typically do not measure the landscape variables within large enough spatial extents, which could lead to underestimation of landscape context effects (Jackson & Fahrig, 2015). To minimize this possibility, we included measurements within radii of up to 6.50 km, the largest extent fully covered by the Crop Inventory for all sampling sites. Fourteen of the crop types included in the Crop Inventory were represented in our landscapes: corn, soybean, cereal, pasture, vegetable, beans, herbs, peas, berries, nursery, orchard, other crop, unseeded, and fallow. We also used the Crop Inventory to estimate the proportional cover of semi-natural habitats, the number of semi-natural habitat types (i.e., semi-natural diversity), and mean field size for each of the 26 distance bands, so that we could include these as covariates in our analyses (see next section). Semi-natural habitats included shrubland, wetland, grassland, deciduous forest, coniferous forest, and mixed-wood forest. Note that we could not use Shannon diversity as our measure of semi-natural diversity because there were some distance bands and sites with no semi-natural habitat. Landscape variables were standardized to mean = 0 and SD = 1 prior to analysis. Landscape variables were measured in ArcGIS (ESRI, Redlands, California).

## Statistical analysis

We used multidiversity (Allan et al., 2014) as our measure of biodiversity. To estimate multidiversity, we first estimated the species richness at each sampling site for each taxonomic group. Note that sampled individuals that could not be identified to species were, where possible, identified to genus or family; however, we refer to this as species richness because the majority of individuals were identified to species. We then standardized the species richness of each taxon across all sites and calculated multidiversity for each sampling site as the mean standardized richness for the eight taxa at that site (as in Martin et al., 2020). A positive multidiversity value indicates higher than average biodiversity at a sampling site and a negative value lower than average biodiversity.

We tested our prediction of positive effects of crop diversity on multidiversity at low to intermediate crop diversity and negative effects at intermediate to high crop diversity (i.e., an  $\cap$ -shaped relationship; Figure 1a). We used linear mixed effects to model multidiversity as a function of crop diversity—including a quadratic term to test for the predicted  $\cap$ -shaped effect of crop diversity on multidiversity—semi-natural cover, semi-natural diversity, and mean field size, with a random effect of sample area

on the model intercept. We included semi-natural cover, semi-natural diversity, and mean field size in this analysis because these three variables are moderately collinear with crop diversity in our study landscapes (see *Results*) and can have strong effects on multidiversity (Janišová et al., 2014; Martin et al., 2020; Sirami et al., 2019). The random effect of the sample area controlled for potential nonindependence of sampling sites within a sample area due to, for example, sampling all sites within a sample area on the same date and by the same surveyor(s).

Evaluation of the effects of a landscape variable, such as crop diversity, on our response variable of interest—multidiversity—was complicated by the fact that the strength, direction, and shape of relationship between a biological response and landscape variable can depend on the spatial extent within which the landscape variable is measured (Miguet et al., 2016). One option is to select an extent a priori based, for example, on the extent used in a previous study or on a biological argument (e.g., Collins & Fahrig, 2017). However, research has shown that methods for a priori scale selection are generally unsuccessful (Miguet et al., 2016). Another approach commonly used in landscape ecology studies is a multiscale analysis, where (1) measures of a landscape variable are calculated in concentric, nested buffers (or extents) centered on the sampling locations for the biological response, (2) a separate model is fitted between the response and landscape variable values for each buffer, and (3) the extent where the effect is strongest is identified as the appropriate extent of measurement (Jackson & Fahrig, 2015). However, this approach assumes that environmental conditions within the surrounding area are equally important up to that appropriate extent, after which environmental conditions have no effect. A possibly more reasonable assumption is that the effect of environmental conditions on a biological response change as a function of distance, that is, a distance-weighted effect (Chandler & Hepinstall-Cymerman, 2016; Miguet et al., 2017).

Based on the preceding considerations, we used distance-weighted measures of our landscape variables in our test for an  $\cap$ -shaped relationship between multidiversity and crop diversity. To do this we had to estimate functions describing how the effect of each landscape variable changed with distance. For this we followed the approach developed by Miguet et al. (2017). First, we specified a set of 50 Gaussian functions to calculate the weight ( $w$ ) for each of the 26 distance bands, where

$$w_i = e^{-\alpha d_i^2}, \tag{1}$$

$\alpha$  is a parameter controlling the shape of the weight-distance distribution, and  $d_i$  is the mean distance of the band  $i$  (in km) from the sampling site. A different  $\alpha$  was used for each function so as to specify its shape (see Appendix S1: Figure S2 for examples). Second, we calculated distance-weighted measures of crop diversity, semi-natural cover, semi-natural diversity, and mean field size for each site, using each of the 50 weighting functions. The distance-weighted measure of a landscape variable ( $X$ ) was calculated as

$$X = \sum_{i=1}^{26} W_i x_i, \tag{2}$$

where  $x_i$  is the landscape variable value calculated for distance band  $i$  and

$$W_i = \frac{w_i a_i}{\sum_{i=1}^{26} w_i a_i}, \tag{3}$$

where  $w_i$  is the weight for distance band  $i$ , calculated using the previously given Equation (1), and  $a_i$  is the area ( $\text{km}^2$ ) in distance band  $i$ . We used Equation (3) to adjust weights to account for area differences among bands. Third, we modeled multidiversity using the linear mixed effects model described previously 50 times, once for each weighting function. Note we also ran the equivalent analysis for 50 negative exponential functions, but the conclusions were identical to those using the Gaussian function, so we present results only using the Gaussian function.

We stress that we used this multiscale analysis to find appropriate distance weightings for the landscape variables. It does not represent multiple tests of a hypothesis because the landscape data are correlated across distance bands, so the 50 statistical models we fit are not independent of each other. We used the model with the largest absolute standardized quadratic effect of crop diversity on multidiversity to evaluate statistical support for our prediction. It would be supported if the 95% CI for the quadratic crop diversity term did not cross zero and the predicted relationship between multidiversity and crop diversity was  $\cap$ -shaped.

We tested our second prediction (Figure 1b) by modeling multidiversity as a function of distance-weighted crop diversity, semi-natural cover, and the interaction of crop diversity  $\times$  semi-natural cover for each of the 50 distance-weighting functions. To test Prediction 2, we did not simply use the distance weighting identified for Prediction 1 because we had no a priori reason to expect that the distance weighting would be the same for the effect of crop diversity (Prediction 1) and the effect of

the interaction between crop diversity and semi-natural cover (Prediction 2). Therefore, we used the model with the largest absolute standardized effect of crop diversity  $\times$  semi-natural cover on multidiversity to evaluate support for our prediction. We also included semi-natural diversity, mean field size, and a random effect of sample area on the model intercept, for the reasons described earlier. We initially allowed for a quadratic multidiversity–crop diversity relationship and for interactions between semi-natural cover and both the linear and quadratic terms for crop diversity; however, support for these models was weaker than for models that included only the linear term and its interaction with crop diversity (Appendix S1: Figures S3 and S4); thus, we focus on results from the latter analysis. Our prediction would be supported if the 95% CI for the interaction effect did not cross zero and there were negative effects of crop diversity when semi-natural cover was low and positive effects when semi-natural cover was high.

To test our final prediction (Figure 1c), we evaluated the relative support for linear versus  $\cap$ -shaped relationships between multidiversity and crop diversity using the Akaike information criterion, corrected for small sample sizes ( $AIC_c$ ), for each of the 50 distance-weighting functions. We modeled the linear relationship between multidiversity and crop diversity using generalized linear mixed effects, including semi-natural cover, semi-natural diversity, mean field size, and a random effect of sample area on the model intercept, for the reasons described earlier. We modeled  $\cap$ -shaped relationships between multidiversity and crop diversity as described for Prediction 1. We used  $AIC_c$  as our metric of model support, rather than the absolute standardized effect size, because these candidate models do not produce comparable effect size estimates for crop diversity. Additionally, we compared the  $AIC_c$  of both models to the  $AIC_c$  for a model that was the same as the aforementioned models, with the exception that it did not include crop diversity effects. Our prediction would be supported if the effect of crop diversity on multidiversity was negative when crop diversity effects were weighted toward the smallest extents, positive when crop diversity effects were weighted toward the largest extents, and  $\cap$ -shaped in between. For the subset of models with support for an  $\cap$ -shaped relationship, we also recorded the crop diversity at which the effect of crop diversity on multidiversity changed from positive to negative. We expected the inflection point to increase as crop diversity was weighted toward longer distances.

We also tested for collinearity among the landscape variables for each of the 50 distance-weighting functions and tested for positive spatial autocorrelation of model residuals for all statistical models using a one-tailed

Global Moran's I and a permutation approach with 5000 permutations to calculate the significance level.

All analyses were conducted in R version 4.0.4 (R Core Team, 2021) using the lme4 package for GLMM (version 1.1.26; Bates et al., 2015), the MuMIn package for  $AIC_c$  (version 1.43.17; Barton, 2020), and the ape package for Global Moran's I (version 5.4.1; Paradis et al., 2004; Paradis & Schliep, 2018).

## RESULTS

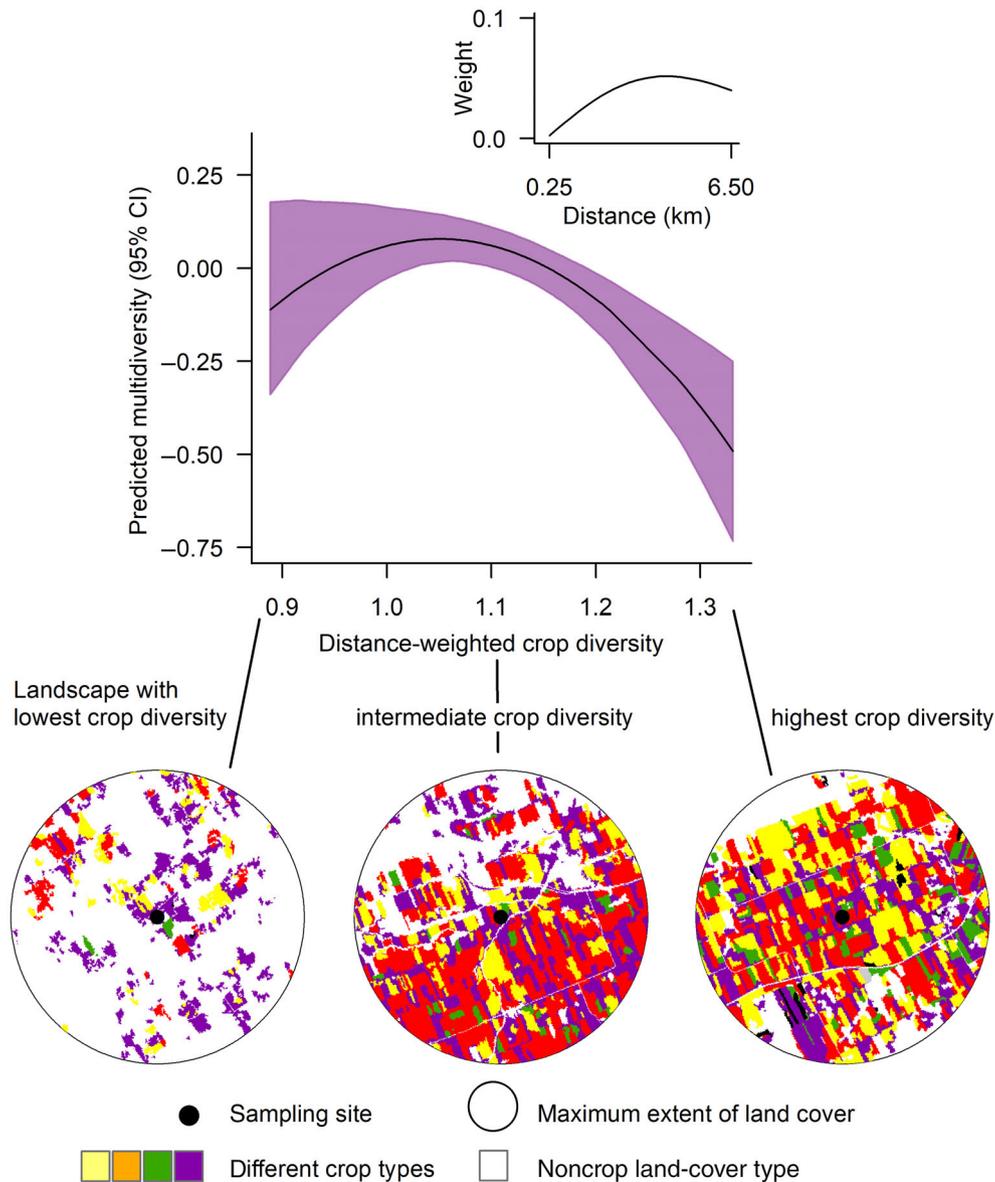
The total number of species identified at a sampling site ranged from 32 to 106 (mean = 61 species), with multidiversity values of  $-0.81$  to  $1.28$  (mean =  $0.00$ ; Appendix S1: Figure S5). Herbaceous plants had, on average, the most species per site (mean = 31, range 8–59), and birds the fewest (mean = 3, range 0–9; Appendix S1: Table S2). Crop diversity values, on average, increased as the distance weighting shifted from short to long distances (Appendix S1: Figure S6a). The same pattern was observed for semi-natural cover and semi-natural diversity, but not for mean field size (Appendix S1: Figure S6b–d).

Landscape variables were generally weakly to moderately correlated. Spearman rank correlations between crop diversity and semi-natural cover ranged from  $-0.45$  to  $-0.08$ , correlations between crop diversity and semi-natural diversity ranged from  $-0.16$  to  $-0.03$ , and correlations between crop diversity and mean field size ranged from  $-0.44$  to  $0.28$ , depending on the distance weighting (Appendix S1: Figure S7). Correlations between semi-natural cover and semi-natural diversity were higher when measurements were weighted toward the shortest distances (Appendix S1: Figure S8). Conversely, correlations between semi-natural cover and mean field size were stronger when measurements were weighted toward the longest distances (Appendix S1: Figure S8).

We found a significant,  $\cap$ -shaped relationship between multidiversity and crop diversity (i.e., a 95% CI that did not cross zero:  $-2.30$  to  $-0.27$ ). The direction of effect on multidiversity was positive up to a threshold crop diversity of  $\sim 1.05$ , above which the effect became negative (Figure 3).

We also found a significant interaction effect of crop diversity  $\times$  semi-natural cover on multidiversity (95% CI:  $0.01$  to  $0.12$ ). The direction of effect of crop diversity on multidiversity was negative when there was low semi-natural cover and positive when there was high semi-natural cover (Figure 4).

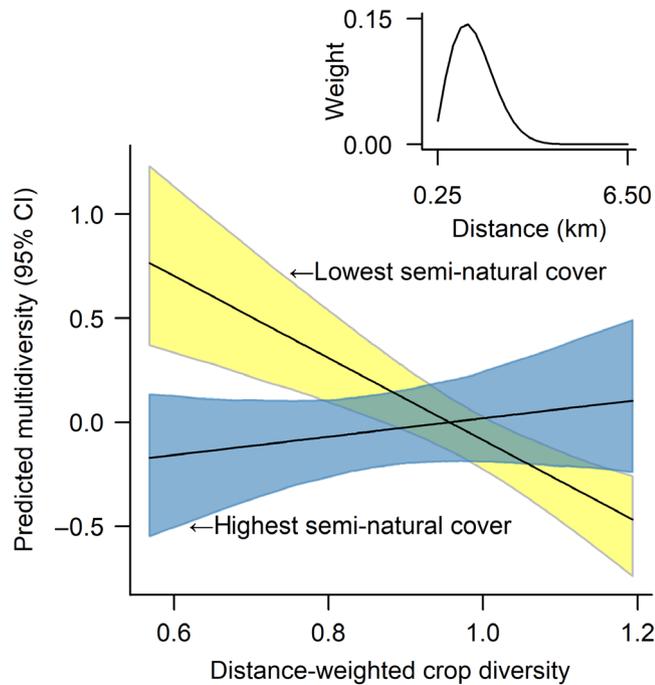
In the preceding analyses, we used distance-weighted measures of landscape variables, relying on a multiscale analysis to identify the appropriate distance-weighting



**FIGURE 3** There was statistical support for an  $\cap$ -shaped relationship between multidiversity (our measure of biodiversity) and crop diversity in the surrounding landscape (95% CI for the quadratic effect of crop diversity on multidiversity did not cross zero:  $-2.30$  to  $-0.27$ ). This figure shows the effect of crop diversity at the mean values of the cover of semi-natural habitats, number of semi-natural habitat types, and mean field size in the landscape. The effects of landscape variables on multidiversity were distance weighted, using the Gaussian distance-weighting function in the inset figure. The inset figure shows the distance weighting with the strongest support, based on the absolute standardized effect size for the quadratic term in the model (Appendix S1: Figure S9). The plotted CI was estimated via bootstrapping ( $n = 5000$ ). Example landscapes depict the range of crop diversity values across our study landscapes.

function (see *Statistical analysis*, above, for details). For the  $\cap$ -shaped relationship between multidiversity and crop diversity, landscape variables were most strongly weighted at  $\sim 4.13$  km from the sampling location (Figure 3, inset, Appendix S1: Figure S9). For evaluation of the interacting effects of crop diversity  $\times$  semi-natural cover on multidiversity, landscape variables were most strongly weighted at  $\sim 1.13$  km from the sampling location (Figure 4, inset, Appendix S1: Figure S10).

The effect of crop diversity on multidiversity was negative when crop diversity effects were weighted toward small to intermediate spatial extents and  $\cap$ -shaped when crop diversity effects were weighted toward the large extents (Figure 5, Appendix S1: Figure S11). For models showing an  $\cap$ -shaped relationship between multidiversity and crop diversity, the inflection point tended to occur at a higher crop diversity when its effects were weighted toward longer distances.



**FIGURE 4** There was statistical support for an interaction effect of crop diversity  $\times$  cover of semi-natural habitats on multidiversity (our measure of biodiversity; 95% CI did not cross zero: 0.01 to 0.12). The effect of crop diversity was more negative in landscapes with low semi-natural cover than in landscapes with high semi-natural cover. This figure illustrates the effects of crop diversity and semi-natural cover when holding the number of semi-natural habitat types and mean field size at their mean values. The effects of landscape variables on multidiversity were distance weighted, using the Gaussian distance-weighting function in the inset figure. The inset figure shows the distance weighting with the strongest support, based on the absolute standardized effect size for the interaction of crop diversity  $\times$  semi-natural cover (Appendix S1: Figure S10). The plotted CI was estimated via bootstrapping ( $n = 5000$ ).

We found no evidence of positive spatial autocorrelation in residuals of our statistical models (all  $p > 0.05$ ).

## DISCUSSION

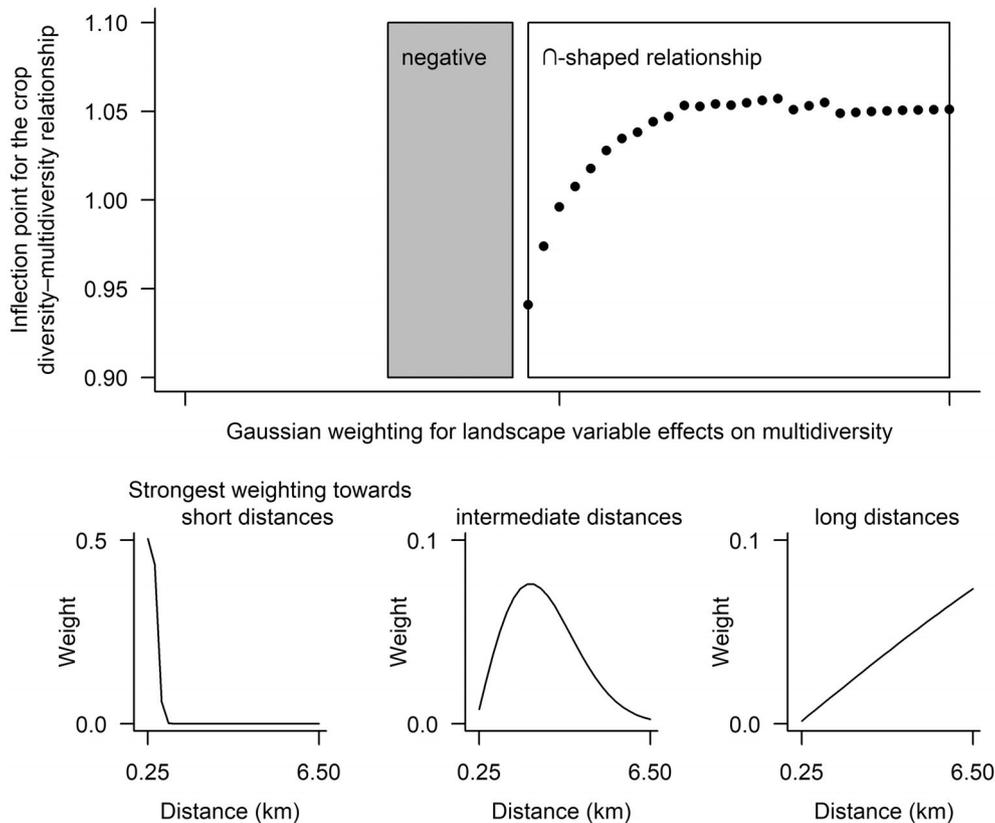
We found support for an area–crop diversity tradeoff, with a significant  $\cap$ -shaped relationship between multidiversity and crop diversity. This is consistent with our expectation that biodiversity responses to crop diversity depend on a tradeoff between increasing the number of crop types in a landscape and decreasing the amount of each single crop type. When crop diversity increases from low to intermediate levels, the increase in the number of crop types should benefit biodiversity by providing habitat for more species. However, above some threshold, further increases in crop diversity should result in too little of

each given crop type to support species that use that crop type as part of their habitat.

The area–crop diversity tradeoff hypothesis is based on the expectation that changes in crop diversity change the amount of habitat available to different species. However, we note that effects of changes in habitat availability on the richness of some taxa could be indirect. For example, our measure of multidiversity included the richness of woody plants, which do not generally grow in crop fields. However, woody plants could be indirectly affected by changes in crop diversity, with effects mediated by the effects of crop diversity on the number of insect pest species and pollinators, for example. Indeed, we previously found effects of crop diversity on the richness of woody plants in field margins in this same study system (Martin et al., 2020). If local habitat quality for nonplant species increases with the number of plant species at the sampling site and plant species richness is affected by crop diversity, then the observed effects of crop diversity on other taxa could occur, at least in part, because crop diversity effected the habitat quality for these taxa.

It is important to note that the evidence for positive effects of crop diversity on multidiversity from low to intermediate crop diversity was weaker than the evidence for negative effects at intermediate to high crop diversity, with high levels of uncertainty around the predicted relationship when crop diversity was low (Figure 3). We investigated whether outliers might be affecting this uncertainty, but we found no support for this speculation. There were only three outliers (Cook's distances  $>4/n$ ), and our conclusions were the same whether or not we included these three sites in our analysis. Instead, the apparent lack of support for the positive effects of crop diversity may reflect the fact that our study did not include landscapes with extremely low crop diversity: The leftmost landscape in Figure 3 had the lowest crop diversity across our study sites. Thus, it is possible that stronger positive effects of crop diversity on multidiversity would have been found if our study had included landscapes with even lower crop diversity, although this speculation requires further testing.

Our findings contrast with those of Sirami et al. (2019), who did not find support for an area–crop diversity tradeoff when studying the effects of crop diversity on multidiversity. One difference between our study and that of Sirami et al. (2019) is that we found stronger correlations among the landscape variables used in our analysis. However, regression-type models, such as the one we used here, generally produce unbiased estimates of an effect, even when variables are collinear (Morrissey & Ruxton, 2018; Smith et al., 2009). If anything, we would expect stronger correlations to reduce detection of the



**FIGURE 5** The effect of crop diversity on multidiversity was negative when crop diversity effects were weighted toward small to intermediate extents and  $\cap$ -shaped when crop diversity effects were weighted toward large extents. For the latter, the inflection point of the multidiversity–crop diversity relationship (where the effect shifted from positive to negative) increased as the measure of crop diversity was weighted toward longer distances. An effect of crop diversity on multidiversity was not statistically supported when the crop diversity measure was weighted toward the smallest distances. We evaluated the relative support for linear and  $\cap$ -shaped relationships between multidiversity and crop diversity using  $AIC_c$  values, using each of 50 Gaussian distance-weighted measurements of the landscape variables. The bottom three figures depict the range of distance-weighting functions evaluated in our multiscale analysis.

relationship, due to the higher uncertainty in parameter estimates. Thus, the difference in levels of collinearity between studies does not explain the difference in our findings. Likewise, differences in the range of crop diversity values used by Sirami et al. (2019) and in our study cannot explain the difference in our findings. Sirami et al. (2019) considered a wider range of crop diversity values (0.00–2.03) than we did (Appendix S1: Figure S6a). However, we would expect a study that considered a wider range of values to be more likely to detect an  $\cap$ -shaped relationship because it would be more likely to include the crop diversity at which the effect shifts from positive to negative. Instead, we speculate that differences between our findings and those of Sirami et al. (2019) occurred because the latter study did not test the hypothesis at a large enough spatial extent. We found the strongest support for an area–crop diversity tradeoff when crop diversity was most strongly weighted at  $\sim 4.13$  km from the sampling location, an extent much larger than the  $\sim 500$ -m landscape extent in Sirami et al.

(2019). This demonstrates why multiscale analyses are valuable: We would probably have failed to detect support for our prediction if we had picked a single extent (or distance-weighting function) for crop diversity a priori.

Correlations between crop diversity and other landscape-scale variables, such as the amount of crop cover or developed cover, could conceivably produce spurious  $\cap$ -shaped relationships between biodiversity and crop diversity. This could occur if, for example, there was an  $\cap$ -shaped relationship between developed cover and multidiversity and developed cover was strongly correlated with crop diversity. However, we suggest this is unlikely in our study. Although we did not include developed cover in our models, the correlations between crop diversity and developed cover were relatively low across extents (Appendix S1: Figure S12). Additionally, all of our sampling sites were in rural areas where most land is either cropped or in semi-natural cover. We note that this does result in strong, negative correlations between

semi-natural cover and crop cover (Spearman rho from  $-0.97$  to  $-0.95$ ). This strong correlation, however, would not translate into a spurious relationship between biodiversity and crop diversity, because by controlling for the effects of semi-natural cover in our statistical models we also effectively controlled for the effects of crop cover. Although the resolution of our land-cover data precludes measurement of the density of hedgerows—which could benefit biodiversity by increasing the connectivity of field margins with other semi-natural land-cover features—previous work in our study region found a relatively weak correlation between crop diversity and hedgerow density across landscapes ( $r = -0.23$ ; Wilson et al., 2017). Correlations between crop diversity and the proportion of the landscape in different crop types could also potentially cause spurious relationships between biodiversity and crop diversity, because different farming practices (e.g., intensity of fertilizer or pesticide use) can be associated with different crop types, leading to different effects of those crop types on biodiversity. We found moderately strong correlations between crop diversity and the covers of cereal, soybean, and vegetable crops; however, our conclusions did not change if we controlled for these variables in our analyses (Appendix S1: Figures S13–S15).

Similarly, it is unlikely that correlations between crop diversity and variables indexing environmental conditions at the sampling site—such as the type of crop in the adjacent field, farming practices used in crop fields, or conditions in the field margin—produced spurious relationships between biodiversity and crop diversity. We did not control for local crop type in our study design, resulting in variation in the type of crop grown adjacent to our sampling sites (Appendix S1: Table S3). However, crop diversity was not related to the local crop type in our study (Appendix S1: Figure S16). Although we could not estimate use of pesticides or fertilizers in fields adjacent to all of our sampling sites, in a previous study of a subset of sites, we found very weak relationships between crop diversity and use of herbicides, insecticides, or fertilizers, which explained between 0.01 and 0.06 of the variance in crop diversity (Martin et al., 2020). We also evaluated the relationships between crop diversity and the field margin width and composition, which were weak (Appendix S1: Figures S17 and S18).

As predicted (Figure 1b), we found that the effect of crop diversity on biodiversity was more likely to be negative in landscapes with less semi-natural habitat and more likely to be positive in landscapes with more semi-natural habitat, when controlling for the effects of semi-natural diversity and mean field size. Other studies found similar interaction effects of crop diversity and semi-natural cover on bird species richness (Wilson et al., 2017) and multidiversity (Sirami et al., 2019). We

note that the positive effect of crop diversity at higher levels of semi-natural cover was weak (Figure 4). This may be because this analysis only included landscapes with  $\leq 60\%$  of the landscape in semi-natural cover. It is possible that the positive effect of crop diversity would be stronger at higher levels of semi-natural cover. Alternatively, we speculate that perhaps the positive multidiversity–crop diversity relationship was weak in landscapes with high semi-natural cover because the semi-natural cover had a weak, positive effect on multidiversity (Appendix S1: Figure S19). This weak effect of semi-natural cover on multidiversity suggests that, in contrast to our expectation, more semi-natural cover did not consistently translate into resources to support more populations of species across our taxonomic groups. Thus, many species in landscapes with high semi-natural cover could still be sensitive to the reductions in the area per crop type that accompany increases in crop diversity. We also note that when semi-natural cover was low, we did not detect a shift from a positive to a negative effect of crop diversity at very low crop diversity levels, nor did we detect a shift from a positive to negative effect at very high crop diversity levels when semi-natural cover was high (Figure 1b, Appendix S1: Figure S3). However, this is not surprising because  $\cap$ -shaped relationships are difficult to detect statistically when the inflection point is near the top or bottom end of the curve.

Additionally, we speculate that the shift in relative importance of the two main drivers of the biodiversity response to crop diversity may be augmented by a shift in species composition. If landscapes with low semi-natural cover were dominated by species that use crops as habitat, we would expect most species in the community to respond negatively to increases in crop diversity due to the associated reduction in area per crop type. In contrast, if landscapes with high semi-natural cover were dominated by species primarily using semi-natural habitats, then we would expect most species to benefit from additional opportunities (e.g., for foraging) available when crop diversity increases, but not to be sensitive to the area per crop type, because they do not depend on crop fields for habitat. Future work is needed to test this speculation.

The interaction effect of crop diversity  $\times$  semi-natural cover could explain why the direction of effect of crop diversity on biodiversity is inconsistent across studies, if studies using landscapes with low to intermediate semi-natural cover generally find negative crop diversity effects and studies using landscapes with intermediate to high semi-natural covers find the opposite. Such cross-study comparison, however, requires estimates of the range of semi-natural cover from each study. Many studies of the

effects of crop diversity on biodiversity do not report this information. Thus, future work is needed to test this idea. Additionally, future work could explore how the effects of two components of crop diversity on multidiversity, that is, the number of crop types and the mean area per crop type, are influenced by the levels of semi-natural cover in the landscape.

Interestingly, our results also suggest that the spatial extent at which crop diversity is measured could help explain why the direction of effect of crop diversity on biodiversity is inconsistent across studies. Specifically, we found that the area–crop diversity tradeoff depended on the distance weighting of the crop diversity effect, with negative effects of crop diversity when its effect was weighted toward shorter distances and  $\cap$ -shaped relationships when its effect was weighted toward longer distances. Additionally, the inflection point of the multidiversity–crop diversity relationship increased as the measure of crop diversity was weighted toward longer distances. This is somewhat consistent with our expectation that, as the spatial extent of measurement increases, the effect of crop diversity should depend more on immigration to the site from elsewhere in the surrounding landscape, leading to a more positive effect of crop diversity on biodiversity at the site. In other words, a landscape with more crop types would provide more species as potential colonists of the site. We note that we did not find support for crop diversity effects on multidiversity when effects were strongly weighted toward the shortest distances. We expected that, if there were too little of a crop type used as habitat at the scale of a local population, then that species would not be present at that site, resulting in negative effects of crop diversity on multidiversity when measuring crop diversity close to the sampling location. We speculate that the extent needed to support a local population is larger than that represented by the shortest-distance measurements of crop diversity for many of the species included in our multidiversity metric, but this remains to be tested.

### Implications for the area–heterogeneity tradeoff hypothesis

Our findings provide support for the area–heterogeneity tradeoff hypothesis (Duelli, 1997; Kadmon & Allouche, 2007). Although this hypothesis has theoretical support (Kadmon & Allouche, 2007), empirical evidence has been mixed, with some studies reporting support (Bar-Massada & Wood, 2014; Elliott et al., 2020; Redon et al., 2014; Wisz et al., 2007) but others not (Ben-Hur & Kadmon, 2020; Costanza et al., 2011; Kim et al., 2018). We hypothesized that the lack of support was due to the interaction of two

factors: (1) other variables can influence the location of the inflection point on the heterogeneity axis and (2) the inflection point of the heterogeneity axis is influenced by the spatial extent of heterogeneity measurements. Our results support this: We found that other characteristics of a landscape (here, the amount of semi-natural cover) and the spatial extent over which heterogeneity is measured influenced the inflection point and the likelihood of detecting negative or positive heterogeneity effects. Overall, our results contribute support for the area–heterogeneity tradeoff hypothesis, and suggest avenues of research for reconciling conflicting past results.

### Management implications

The results of this study suggest that increasing crop diversity is not a reliable approach to increase biodiversity in the cropped areas of landscapes. The interaction effect with semi-natural habitat suggests that policies to increase crop diversity are unlikely to benefit biodiversity in agricultural landscapes where conservation action is most urgently needed, that is, those with the lowest semi-natural cover. Additionally, our results suggest that efforts to diversify crop types could reduce local populations by reducing the available area of the crop type a given species can use as habitat. Other approaches are needed that can more consistently promote biodiversity across agricultural landscapes. For example, reducing mean field sizes consistently increases biodiversity across studies and taxonomic groups (this study, Appendix S1: Figure S20; Alignier et al., 2020; Ekroos et al., 2019; Fahrig et al., 2015; Hass et al., 2018; Martin et al., 2020; Sirami et al., 2019; Zhou et al., 2018), suggesting that policies/guidelines aimed at reducing crop field sizes could effectively support biodiversity in agricultural landscapes without taking land out of production.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data and code (Khan et al., 2023) are available in Figshare at <https://doi.org/10.6084/m9.figshare.14724732>.

The land-cover data sets utilized for this research are from the Agriculture and Agri-Food Canada Annual Crop Inventory (Agriculture and Agri-Food Canada, 2013) available at <https://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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