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Influence of crop type, heterogeneity and woody structure on avian biodiversity in agricultural landscapes

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ABSTRACT

Agriculture is a primary factor underlying world-wide declines in biodiversity. However, different agricultural systems vary in their effects depending on their resemblance to the natural ecosystem, coverage across the landscape, and operational intensity. We combined data from the North American Breeding Bird Survey with remotely sensed measures of crop type and linear woody feature (LWF) density to study how agricultural type, woody structure and crop heterogeneity influenced the avian community at landscape scales across a broad agricultural region of eastern Canada. Specifically, we examined whether 1) avian diversity and abundance differed between arable crop agriculture (e.g., corn, soy) and forage (e.g., hay) and pastoral agriculture, 2) whether increasing the density of LWF enhances avian diversity and abundance, and 3) whether increasing the heterogeneity of arable crop types can reduce negative effects of arable crop amount. Avian diversity was lower in landscapes dominated by arable crop compared to forage agriculture likely due to a stronger negative correlation between arable cropping and the amount of natural land cover. In contrast, total avian abundance did not decline with either agricultural type, suggesting that species tolerant to agriculture are compensating numerically for the loss of non-tolerant species. This indicates that bird diversity may be a more sensitive response than bird abundance to crop cover type in agricultural landscapes. Higher LWF densities had positive effects on the diversity of forest and shrub bird communities as predicted. Higher crop heterogeneity did not reduce the negative effects of high crop amount as expected except for wetland bird abundance. In contrast, greater crop heterogeneity actually strengthened the negative effects of high crop amount on forest bird abundance, shrub-forest edge bird diversity and total bird diversity. We speculate that this was due to negative correlations between crop heterogeneity and the amount of shrub and forest habitat patches in crop-dominated landscapes in our study region. The variable response to crop heterogeneity across guilds suggests that policies aimed at crop diversification may not enhance avian diversity on their own and that management efforts aimed at the retention of natural forest and shrub patches, riparian corridors, and hedge-rows would be more directly beneficial.

1. Introduction

Agricultural expansion and intensification has been a principal driver of biodiversity loss in temperate and tropical regions (Donald et al., 2001; Kremen et al., 2002; Tscharntke et al., 2005; Mahood et al., 2012). As the human population approaches an expected 9 billion mid-century, a critical conservation question is: how can we maintain biodiversity amidst the need for increased agricultural yields (Godfray et al., 2010)? The designation of protected areas free of agriculture is important, as some species are intolerant to any form of agricultural conversion (Maas et al., 2009; Mahood et al., 2012), but there is a limit to how much land can be set aside because of the resulting loss in yield. Therefore, we also need to understand how to maximize biodiversity to the extent possible within a working agricultural landscape (Tscharntke et al., 2005; Bátary et al., 2010a). Knowledge of how and why different agricultural production systems influence biodiversity is a key step in this process.

Agricultural systems are defined by decisions such as the extent of

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pastoral versus crop lands, the varieties of crops grown, the configuration of different crop and natural land covers, and the intensity of techniques used to grow crops. The degree to which an agricultural system negatively impacts biodiversity depends in part on how it transforms the landscape. This influence can vary along two axes related to the extent to which the system occupies the landscape and how strongly the system contrasts with the natural cover types that agriculture replaced (Cunningham et al., 2013). Agricultural systems can vary widely in their contrast to the natural ecosystem, from expansive crop monocultures with typically low biodiversity to wildlife-friendly systems that retain large proportions of the native faunal and floral communities (Donald, 2004; Tscharntke et al., 2012; Liu et al., 2013).

Positive relationships are typically observed between biodiversity and total landscape heterogeneity, including both natural and agricultural cover types (e.g., Jonsen and Fahrig, 1997; Benton et al., 2003; Wiebull et al., 2008). However, it is also important to understand whether biodiversity benefits specifically from a greater diversification of the agricultural components of the landscape as these may be easier to manage than the natural components. Crop heterogeneity might be beneficial for biodiversity if multiple crop types support different species or allow single species to meet different resource requirements (Dunning et al., 1992; Fahrig et al., 2011). Crop heterogeneity might also be beneficial if the separation of different crops leads to a greater retention of semi-natural habitats such as hedge rows, riparian corridors and grassy strips at field edge boundaries (Benton et al., 2003; Duelli and Obrist, 2003; Weibull et al., 2008; Evans et al., 2014). Evidence supports the benefits of crop heterogeneity for biodiversity at spatial scales within and between farm fields (Vandermeer et al., 1998; Henderson et al., 2009; Malézieux et al., 2009). However, results are mixed at landscape scales with positive relationships in some studies (Siriwardena et al., 2000; Billeter et al., 2008; Lindsay et al., 2013) but not others (Fahrig et al., 2015; Hiron et al., 2015). Variation in the benefits of crop heterogeneity for biodiversity across regions and taxa may be related to factors such as the extent and scale at which taxonomic groups use agricultural cover types and the role of semi-natural habitat for those groups (Piha et al., 2007; Gabriel et al., 2010; Fahrig et al., 2015).

Much of our knowledge of the impacts of agriculture on biodiversity is at the field and farm scales, but there is a growing recognition of the importance of landscape-scale studies. Most landscape-scale research on agricultural impacts thus far has been conducted in European systems (e.g. Billeter et al., 2008; Gabriel et al., 2010; Fischer et al., 2011). By contrast, there is less known about the extent to which different agricultural systems support biodiversity at landscape scales in North America. Landscape-scale studies are difficult to conduct because of the effort and resources involved but the integration of two data types hold potential for such research. First, recent advances in remote sensing allow us to identify the composition and configuration of agricultural landscapes with greater precision than was previously possible (Fisette et al., 2013; Van der Zanden et al., 2013; Pasher et al., 2016). Second, large, volunteer-based efforts (i.e. citizen science) allow us to expand the spatial scope of analyses far beyond the limits of traditional field studies (Dickinson et al., 2010). Among vertebrate taxa, monitoring data are often the most spatially and temporally extensive for birds (e.g., PECBMS, 2012; Sauer et al., 2014). Combined with the diversity of habitat use and broad geographic coverage across avian taxa, this makes birds excellent and frequently used indicators for the effects of human activity on biodiversity (Gregory and van Strien, 2010; Suarez-Rubio et al., 2013; Herrando et al., 2014; Morelli et al., 2014). In this study, we combined data from the North American Breeding Bird Survey (BBS, Pardieck et al., 2017) with remotely sensed measures of land cover type and linear woody feature (LWF) density (Fisette et al., 2013; Pasher et al., 2016) to examine how the amount, type and heterogeneity of agriculture influenced avian diversity and abundance across a broad agricultural region of eastern Canada.

Our first objective examined, at the landscape scale, whether the effects of agriculture on avian diversity and abundance differed depending on whether the agricultural system was 1) forage (e.g., hay) and pastoral agriculture (hereafter "forage"), or 2) crop agriculture excluding forages (hereafter "arable crop", e.g., oilseeds, cereals, grains and pulse crops). Of these two agricultural systems, forage and pasture typically receive lower agrochemical inputs, lower tillage and have more permanent cover between years compared to arable crops (Boutin and Jobin, 1998). Our second objective tested the hypothesis that a greater density of LWF enhances avian diversity and abundance in agricultural landscapes (Hinsley and Bellamy, 2000; Bátary et al., 2010b). We expected these benefits to occur primarily for forest and shrub bird communities. Our final objective tested the hypothesis that increasing the heterogeneity of arable crop types enhances biodiversity by creating greater compositional diversity and a higher retention of semi-natural habitats in the landscape. Based on this hypothesis, we expected to observe 1) a positive relationship between indices of arable crop heterogeneity and avian diversity and abundance, and 2) that increasing the heterogeneity of arable crop types would lessen negative impacts of the amount of arable cropping.

2. Methods

2.1. Survey region

We measured agricultural effects on avian diversity across regions of eastern Ontario and southwestern Quebec, Canada, covering a latitudinal span of ~590 km and a longitudinal span of ~970 km (Fig. 1). Prior to European settlement, the region was largely a combination of deciduous and mixed forests interspersed with lakes and wetlands. Extensive clearing of forests and draining of wetlands for logging and agriculture occurred during the 18th and 19th centuries. Forest regeneration has occurred since the mid-20th century, particularly in eastern Ontario and southern Quebec, although forest cover is still limited in southern Ontario (Butt et al., 2005).

2.2. Avian surveys

We used data from the North American Breeding Bird Survey (BBS, Pardieck et al., 2017) to create survey transects in 131 replicate 20 km^2 landscapes. The BBS was initiated in 1966 and is conducted by experienced observers each year from late May through early July. The survey comprises thousands of ~40 km roadside routes across North America. Each route is composed of 50, 3 min (400 m radius) point counts spaced ~0.8 km apart that are ordinarily summed to create a single estimate of abundance for each species on that route (Sauer et al., 2014). For the purposes of our analysis, we created two transects from each BBS route located in the study area. The first transect included stops 1 through 11, and the second transect included stops 21 through 31. With ~0.8 km between stops, the total distance for each transect was ~8 km and the two transects on each route were separated by ~8 km. This separation allowed us to avoid any spatial autocorrelation that may have occurred had we used consecutive transects. For 11 of the 71 BBS routes included in the study, we only used one transect because land cover imagery was not available for the other transect. We used a single year of BBS data for each transect. The crop mapping data used in this analysis were from 2012, so we selected BBS data for 2012 when possible (115 of 131 transects). However, some BBS routes were not surveyed in 2012, so we used the next closest year with data (9 transects from 2013, 5 from 2009 and 2 from 2008). It is possible that there were some changes in land cover between the timing of the land cover analysis in 2012 and the BBS survey for these transects. However, given the large size of the replicate landscapes, i.e. 20 km^2 areas, we reasoned that the influence of such land cover changes on our landscape variables (arable crop amount, forage amount and arable crop diversity) was slight and unlikely to influence our results.

All species were identified to one of 6 guilds (forest, shrub-forest

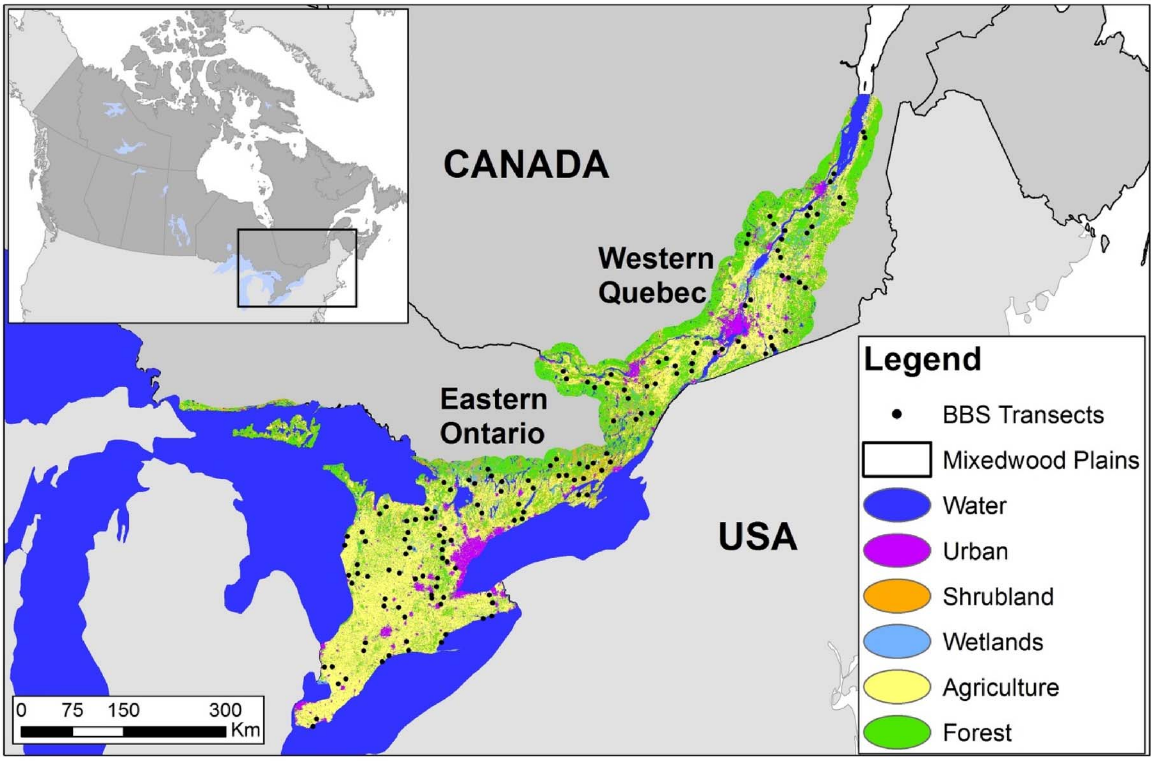

Fig. 1. Study area location showing land cover and bird survey transect locations in eastern Ontario and western Quebec, Canada. Each transect includes 11 stops (8 km total) from a Breeding Bird Survey route. We quantified land cover, crop heterogeneity and linear woody feature density in a 20 km^2 landscape around each transect.

edge (hereafter 'shrub-edge'), grassland, wetland, generalist or aerial forager) based on information on habitat associations provided in the Birds of North America Online (Rodewald, 2015) and the State of Canada's Birds (NABCI, 2012). The BBS data included 21,345 individuals of 138 species across the 6 guilds (forest: 58 species, 3284 individuals; shrub-edge: 20 species, 3344 individuals; grassland: 14 species, 2474 individuals; wetland: 27 species, 1469 individuals; generalist: 11 species, 9846 individuals; and aerial forager: 8 species, 928 individuals) (SI Table 1).

We estimated avian diversity and abundance within each landscape for all guilds and the total bird community. Bird diversity was measured by calculating a Shannon index (Shannon, 1948), which incorporates richness and the relative abundance of each species in the landscape:

$$H = -\sum_{i=1}^{s} p_i \cdot \ln p_i$$

where s is species richness for the landscape and p_i is the proportion of s made up of species i. We calculated p_i for each species using the summed estimate of abundance of each species across the 11 stops on each transect. We also summed the abundance of all species in a guild to create the landscape-level abundance for each guild. The methods used to conduct the BBS did not allow us to incorporate detectability in the estimation of abundance. However, because we have a large sample size and analyzed responses for guild diversity and abundance across a large spatial scale, we expect that any influence of detectability would have a minimal influence on our results.

2.3. Land cover composition

We used the 2012 annual crop inventory mapping produced by Agriculture and Agri-Food Canada (AAFC, Fisette et al., 2013) to obtain land cover information for the study region. This data product is assembled at a 30-m spatial resolution and is considered the most accurate and spatially consistent land cover information for regions of southern Canada. It is used to monitor trends in agriculture. The entire AAFC dataset consists of 66 classes of which 31 natural, agricultural and urban land cover classes were represented in the study region. These included 21 crop types that were separated into five categories by AAFC: oilseeds, grains, cereals, pulses and special crops. Five of these special crop types were woody plants: orchards, vineyards, nurseries, berries and fruits. These five crops were left out of the analysis because they are rare (combined they represented 0.79% of total agricultural amount) and mainly restricted to the southern part of the study area. Proportions of all other crop land covers were re-scaled after removing woody crops from the total. The AAFC dataset does not separate hay and alfalfa; these are combined with pasture land in a single class called forage (hereafter 'forage agriculture'). All crops other than woody crops and forage agriculture were then combined as 'arable crop agriculture'. The final dataset consisted of 10 primary land covers (arable crop, forage, grassland, barren land, wetland, deciduous forest, coniferous forest, mixed forest, water and urban). We calculated a Shannon index of diversity for arable crop as an indication of crop heterogeneity on each transect

We measured the amount of each land cover type within a 2-km wide landscape (i.e. 1 km on each side of the transect) surrounding each of the BBS transects. We chose this width because the BBS includes observations out to 400 m from each survey point and so a 1 km buffer on either side of the transect line would likely cover the territories of the species detected. With the 1 km buffer on either side of the 8 km transect (including the ends), each landscape represents a 20 km^2 area. Variables for proportion of arable crop and proportion of forages were not standardized thus allowing us to directly compare the relative change in avian diversity or abundance for a given change in each variable.

Information on LWF was extracted from a database produced by Pasher et al. (2016) who used a line intersect sampling strategy to sample features from high resolution airborne imagery. Sampling was conducted manually by placing points where interpreters identified intersections of the sampling transect and LWF. For this analysis, we took the total number of points on LWF identified within the 2 km buffered region surrounding each BBS transect. Based on Pasher et al. (2016) and Corona et al. (2004), the number of points is directly proportional to the estimated LWF density (m/ha) for a given landscape.

2.4. Statistical analysis

To examine the influence of agricultural type (arable crop or forage), arable crop heterogeneity and LWF density on avian biodiversity, we used a linear model when avian diversity was the response variable and a negative binomial generalized linear model (Venables and Ripley, 2002) when avian abundance was the response variable. The latter was used for the abundance data to accommodate over-dispersion that is typically present in count data. We compared support for models using corrected Akaike's Information Criterion (AICc, Burnham and Anderson, 2002). Our modeling approach proceeded in three steps. We first ran two models with either a single variable for total proportion of agriculture (i.e. arable crop and forages combined) or two variables representing the proportion of arable crops and the proportion of forages. Support for the latter model indicated a difference in the effects of the two agricultural types on bird diversity or abundance (Objective 1). All subsequent models included the proportion of arable crop and the proportion of forage as separate variables because this model was needed to test for the interaction of arable crop amount by crop heterogeneity. In the second step we added LWF density to the model with arable crop and forage, and compared AICc between models with and without LWF density (Objective 2). Finally, we added arable crop heterogeneity to the arable crop and forage amount model with and without LWF density. The model with all four variables (arable crop amount, forage amount, arable crop heterogeneity and LWF density) was our global main effects model and we compared support for this model to one with an interaction between arable crop amount and arable crop heterogeneity to assess whether negative effects of arable crop amount would be lessened in more diverse arable crop landscapes (Objective 3). Interactions were fit with cross-product residuals to eliminate the correlation between the interaction terms in examining the main effects (Lance, 1988). Our most complex models with the interaction term had five explanatory fixed effects variables and the intercept. Thus, with our sample size of 131 landscapes, we always had at least 21 samples per parameter.

Model fit was evaluated by assessing normality of residuals for diversity models and comparing residuals with fitted values to assess homogeneity of variance for both diversity and abundance models. For the aerial forager guild, one or fewer individuals were detected on 33 of 131 transects, resulting in poor model fit. Therefore, we included aerial foragers in calculations of total avian diversity and abundance, but did not consider this guild independently. In addition to examining support for models containing each variable, we used the coefficient effect sizes and 95% confidence intervals to infer significant effects of agricultural variables. We report coefficients from the global main effects model if there was no support for the arable crop amount by heterogeneity interaction or the global interaction model if there was support for the interaction. By reporting estimates from the global model we are showing the effect size of each variable while accounting for the influence and relationship with other variables. If our study had contained a large number of variables in an exploratory analysis then it may have been necessary to identify a reduced set of influential variables prior to examining effect sizes. However, our four main explanatory variables were carefully considered based on a priori hypotheses and therefore it was preferable to report effect sizes from the global main effects or global interaction effects model. We examined the correlations among all variables and estimated a variance inflation factor (VIF) to assess multicollinearity. The maximum correlation was −0.39 between proportion of arable crop and proportion of forage (S1 Table S2) and the variance inflation factor was 1.33, indicating no evidence for issues of multicollinearity (Kutner et al., 2004). Analyses were conducted in R version 3.3.3 (R Core Team, 2017). The R package MASS (Venables and Ripley, 2002) was used to run negative binomial generalized linear models.

3. Results

3.1. Agricultural land cover characteristics

Agricultural land represented 57.5% of total cover across all landscapes, while natural land cover classes (including waterbodies) represented 39.2% and urban areas represented 3.3%. The average proportion of arable crop and forage agriculture within landscapes was 31.7% (range: 0.05–92.7) and 24.6% (range: 0.7–61.4) respectively. Only 7% of the 131 landscapes had less than 20% combined agriculture. The density of LWF averaged 10.41 m/ha and ranged from 0 to 35.17 m/ha across landscapes. Corn and soy were the dominant crop types representing 46% and 38% respectively of the total arable crop amount, while cereal crops (barley, oats, wheat) represented ∼11%.

3.2. Objective 1: effects of arable crop vs. forage on avian diversity and abundance

Our model results suggest a greater relative decline in total, forest and wetland bird diversity with increasing amount of arable crop compared to forage, while grassland bird diversity increased with both crop types, but more strongly with forage (Table 1 compare model "C + F" with model "A", Fig. 2a, Table S3). Diversity of the shrub-edge guild declined similarly as amount of arable crop and forage increased in the landscape, while generalist guild diversity did not vary with amount of arable crop or forage (Table 1, Fig. 2a).

Relationships between the amount of the two agricultural types and abundance were similar to the patterns highlighted above for guild diversity, but in most cases the effect sizes were more positive (Table 2, Fig. 2b). Only forest bird abundance was negatively affected by both agricultural types while wetland bird abundance was negatively affected by only amount of arable crop (Fig. 2b). For the shrub-edge

Table 1
Akaike's Information Criterion (AICc) results for effects of agriculture on avian diversity in 131 landscapes in eastern Canada. Crop (C) = proportion of arable crop, forage (F) = proportion of forage, agriculture (A) = combined proportion arable crop and forage, heterogeneity (H) = Shannon index of arable crop diversity, L = density of linear woody features. ΔAIC_c = change in AIC_c with the top model equal to 0 (bolded for each guild), w_i = model weight. See Fig. 2 for coefficient effect sizes.

Model	Total		Forest		Shrub-edge		Grassland		Generalist		Wetland	
	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
C*H + F + L	**0.00**	0.39	0.57	0.29	**0.00**	0.83	2.63	0.16	7.08	0.02	5.03	0.04
C + F + H + L	3.49	0.07	**0.00**	0.48	4.40	0.09	1.85	0.24	6.82	0.02	4.10	0.07
C + F + L	1.36	0.20	4.29	0.05	6.28	0.04	12.88	0.00	5.79	0.03	2.11	0.18
C + F + H	3.28	0.08	3.88	0.06	6.82	0.03	**0.00**	0.60	5.41	0.04	2.01	0.19
C + F	1.12	0.22	5.83	0.02	10.84	0.00	12.55	0.00	4.07	0.08	**0.00**	0.51
A	3.98	0.05	7.12	0.01	8.78	0.01	12.76	0.00	2.07	0.21	7.14	0.01
Intercept	34.42	0.00	40.15	0.00	31.30	0.00	20.46	0.00	**0.00**	0.60	14.42	0.00

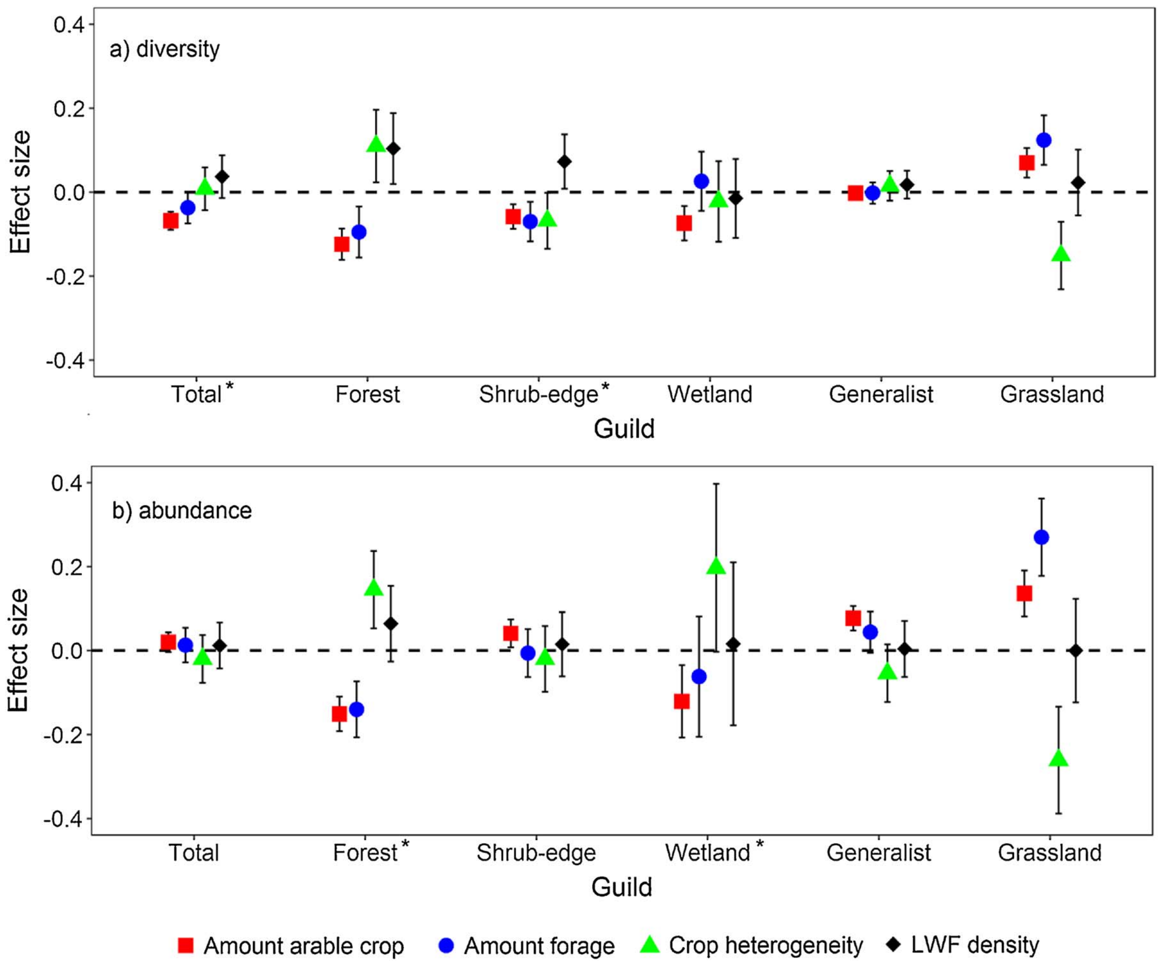

Fig. 2. Model coefficient effect sizes for the influence of arable crop amount, forage amount, arable crop heterogeneity and linear woody feature (LWF) density on avian diversity (top panel) and abundance (bottom panel). To show effects of all four variables we report the mean and 95% confidence intervals for each response from either the global main effects or interaction model depending on which model had the highest support. An asterisk indicates cases where there was support for an interaction effect between arable crop amount and arable crop heterogeneity (see Fig. 3).

guild, abundance actually increased with arable crop agriculture in contrast to the negative response of diversity. Generalist guild abundance increased with both agricultural types, although slightly more strongly with arable crop amount.

3.3. Objective 2: effects of linear woody features on avian diversity and abundance

Our hypothesis that LWF would enhance the diversity of the forest and shrub-edge bird communities was supported with higher model support and coefficient confidence intervals excluding 0 for both guilds (Table 1, Fig. 2a). In contrast, we did not find support for higher abundance of these two guilds in relation to LWF densities. There were no significant effects of LWF density on diversity or abundance of any other guild (Table 1, Fig. 2).

3.4. Objective 3: effects of arable crop heterogeneity on avian diversity and abundance

Higher crop heterogeneity had positive effects on forest bird diversity and negative effects on grassland bird diversity and abundance; in these three cases the effects of crop heterogeneity were independent

Table 2
Akaike's Information Criterion (AICc) results for effects of agriculture on avian abundance in 131 landscapes in eastern Canada. Crop (C) = proportion of arable crop, forage (F) = proportion of forage, agriculture (A) = combined proportion arable crop and forage, heterogeneity (H) = Shannon index of arable crop diversity, L = density of linear woody features. ΔAIC_c = change in AIC_c with the top model equal to 0 (bolded for each guild), w_i = model weight. See Fig. 2 for coefficient effect sizes.

Model	Total		Forest		Shrub-edge		Grassland		Generalist		Wetland	
	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i
C*H + F + L	7.95	0.01	**0.00**	0.68	6.04	0.02	3.94	0.09	4.40	0.03	**0.00**	0.54
C + H + F + L	5.97	0.02	3.36	0.13	3.83	0.05	2.20	0.23	2.18	0.10	7.12	0.02
C + F + L	4.22	0.05	9.26	0.01	1.79	0.15	14.63	0.00	2.25	0.10	6.52	0.02
C + F + H	3.96	0.06	3.19	0.14	1.90	0.14	**0.00**	0.68	**0.00**	0.31	4.97	0.05
C + F	2.41	0.12	7.44	0.02	**0.00**	0.36	12.75	0.00	0.30	0.27	4.41	0.06
A	0.46	0.33	6.25	0.03	1.33	0.19	16.05	0.00	1.01	0.19	2.44	0.16
Intercept	**0.00**	0.41	43.68	0.00	2.89	0.09	29.20	0.00	17.14	0.00	2.41	0.16

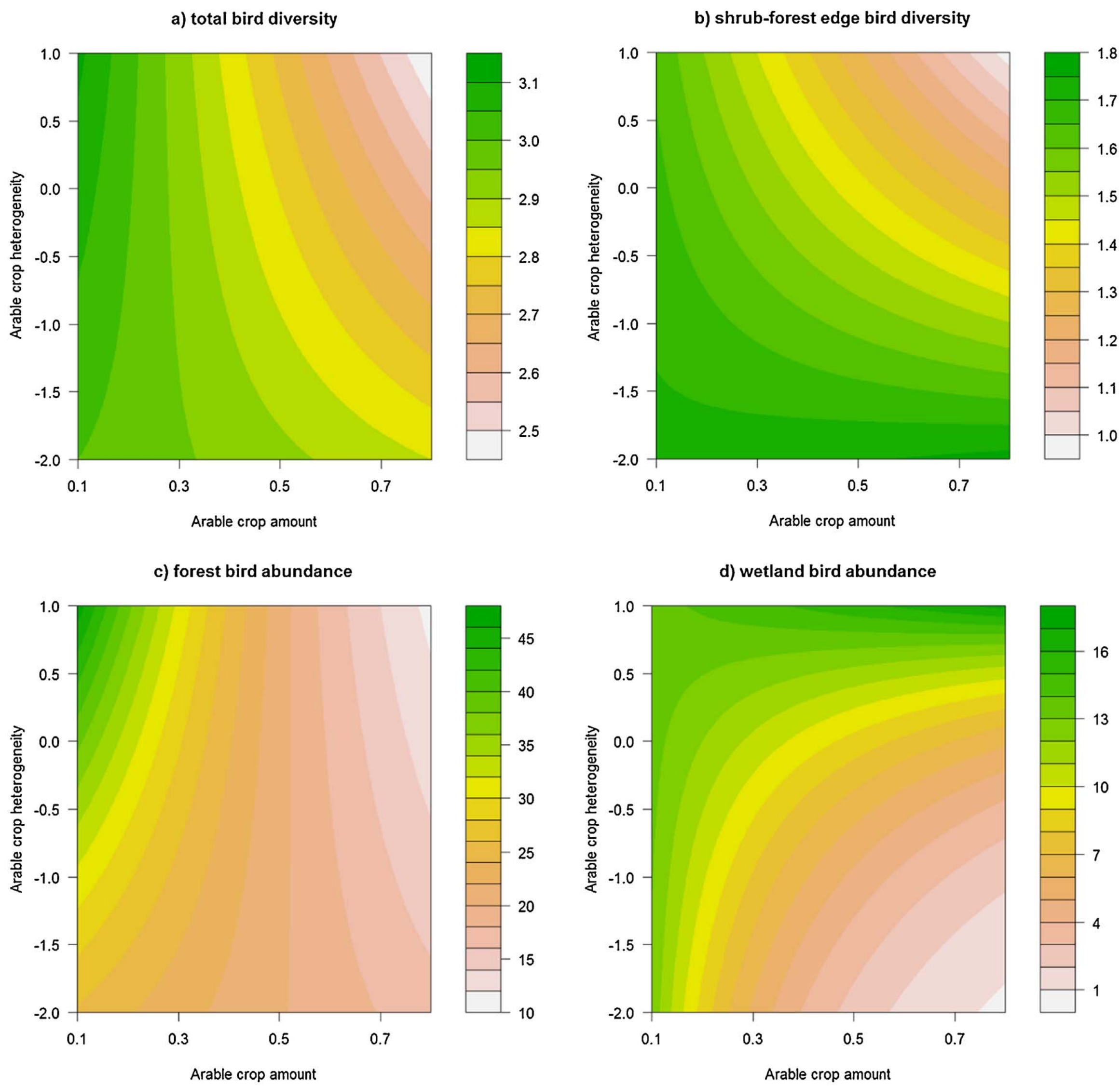

Fig. 3. Contour plots showing the interaction between arable crop amount and arable crop heterogeneity on a) total bird diversity (Shannon index), b) shrub-forest edge bird diversity, c) forest bird abundance and d) wetland bird abundance. Figures were generated by predicting responses from the interaction model across combinations of arable crop proportions (0.10–0.80) and arable crop heterogeneity (standardized values of −2.0 to 1.0) observed in the dataset. For all predictions, LWF density was held at a standardized value of 0 and proportion of forage agriculture was held fixed at 0.15.

of the effect of crop amount (Fig. 2, Tables 1 and 2). Greater crop heterogeneity did not reduce the negative effects of arable crop amount on avian diversity as hypothesized. In fact, we observed the opposite effect on total and shrub-edge diversity, where landscapes with high amounts of arable crop cover had lower diversity when crop heterogeneity was high than when it was low (Table 1, Fig. 3a and b). For forest bird abundance, greater crop heterogeneity enhanced abundance in landscapes with low amounts of crop but had a negative effect in landscapes with a high amount of crop cover (Table 2, Fig. 3c). Our hypothesis was supported only in one case; wetland bird abundance was maintained across the gradient of crop amount in landscapes with high but not low crop heterogeneity (Table 2, Fig. 3d).

4. Discussion

We combined citizen science and remotely sensed mapping of agricultural landscapes to examine how the type and heterogeneity of agriculture influenced avian diversity and abundance across a broad agricultural region of eastern Canada. Our study found several key results. First, landscapes containing mainly arable crop agriculture, primarily represented by row crops (e.g., corn, soy), supported lower avian diversity than landscapes containing mainly forage crops (e.g., hay, alfalfa) and pasture. Second, avian community abundance did not decline with increasing amounts of arable crop agriculture, implying that species tolerant to arable cropping numerically compensated for the loss of individuals due to declining avian diversity. Third, higher densities of LWF resulted in a higher diversity of the forest and shrub bird communities. Finally, higher crop heterogeneity did not reduce the negative effects of high crop amount on the diversity of the avian community.

Arable crop agriculture was associated with lower total bird diversity than forage crop and pastoral agriculture. Characteristics of the two agricultural types and their correlation with natural land covers in our study region highlight several factors that likely contribute to the more negative influence of arable cropping on the bird community. First, the amount of natural cover and the density of LWF is often strongly, negatively correlated with the amount of arable crop agriculture but not with the amount of forage agriculture (SI Table 2). Second, while the average proportion of each agricultural type was similar across the 131 landscapes (0.32 and 0.25 for arable crop and forage respectively), arable crop agriculture comprised a high proportion of many landscapes. The maximum proportion of forage agriculture on any landscape was 0.61, whereas 22 landscapes had arable crop proportions exceeding 0.61 with a maximum of 0.93. Finally, patch size estimates based on FragSTATS (McGarigal et al., 2012) showed that the average size of arable crop patches (23.26 ha + 2.35(SE)) was more than twice the average size of forage patches (10.38 ha + 0.58). Our findings here are consistent with a finer-scale study in eastern Ontario where diversity was higher on farms that contained more pasture and non-agricultural habitat than those where row crops represented a higher proportion of farm area (Freemark and Kirk, 2001). Our results are also similar to those from several studies in other regions, particularly in Europe, where agricultural practices that retained natural and semi-natural land covers adjacent to farmland had positive benefits for biodiversity (Duelli and Obrist, 2003; Billeter et al., 2008; Weibull et al., 2008; Lindsay et al., 2013; Wuczyński, 2016). In our study region, there has been a general trend to fewer, larger farms and a shift away from forage agriculture towards a higher production of corn and soybean (Agriculture Canada, 2013). While total bird diversity declines with increasing amounts of both agricultural types, we predict that a continued shift to more intensive arable crop agriculture will lead to greater declines in avian diversity in this region.

Our comparison of how agriculture influences bird diversity versus abundance reveals that declines in some species might be compensated by an increase in others. Forest bird diversity and abundance declined with increasing arable crop coverage indicating consistent responses across species in the guild. In contrast, the shrub-edge guild showed strong declines in diversity but an increase in abundance as the amount of arable crop increased. This result suggests that many species in the guild were negatively affected by arable crops but that the abundance of some species increased even though arable crop cover is often negatively correlated with the amount of shrub and forest habitat on the landscape. For example, two common shrub and edge species in our study, Northern Cardinal (*Cardinalis cardinalis*) and Song Sparrow (*Melospiza melodia*), both showed weak, yet positive correlations with proportion of arable crop ($r = 0.21$ and $r = 0.12$ respectively). Although these species require shrub and edge habitat at fine scales, their abundance at the landscape scale may be higher in open, agricultural landscapes than in forested landscapes as long as small patches of suitable shrub and edge habitat are retained. More positive responses of abundance than diversity to increasing arable crop amounts were also observed for total avian abundance as well as generalist and grassland guild abundance. While such compensation by agriculture-tolerant species could maintain avian community abundance, the disappearance of particular species likely results in the loss of important functional roles within the ecosystem (e.g., Larsen et al., 2005; Gavier-Pizarro et al., 2012). Future studies should evaluate the turnover and functional resiliency of the community across gradients of agricultural intensity (e.g., Winfree and Kremen, 2009; Karp et al., 2011).

We found support for our hypothesis that the retention of LWF in agricultural landscapes enhances the diversity of forest and shrub-edge bird communities. These features included riparian strips and hedge rows between fields and along roads. The retention of semi-natural habitats adjacent to agricultural land is known to benefit the diversity of birds (Lindsay et al., 2013; Evans et al., 2014; Wuczyński, 2016) and other taxa including vascular plants (Billeter et al., 2008) and arthropods (Duelli and Obrist, 2003; Weibull et al., 2008). For birds, hedge rows offer a range of benefits for nesting, roosting and maintaining connectivity among larger patches (Hinsley and Bellamy, 2000; Benton et al., 2003). Bátary et al. (2010b) also showed that the benefits of hedges for bird diversity were highest in simple landscapes dominated by agriculture. While numerous studies at smaller spatial scales have emphasized the benefits of hedge rows and other semi-natural habitats, we believe this study to be one of the few to remotely quantify these linear elements across a broad geographic area and confirm their benefits for forest and shrub bird communities at landscape scales in agricultural regions.

Our study revealed variation in how individual guilds responded to the amount of agriculture and the density of LWF. Differences were most notable between the response of the forest and shrub bird communities compared to the grassland bird community. Diversity of forest and shrub-edge guilds declined with higher proportions of both agricultural types, while grassland bird diversity increased. Linear woody features had positive benefits only for the diversity of the forest and shrub-edge bird communities. This variability across guilds likely relates to how the structure of agricultural lands favor different guilds relative to the natural ecosystem that agriculture replaced (Donald, 2004; Cunningham et al., 2013). Our study region was formerly dominated by deciduous and mixed deciduous-coniferous forest (Butt et al., 2005). Species that select forest, forest edge and shrub habitats represented the majority of species detected and thus, measures of total avian diversity reflect to a greater extent the response of these guilds to agriculture. The variable guild-level responses highlight the complexity in conserving biodiversity across multiple taxa that differ in habitat associations and their tolerance to agricultural conversion (Billeter et al., 2009; Gabriel et al., 2010; Smith et al., 2011). In our study region, total avian biodiversity would be enhanced to a greater extent by management actions that enhance the diversity of the forest and shrub bird communities given their higher species richness (57% of the species in this analysis). The grassland bird community only represented 10% of the species in this analysis yet include species of conservation concern such as Bobolink (*Dolichonyx oryzivorus*) and Eastern Meadowlark (*Sturnella magna*) that do not select forest and shrub habitat. The use of optimization analyses to identify agricultural landscapes that jointly maximize diversity of the forest/shrub and grassland bird communities to the extent possible would be an interesting and important area of future research (Wilson et al., 2009).

We hypothesized that increasing the heterogeneity of arable crops would lessen negative effects of crop amount on avian diversity and abundance if it promoted greater structural diversity within the production system and the retention of higher amounts of semi-natural habitat adjacent to fields (Vandermeer et al., 1998; Benton et al., 2003; Weibull et al., 2008). There was support for this hypothesis only for wetland bird abundance, while higher crop heterogeneity actually strengthened negative effects of crop amount on the diversity of the forest and shrub-edge bird communities. The unexpected negative effect of crop heterogeneity might be explained by relatively strong and negative correlations across our landscapes between crop heterogeneity and the amount of shrub land cover ($r = -0.48$) and to a lesser extent forest cover ($r = -0.14$). It is unclear why higher crop heterogeneity shows this particularly strong correlation with amount of shrub cover. One possibility is that the expansion of farm size in Ontario and Quebec (Agriculture Canada, 2013) means that semi-natural shrub habitats that formerly fell along property boundaries now lie within properties where they may be removed if perceived as a lost opportunity to increase agricultural yield and an obstacle to more efficient farming operations. In high crop production landscapes, the main crop types are frequently grown adjacent in large fields without semi-natural boundary habitat (Fig. 4). In such cases, increasing the variety of crops grown will not necessarily benefit the avian community if the expected retention of semi-natural habitat between crop fields is absent. Thus, alternative strategies may be needed to retain semi-natural land cover. In addition to benefits for biodiversity, the retention of semi-natural lands would help limit soil erosion, provide windbreaks for crops and riparian corridors for runoff, and support faunal communities that provide pollination and pest control services (Marshall and Moonen, 2002; Swinton et al., 2007; Tscharntke et al., 2012).

In summary, the joint application of citizen science monitoring data with remotely sensed land cover measurements allowed us to evaluate how landscape scale amount and heterogeneity of agriculture impact avian biodiversity. The regional scope of this study allowed us to examine the direct relationship between agricultural variables and avian

Fig. 4. Forage agriculture (left panel) with hay fields, linear woody features and grassy strips along field boundaries, and arable crop agriculture (right panel) showing adjacent mixed crops with cereals (foreground), soybean (middle) and corn (background).

diversity and abundance, as well as determine how different agricultural systems influence the natural landscape. The broad coverage of the North American Breeding Bird Survey and the availability of remotely sensed land cover data would make it straightforward to extend the analyses from this study to address similar landscape-scale questions in other ecosystems and even to facilitate cross-ecosystem comparisons.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.07.059.

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