RESEARCH ARTICLE

The homogenizing influence of agriculture on forest bird communities at landscape scales

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Abstract

Context Agricultural expansion is a principal driver of biodiversity loss, but the impacts on community assembly in agro-ecosystems are less clear, especially across regional scales at which agricultural policies are applied.

Objectives Using forest-breeding birds, we (1) tested whether increased agricultural coverage resulted in species communities that were random or more similar than expected, (2) compared the relative influence of agriculture versus distance in structuring communities, and (3) tested whether different responses to agriculture among functional guilds leads to a change in functional diversity across gradients of agriculture.

Methods Species abundances were sampled along 229 transects, each 8 km, using citizen science data assembled across a broad region of eastern Canada. Agricultural and natural land cover were each summed within three different-sized buffers (landscapes) around each transect. A null modeling approach was used to measure community similarity.

Results Communities were most similar between landscapes that had high agricultural coverage and became more dissimilar as their respective landscapes differed more strongly in the amount of agriculture. Community dissimilarity increased with geographic distance up to about 200 km. Dissimilarity with increasing agriculture was largely due to the disappearance of Neotropical migrants, insectivores and foliage-gleaners from the community as agriculture increased. Functional diversity declined with increasing agriculture but less strongly than species richness and only when agriculture exceeded 40% of the landscape.

Conclusions Our results support the hypothesis that increasing agricultural coverage produces a filtering towards communities of agriculture-tolerant forest birds with a loss of functional diversity and high site-to-site community similarity.

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Introduction

The expansion of agricultural land is a principal driver of global declines in biodiversity (Donald et al. 2001; Tscharntke et al. 2012). These impacts are expected to increase over the next few decades as the human population continues to grow and food demand rises (Tilman et al. 2011). The effects of natural land cover removal for agriculture (e.g. cropland, pasture) on species alpha diversity are well studied and typically negative (Benton et al. 2002; Flynn et al. 2009; Flohre et al. 2011). In contrast, we know less about how agricultural expansion affects species turnover or beta diversity, i.e., community similarity between sites or landscapes within a region. An understanding of the factors affecting community similarity is important because community composition has direct implications for functional diversity and associated ecosystem resiliency (Cadotte et al. 2011; Karp et al. 2011). Furthermore, understanding the factors affecting community similarity at regional scales has applied conservation implications, as agricultural land use policies in agro-ecosystems are typically established across broad regions (Socolar et al. 2016).

Habitat loss has been predicted to increase community similarity between landscapes by filtering community composition, with the result that certain species or guilds will be over-represented relative to the regional species pool as habitat availability declines (Tscharntke et al. 2008; Karp et al. 2012; Jeliazkov et al. 2016; Socolar et al. 2016). We refer to this as the *filtering hypothesis* and it has been supported by studies documenting increased community similarity in agricultural landscapes following the removal of natural land cover. For example, in highly agricultural landscapes, communities of plants (Flohre et al. 2011), soil microbes (Flores-Rentería et al. 2016), arthropods (Ekroos et al. 2010) and birds (Karp et al. 2012; Vallejos et al. 2016) were more similar to one another than communities in landscapes with higher proportions of natural cover types. In contrast, the *random assembly hypothesis* suggests that habitat availability is not structuring communities and

therefore the communities of two landscapes with comparable habitat composition will be no more similar than expected if randomly selected from the regional species pool (Chase and Myers 2011; Chase et al. 2011). Community similarity tends to decline with geographic distance (Nekola and White 1999; Pomara et al. 2013) and the relationship between distance and similarity may be more evident if the deterministic influence of agriculture is weak or absent.

There remain at least two important knowledge gaps with respect to the effects of agricultural expansion on community similarity. First, there are often scale-dependent effects where even for the same taxon there can be an influence of agriculture at one scale but not another (Flohre et al. 2011; Jeliazkov et al. 2016). Most studies to date have focused on smaller spatial scales and there is a need to better understand the influence of agriculture on community similarity at landscape scales across broad ecoregions. Second, species life histories and behavioral traits can have a strong influence on how they respond to the loss of habitat due to agriculture (Waltert et al. 2005; Karp et al. 2011; Newbold et al. 2013; Bregman et al. 2014). If particular guilds are susceptible to agriculture then we might also expect a decline in functional diversity, defined as the value and range of species traits that influence ecosystem functioning (Tilman 2001). Yet, the relationship between functional diversity and the extent of agriculture is complex and also depends on the degree of functional redundancy (Flynn et al. 2009; see also Díaz and Cabido 2001). If there is low functional redundancy then declines in functional diversity will closely match declines in species richness across gradients of agriculture. However, if functional redundancy is high then functional diversity will be less sensitive and decline less steeply than species richness (Flynn et al. 2009). A knowledge of guild level responses to agriculture and the associated changes in functional diversity, if any, has important implications for predicting how agricultural expansion impacts ecosystem function (e.g. Tilman et al. 1997; Cadotte et al. 2011; Karp et al. 2011).

In this study, we used a null modelling approach (Chase et al. 2011) with forest-breeding birds to examine support for the *filtering* versus *random assembly hypotheses* in the context of landscape-scale forest loss for agriculture. Specifically, we (1) examined how similarity of the community changes among

landscapes as species richness declines with increasing amounts of agriculture, (2) compared the relative influence of agriculture versus geographic distance in structuring communities, and (3) examined whether different responses to agriculture among guilds leads to a change in forest bird functional diversity across gradients of agriculture. The data were drawn from a broad region of eastern Canada covering approximately 560 km latitude and 990 km longitude (Fig. 1).

We chose to study forest-breeding birds as a model taxon for two reasons. First, our previous research in the region showed that within-landscape species richness in this group is negatively affected by the amount of agricultural land cover (Wilson et al. 2017). Therefore, forest birds allowed us to examine the two hypotheses above on how agricultural expansion affects community similarity when it expands into a naturally forested ecoregion (Butt et al. 2005). Second, the forest-breeding guild contains species varying in migratory status, diet, foraging strata and size. This variation allowed us to examine whether any effects of landscape homogenization on species richness are related to particular effects of agriculture on specific guilds and the extent to which these changes influence functional diversity.

For the *filtering hypothesis*, we first predicted that (1) landscapes with more agriculture would have higher similarity in their communities due to filtering and (2) similarity between communities would decline as their respective landscapes differed more strongly in the amount of agriculture. Previous research in other regions in North America found that long distance migrants tend to be more sensitive to forest loss than short distance migrants (Lynch and Whigham 1984; Schmiegelow et al. 1997; Hobson and Bayne 2000). Global comparisons of the response of foraging guilds to forest loss also found that insectivores were more sensitive than granivores and frugivores in both temperate and tropical regions, although effects were stronger in the latter (Bregman et al. 2014). Given the results of these earlier studies, we also predicted under this hypothesis that Neotropical migrants and insectivores would be more susceptible to the amount of agriculture in the landscape, while short-distance migrants and granivores would be less susceptible. The insectivorous and Neotropical migrant guilds are species rich and therefore, if these guilds are most susceptible to agriculture, then we also predicted that functional diversity should decline more slowly than species richness as agricultural amount increases because large numbers of species need to
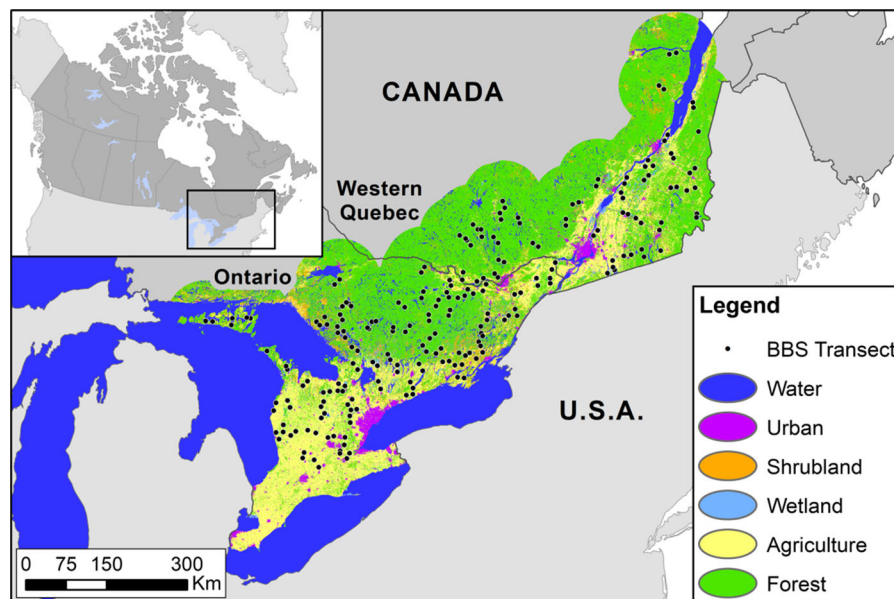

Fig. 1 Study region showing land cover and bird survey transect locations in eastern Ontario and southern Quebec, Canada. Each transect includes 11 stops (8 km total) from a Breeding Bird Survey route. We quantified agricultural and natural land cover amounts within landscapes at three spatial scales (20 km², 84 km², 180 km²) around each transect

disappear from the landscape before a loss of functional diversity is observed.

In contrast, for the *random assembly hypothesis*, we predicted that (1) community similarity would not vary with the amount of agriculture in the landscape and (2) geographic distance would be a stronger predictor of community similarity than agriculture. Under this hypothesis we predicted that even as species richness declines with increasing amount of agriculture there would be no particular guilds that are more or less susceptible. An even response to agriculture across guilds was also predicted to result in a similar rate of decline for species richness and functional diversity across increasing gradients of agriculture.

Methods

Study region

Prior to European settlement, the study region was primarily a combination of deciduous and mixed forests interspersed with lakes and wetlands. During the eighteenth and nineenth centuries, deforestation increased for logging and agriculture. Forest regeneration has occurred since about the mid-twentieth century particularly in eastern Ontario and southern Quebec, although forest cover remains limited in southern Ontario (Butt et al. 2005). Approximately 30% of the study region is agricultural land with corn, soybean and pasture land (e.g. hay, alfalfa) being the dominant crops and representing about 92% of total agriculture (see Supporting Information Table A1 for individual class proportions). Agricultural lands in the region contain varying extents of semi-natural habitats (e.g. hedge rows, riparian strips) that have been shown to enhance the diversity of forest and shrub-breeding avian guilds (Wilson et al. 2017). The breeding season climate of the study region varies along a spatial gradient: from the southwest to the northeast, mean June temperatures decline by about 2° while total June precipitation increases by approximately 25 mm (data from https://climate-viewer.canada.ca).

Avian surveys and land cover composition

The BBS is a volunteer-based survey initiated in 1966 and conducted annually on over 4000 roadside routes across North America between late May and early July (Environment Canada 2017; Sauer et al. 2017). Each route is 39.2 km long and contains 50 stops at 800 m intervals where the observer conducts a 3 min point count of all birds seen or heard within 400 m. For our analysis, we first identified all BBS routes from the Lower Great Lakes and St. Lawrence Plain Bird Conservation Region with at least one survey between 2010 and 2014. As described above, landscapes within these regions were once heavily forested and have now been converted to agriculture to varying degrees. To ensure we had a large gradient representing forest-dominated to agriculture-dominated sites we also included a small number of routes from the southern-most section of the Boreal Hardwood Transition ecoregion. Following this selection we had 135 BBS routes from across southern and eastern Ontario and southern Quebec. We subsequently excluded 18 of these routes from the southernmost ecoregion in Ontario (Ecoregion 7, Crins et al. 2009) as it shows distinct vegetation from the rest of the study region and includes some avian species with restricted ranges. For the remaining 117 routes (Fig. 1), we used the bird survey information at the stop level to create two "transects" consisting of stops 1 to 11 and stops 21 to 31 from each route (n = 234 transects). We omitted stops 12 to 20 to limit spatial autocorrelation between transects on the same route. We subsequently removed five transects due to incomplete land cover information and our final analysis was based on 229 transects. Abundance data for each species was summed over the 11 stops within each transect and therefore transects represent the individual sampling units in this study. By using 11 stops over an 8 km transect, we obtained sufficient information to describe each 'community' in terms of both its species composition and relative abundances of species; apart from that consideration, the choice of transect length was arbitrary. For additional detail on the designation of transects and survey methodology see Wilson et al. (2017).

The methods used to conduct the BBS do not allow us to explicitly estimate species detectability when estimating abundance. Therefore, to estimate the average annual abundance for each species on each transect we averaged abundances over a 5-year window (2010–2014) around our focal study year of 2012 when the land cover data were assembled (see below). This approach of using a 5-yr average should

help minimize cases where a species was missed in one or more years and is similar to approaches taken by other authors when using the BBS to examine impacts of landscape change on avian communities (e.g. Donovan and Flather 2002). Because of the large sample size and spatial scale of our analysis as well as our 5-year averaging approach, we expect that any variation in detectability should have a minimal influence on our results. To check whether our sample sizes were sufficient to sample the community of species we also estimated how many transects were needed to detect 95% and 99% of the regional species pool (see "Results" section). We note that our estimates are a relative and not an absolute measure of abundance for each species in the community.

Land cover was summarized at three spatial scales: 1 km, 3 km and 5 km on either side of each transect line including the ends. This resulted in landscapes that were approximately 20 km^2 (1 km buffer), 84 km^2 (3 km buffer) and 180 km^2 (5 km buffer) in size. Because transects ran along roads and were not always straight, the size of the landscape varied slightly among them. The 1 km scale was chosen as the smallest scale because this should represent the land covers at the territory scale for the majority of species detected within the maximum radius (400 m) for each survey point (Wilson et al. 2017). However, we also wished to determine whether community composition was affected more strongly by landscape composition at increasing spatial scales. Previous work indicates that it is difficult to make any a priori assumptions of the scale at which the landscape context has its largest effect, i.e., the 'scale of effect' (Jackson and Fahrig 2014; Farrell et al. 2019). For many routes along the northern and southern edges of the region, we were unable to assemble land cover beyond 5 km and therefore, this buffer width was the maximum scale we evaluated. We then also summarized land cover within a 3 km buffer as an intermediate scale.

We extracted land cover data from the 2012 annual crop inventory from Agriculture and Agri-Food Canada (Fisette et al. 2013). This 30 m resolution data set provides extensive and detailed information on up to 66 classes of land cover data, including agricultural and natural vegetation classes. Within the three scales for each landscape we determined the total number of 30 × 30 m pixels for each land cover class and converted these to proportions based on the total number of pixels in each landscape. The raster was Sieve filtered

to reclassify patches of 2 pixels or less, assigning them to the class of the largest neighbouring patch. Roads were incorporated and included as urban land cover. We added the proportions of cropland (including cereals, pulses, fruits and vegetables) and pasture to determine the total proportion of agricultural land within each landscape at each spatial extent around each transect. At each spatial extent, we grouped landscapes into four categories for comparisons of community assembly in relation to amount of agriculture: (1) high agriculture ($\geq$ 50% of the landscape in agricultural land cover), (2) moderate agriculture (30% to < 50% agriculture), (3) low agriculture (10% to < 30% agriculture) and (4) very-low agriculture (< 10% agriculture). As per our predictions for the filtering and random assembly hypotheses, classifying amount of agriculture in this way allowed us to compare (1) if landscapes with more agriculture have higher similarity in their communities and (2) if similarity between communities declines as landscapes differ more strongly in the amount of agriculture.

Avian community

Our analysis focused on species that are found within forested landscapes but included species that breed in forest, forest-edge and shrubby wooded habitats at finer patch scales. These assignments were based on the State of Canada's Birds (NABCI 2012) combined with information from the Birds of North America (Rodewald 2018). Hereafter we refer to this group as the 'forest bird community' although associations with continuous forest vary within the group. The study region also includes avian species that breed in open grassland and agricultural habitats (e.g. see Wilson et al. 2017); however, we excluded these species from our analysis because our objective was to use forest birds as a model to test hypotheses on community similarity when agriculture extends into a naturally forested ecosystem. We also excluded four non-native species from this analysis.

We categorized species by three categorical guilds (migratory status, diet, foraging strata) as well as size (body mass) to examine how guild association influenced response to the expansion of agriculture and any resulting effects on functional diversity. Migratory guild designations included resident, short-distance migrant and Neotropical migrant based on descriptions of the wintering range from the Birds of North

America (Rodewald 2018) and eBird distribution maps (eBird 2018). Species were defined as residents if there was no directional change in their breeding and winter distributions. Short-distance migrants were species where the winter distribution lies south of the breeding distribution, but where the majority of the species distribution is north of the Tropic of Cancer in all seasons. Neotropical migrants were those species that breed in Canada and primarily over-winter south of the Tropic of Cancer including the Caribbean (Hagan and Johnston 1992). In cases of species with both migratory and resident populations, we used the Birds of North America (Rodewald 2018) to classify them based on the migratory status of the populations breeding within our study region.

Diet and foraging strata were based on information in Elton Traits 1.0 (Wilman et al. 2014) and the Birds of North America (Rodewald 2018). Diet guild categories were assigned based on the majority diet in Wilman et al. (2014) and included vertebrates (hereafter 'carnivore'), insectivore, nectarivore, frugivore, granivore, herbivore and omnivore (defined as species that consumed a mixed diet that included vertebrates and/or scavenging). Foraging strata included four categories based on the location where the majority of food is obtained: aerial (including aerial foragers and hawkers), bark forager, foliage gleaner and ground gleaner. Many species are not restricted to a single diet or foraging strata guild but the assignments used represented the majority diet or strata for that species across the annual cycle. Finally, we obtained estimates of average mass for each species (Sibley 2000). Guild assignments and body mass for all species are included in Appendix Table A2.

Statistical analyses

Influence of proportion agriculture and distance between transects on community similarity

To test our predictions for the *filtering* versus *random assembly* hypotheses, we first estimated the community similarity between all pairs of transects. We then grouped all pairs of transects into the ten possible pairwise combinations of the four agriculture categories (VL–VL, L–L, M–M, H–H, VL–L, VL–M, VL–H, L–M, L–H, and M–H). This allowed us to determine (i) whether similarity increased with increasing agriculture amount and (ii) whether

community similarity declined with increasing difference in amount of agriculture between landscape pairs. We did this at each of the three spatial extents for agriculture amount, i.e. within 1 km, 3 km and 5 km of the transects.

Pairwise community similarity was estimated using a method developed by Chase et al. (2011), which examines whether community composition differs from that expected if communities are randomly assembled from a given pool of available species (i.e., a null modelling approach). A null distribution of community assemblages was created by randomly drawing species from the regional species pool (γ diversity), with each species having a probability of being drawn that is equal to its proportional abundance. The number of species drawn for each transect was determined by its observed alpha diversity, where alpha diversity refers to the number of species on each transect. Gamma diversity refers to the total diversity of the entire study region shown in Fig. 1. We then calculated Raup-Crick (RC) dissimilarity values (Raup and Crick 1979) between each pair of transects and compared the dissimilarity value to the null distribution to yield a score between -1 and 1 (referred to herein as dissimilarity scores). A low negative value for a given pair of transects indicates that the communities on the two transects were more *similar* than expected based on the null distribution, whereas a high positive value indicates that the communities on the two transects were more *dissimilar* than expected by chance. A value of zero indicates the communities from the two transects could have been randomly drawn from the regional species pool. This procedure resulted in 26,107 comparisons between transect pairs.

Using the Raup-Crick dissimilarity scores we then tested for differences among the 10 pairwise combinations of agriculture (above) on forest bird community assembly. We included distance between transects to control for its effect on community dissimilarity. To avoid using all 26,107 transect pairs for statistical analysis we randomly selected 200 pairs from each of the ten pairwise combinations of agriculture (e.g. H–H, H–M, etc.), determined at the largest spatial scale. This resulted in a sample size of 2000 transect pairs (7.7% of all transect pairs). The agriculture category that a transect falls within can change with the scale over which land cover is measured and therefore while the overall sample size

remained the same, the number of transect pairs in each of the 10 pairwise combinations of agriculture was not exactly 200 at the 1 km and 3 km scales. Because the Raup-Crick scores are bounded between − 1 and 1, we first normalized the scores to fall between 0 and 1 and then used a beta regression (Cribari-Neto and Zeileis 2010) to examine support, based on AIC model selection, of the effects of agriculture combination at the three spatial scales and distance between transects, on community dissimilarity between transects. The pairwise agriculture combinations were treated as a categorical variable where each pair of transects fell into one of the 10 pairwise combinations as described above. Geographic distance between the two transects was included as a continuous variable.

Influence of amount of agriculture on guild abundance, species richness and functional diversity

To compare how amount of agriculture influenced abundance across migratory status, diet, foraging strata, and size, we first calculated the abundance of all guilds on each transect. These abundances were then used to calculate the average percent of total abundance represented by each of the guilds in landscapes with high, moderate, low and very low agriculture. For example, a Neotropical migrant estimate of 60% in very low agriculture would mean that on average 60% of the total avian abundance on transects in landscapes with < 10% agriculture are Neotropical migrants.

We estimated forest bird functional diversity using Petchey and Gaston's FD (2002, 2006), which estimates functional diversity as the total branch length of a functional dendrogram of species traits and has been used elsewhere as a measure of functional diversity in response to agricultural intensification (Flynn et al. 2009; Karp et al. 2012). As our data included categorical and continuous species traits, the estimation of Petchey and Gaston's FD first required us to calculate a Gower distance matrix followed by a hierarchical cluster analysis on the matrix using UPGMA (unweighted pair-group method with unweighted mean, Petchey and Gaston 2006; Podani and Schmera 2006). Analyses of functional diversity were performed with the vegan package (Oksanen et al. 2019) in R version 3.6.0 (R Core Team 2017).

We used a linear model to examine the relationship between proportion agriculture and both species richness and functional diversity and we tested a linear and a curvilinear fit to the data in each case. Support for an effect of agriculture on species richness and functional diversity was determined based on a drop in AIC relative to the intercept-only model without proportion agriculture. We then compared the percent decline in functional diversity versus species richness in high, moderate and low agriculture landscapes relative to landscapes with very low agriculture.

Results

The proportion of agriculture across landscapes averaged 0.305 ± 0.018 at the 1 km scale (range 0–0.931), 0.282 ± 0.018 at the 3 km scale (0–0.902) and 0.274 ± 0.017 at the 5 km scale (range 0–0.879). The proportion of agricultural land and forest cover were highly negatively correlated with $r = - 0.86$ and $p < 0.001$ at all three scales (Table A3, Fig A1). The BBS data consisted of 110,626 individuals of 110 species of forest and forest-edge birds (residents: 12,664 individuals, 26 species; short-distance migrants: 65,220 individuals, 33 species; Neotropical migrants: 32,742 individuals, 51 species). The community was well sampled across the study region with 95% of the species detected with coverage of any random selection of 42% of the transects and > 99% of species detected with random selection of any 79% of the transects (Fig A2).

Influence of agriculture on forest bird community similarity

Mean Raup-Crick dissimilarity scores were $- 0.66 \pm 0.01$ indicating that on average, forest bird communities were considerably more similar than expected at random. Our results provide strong support for the *filtering hypothesis* where communities were more similar than expected by chance for transect pairs whose landscapes both had high or moderate amounts of agriculture (mean RC dissimilarity = − 0.97 and − 0.92 respectively) in comparison to pairs whose landscapes both had low or very low amounts of agriculture (mean RC dissimilarity = − 0.66 and − 0.72 respectively) (Fig. 2;
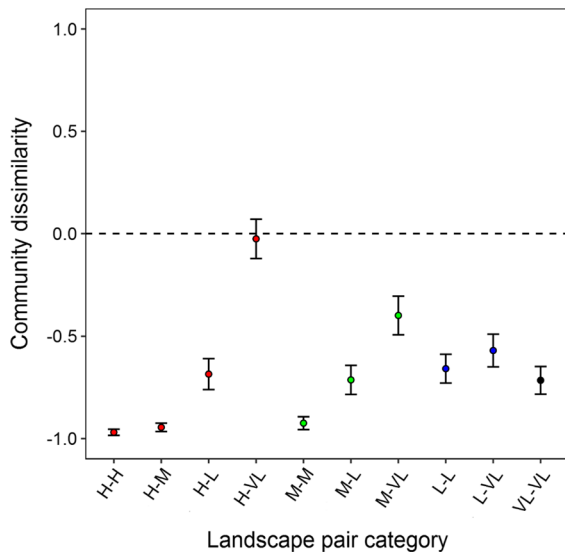
Fig. 2 Raup-Crick dissimilarity of the forest bird communities. Each value is the mean (95% CI in brackets) Raup-Crick dissimilarity for transect pairs in each of 10 pairwise combinations of agriculture categories. Within a pairwise combination, the two transects in each pair are surrounded by the two indicated categories of proportion agriculture within a 5 km buffer: H = high ($\geq 50\%$ agriculture in the landscape), M = moderate (30% to < 50%), L = low (10% to < 30%), VL = very low (< 10%). For example, the H–L value is the mean RC dissimilarity for transect pairs where one transect in the pair was surrounded by a landscape with high agriculture amount and the other with low agriculture amount. RC values that are low and negative, and high and positive, respectively, indicate transect pairs where the bird communities were more similar or less similar than expected if assembled randomly from the available gamma diversity and species abundances across all transects, constrained to the observed alpha diversity for the given transect. Colours distinguish the comparison of a category against each category with equal or lower agriculture amount. Each comparison was based on n = 200 pairs

Table 1). Consistent with our predictions for the filtering hypothesis, we also found the highest dissimilarity between transects in pairs whose landscape categories differed most in amount of agriculture (Fig. 2). The amount of agriculture at the largest 5 km scale (~ 180 km^2 landscape) around each transect pair better explained the influence of agriculture on community similarity than the finer 3 km (~ 84 km^2) and 1 km (~ 20 km^2) buffers (AIC of the 5 km model = 32.9 and 65.0 units lower than the 3 km and 1 km models respectively, Table 1). However, model coefficients for the effect of agriculture were very similar at all three scales (Table A4).

Table 1 Influence of surrounding agriculture and distance between sample transects on Raup-Crick dissimilarity of forest bird communities

Model	K	ΔAIC	w_i	pseudo R^2
Agriculture (180)[a] + distance^2	13	0.0	1.00	0.37
Agriculture (84) + distance^2	13	23.0	0.00	0.36
Agriculture (180) + distance	12	30.9	0.00	0.36
Agriculture (20) + distance^2	13	54.7	0.00	0.34
Agriculture (180)	11	156.5	0.00	0.27
Agriculture (84)	11	189.4	0.00	0.26
Agriculture (20)	11	221.5	0.00	0.23
Distance.sq	4	400.5	0.00	0.09
Distance	3	405.7	0.00	0.09
Null	2	513.2	0.00	0.00

Surrounding agriculture is a categorical variable with pairwise combinations of high ($\geq 50\%$ agriculture in the landscape), moderate (30% to < 50%), low (10% to < 30%) and very low (< 10%) agriculture amount for the landscapes surrounding the two transects in each transect pair. Analyses were conducted using beta regression and models are ranked based on Akaike's Information Criterion. Distance^2 and distance respectively refer to quadratic and linear effects of distance between transects on Raup-Crick dissimilarity

[a]Numbers in brackets refer to the landscape scale at which agriculture was measured around transects (5 km buffer = 180 km^2, 3 km buffer = 84 km^2 or 1 km buffer = 20 km^2)

Influence of distance between transects on forest bird community similarity

We found that community dissimilarity was also influenced by the distance between two transects and that a model containing a curvilinear distance effect was better supported than a model with a linear distance effect (30.9 AIC units lower, Table 1). Dissimilarity increased with distance up to about a 200 km separation between transects and then remained similar at a dissimilarity of about -0.5 to -0.7 for distances between 200 and 800 km (Fig. 3). Beyond 800 km the communities were as dissimilar as expected if randomly assembled. The pseudo R^2 from models with only the effects of the pairwise combination of agriculture categories explained approximately three times more of the variance in community dissimilarity than distance between transects (Table 1), suggesting community similarity between landscapes is more strongly driven by the amount of
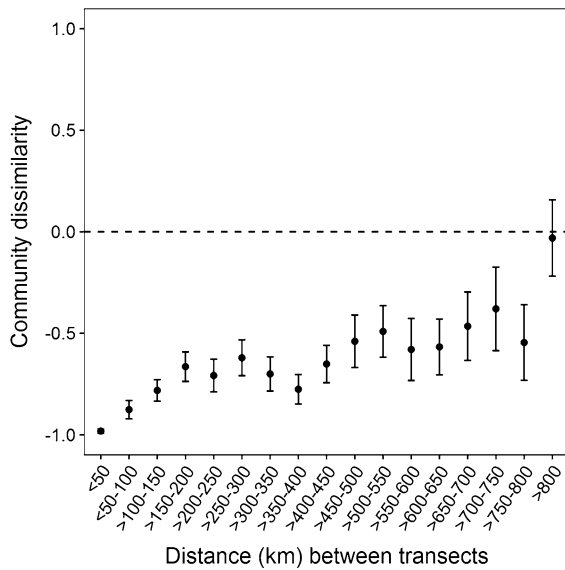
Fig. 3 Raup-Crick community dissimilarity (mean and 95% CI) of the forest bird communities in eastern Canada in relation to the distance between sample transects. Low, negative and high, positive values respectively indicate transect pairs where the bird communities are more similar or less similar than expected if assembled randomly from the available gamma diversity and species abundances across all transects, constrained to the observed alpha diversity for the given transect

agriculture than the geographic distance between them.

Influence of agriculture on guild abundance, species richness and functional diversity

As the amount of agriculture in the landscape increased there was a decrease in the proportion of the community represented by Neotropical migrants and insectivores, as predicted, along with foliage gleaners and bark foragers. With increasing agriculture, we observed an increase in short-distance migrants and granivores as predicted, although their abundance peaked at moderate amounts of agriculture (30–50%), before declining slightly when agriculture exceeded 50% of the landscape (Table 2). The proportion of the community represented by omnivores and ground gleaners also increased with higher agricultural coverage (Table 2). Finally, we observed an increase in the average abundance-weighted mass of individuals with higher amounts of agriculture indicating that abundance of small species declined as agriculture increased (Table 3).

The species richness of forest birds declined in a curvilinear manner with increasing proportion agriculture ($\hat{\beta}_{ag} = -2.99 \pm 7.10$ (SE), $\hat{\beta}_{ag^2} = -20.62 \pm 9.63$, Table 3; Fig. 4). The AIC values of the quadratic and linear models respectively for species richness versus proportion agriculture were 62.66 and 60.06 units lower than the intercept-only model. Forest bird functional diversity on transects declined similarly with increasing proportion of agriculture in the landscape and the relationship again was best explained by a quadratic model ($\hat{\beta}_{ag} = 0.99 \pm 0.68$ (SE), $\hat{\beta}_{ag^2} = -2.51 \pm 0.93$, Table 3; Fig. 4). The AIC of the quadratic and linear models respectively were 15.78 and 12.95 units lower than the intercept-only model. While both species richness and functional diversity declined in a curvilinear manner, the shape of the decline differed. Species richness declined immediately with increasing proportion of agriculture whereas functional diversity initially increased with agriculture, peaked at 20% coverage and did not decline strongly until agriculture exceeded more than 40% of the landscape. This pattern supported our prediction that when guilds most susceptible to agriculture are species rich, functional diversity will decline more slowly than species richness as the amount of agriculture in the landscape increases (Table 3; Fig. 4).

Discussion

Our study highlights the importance of the extent of agricultural land cover as a factor shaping avian communities across broad geographic scales. We focused on two hypotheses for how community similarity between landscape pairs varies with changing agricultural cover. Of these hypotheses, we found convincing support for the *filtering hypothesis*. The expansion of agriculture resulted in a filtering towards more similar forest bird communities in landscape pairs with high agriculture (and low forest) cover, largely due to the decline in richness and abundance of particular guilds (Neotropical migrants, insectivores, foliage gleaners, and smaller-bodied species). Moreover, while similarity also declined as the distance between transects increased, the influence of the amount of surrounding agriculture explained more of the variance in community similarity. Our study shows

Table 2 Average abundance of each migratory, diet and foraging strata guild on transects in relation to the four agricultural categories: high (≥ 50% agriculture in the landscape), moderate (30% to < 50%), low (10% to < 30%), very low (< 10%)

Guild	High	Moderate	Low	Very low
Migratory status				
Neotropical	15.28 ± 1.15	26.91 ± 2.62	36.43 ± 2.92	46.26 ± 1.64
Short-distance	53.39 ± 1.87	55.71 ± 2.80	51.29 ± 3.33	40.10 ± 1.69
Resident	25.19 ± 1.50	29.96 ± 1.37	29.34 ± 1.68	23.46 ± 1.12
Diet				
Carnivore	0.11 ± 0.02	0.11 ± 0.03	0.09 ± 0.02	0.09 ± 0.02
Frugivore	1.99 ± 0.31	2.75 ± 0.32	2.91 ± 0.43	1.83 ± 0.20
Nectarivore	0.02 ± 0.01	0.04 ± 0.01	0.11 ± 0.04	0.12 ± 0.03
Granivore	30.73 ± 1.27	30.89 ± 1.66	28.68 ± 2.10	20.12 ± 0.92
Herbivore	0.78 ± 0.18	0.70 ± 0.19	0.66 ± 0.18	0.19 ± 0.05
Insectivore	34.22 ± 1.50	51.02 ± 3.41	60.32 ± 4.03	70.83 ± 2.23
Omnivore	26.01 ± 1.77	27.09 ± 1.26	24.26 ± 1.49	16.65 ± 0.97
Foraging strata				
Aerial	2.54 ± 0.25	3.60 ± 0.35	4.15 ± 0.52	2.53 ± 0.19
Bark Forager	0.88 ± 0.12	2.31 ± 0.26	3.40 ± 0.35	5.51 ± 0.34
Foliage Gleaner	19.95 ± 1.38	29.25 ± 2.24	36.31 ± 3.16	40.48 ± 1.27
Ground Gleaner	70.50 ± 2.45	77.42 ± 3.63	73.19 ± 3.70	61.31 ± 2.24

Values are the mean and SE across the 229 transects

Table 3 Total community abundance (mean ± SE), species richness, functional diversity (Petchey and Gaston's FD) and abundance weighted mean mass along transects in landscapes with high (≥ 50% agriculture in the landscape), moderate (30% to < 50%), low (10% to < 30%) and very low (< 10%) agriculture

Measure	High	Moderate	Low	Very low
Abundance	93.23 ± 3.21	112.78 ± 5.41	117.91 ± 6.56	111.04 ± 3.05
Species richness	30.84 ± 1.07	38.51 ± 1.28	41.56 ± 1.19	42.35 ± 0.90
Functional diversity	5.59 ± 0.11	6.10 ± 0.11	6.20 ± 0.11	6.10 ± 0.09
Weighted mass (g)	163.58 ± 11.05	144.94 ± 9.64	135.27 ± 8.76	91.72 ± 3.84
Δ Species richness	− 27.18	− 9.07	− 1.87	–
Δ Functional diversity	− 8.36	0	1.63	–

Values for Δspecies richness and Δfunctional diversity are the % percent change in each measure in the respective agricultural category relative to that in very low agriculture

the homogenizing influence of agriculture across one of the broadest geographical regions assessed to date.

Studies of change in community composition across large regions of tens to hundreds of kilometres are rare, in large part due to the logistical difficulties of sampling over such broad areas. We overcame this challenge by integrating citizen science data with remotely sensed measures of land cover. Our results mostly complement other broad-scale studies showing community homogenization of forest biodiversity in areas of intensive land-use. In Costa Rica, Karp et al. (2012) found that intensive agriculture created similar vegetation communities at between-ecoregion scales,

which resulted in high similarity in the avian community and reduced the positive effect of distance on beta diversity typically observed in tropical forests in the region. In the Atlantic Forest in Brazil, Vallejos et al. (2016), who also used citizen science data, showed a directional shift of the avian community towards disturbance-tolerant species along a gradient from mostly natural to rural to urban sites. Studies of other taxa, including plants in North America and Europe (Vellend et al. 2007) and lepidopterans in Finland (Ekroos et al. 2010), show similar patterns of community homogenization with increasing land-use intensity. While these studies and ours point to the
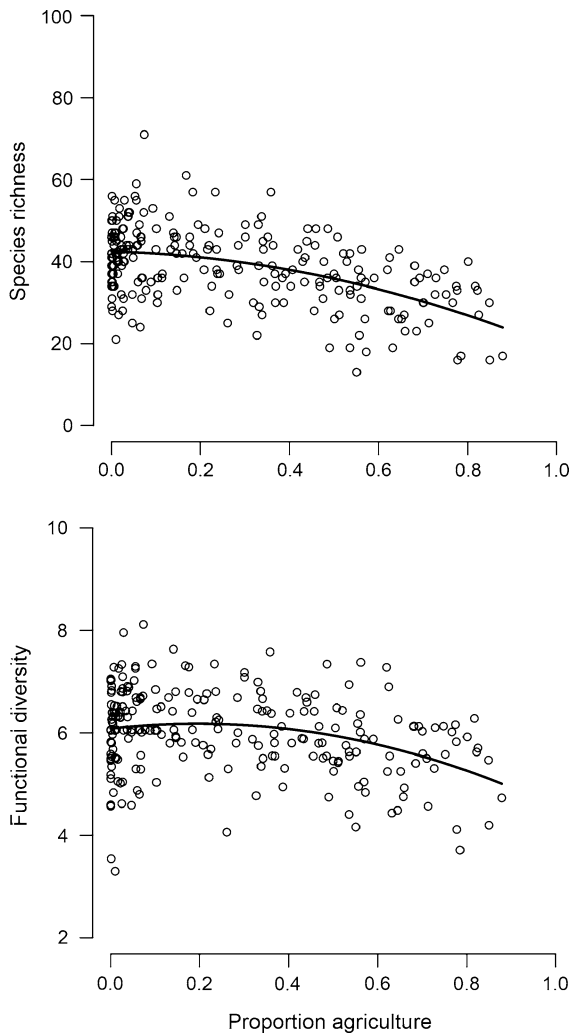
Fig. 4 Forest bird species richness (top panel) and functional diversity (bottom panel) in relation to proportion of agriculture across landscapes in eastern Canada. Proportion of agriculture is measured at a 5 km buffer around each side of an 8 km Breeding Bird Survey transect resulting in a 180 km² landscape. Functional diversity is based on Petchey and Gaston's FD (2006)

important role of agriculture in shaping community composition, these responses are not universally observed. In a study in southwestern France, Baselga et al. (2015) examined temporal turnover of the local bird community over a 26-year period in relation to agricultural land cover change. They found little evidence that community similarity was impacted by the increasing extent of agricultural land cover over time, and suggested that stochastic processes related to how species populations appear and disappear in an

area were more important in determining local community assemblage changes over time.

While agriculture was a stronger determinant of community composition than distance between communities, we still found that transects that were closer together had more similar communities. This influence of distance was evident up to about 200 km after which there was little change in the relationship between distance and similarity. Model comparisons showed a significant influence of distance even after controlling for the influence of surrounding agriculture and thus the effect was not simply an artefact of homogeneity of the community in intensive agricultural areas. Dispersal limitation may be one reason for this effect of distance on community similarity (Nekola and White 1999; Pomara et al. 2013). Previous estimates for North American birds, including many of those in our study, indicate natal and dispersal distances are often in the 0 to 100 km range (Tittler et al. 2008; Martin and Fahrig 2018), although they can be in the order of hundreds of kilometers for some species (e.g. Rushing et al. 2015; Wilson et al. 2018a). Our results of decreasing similarity with distance up to 200 km potentially indicate a dispersal influence within this range but further study would be needed to conclude this with certainty. At large distances, factors such as environmental tolerance or the availability of suitable habitat may also influence species abundance (Brown 1984; Pulliam 2000) resulting in lower community similarity.

While the forest-to-agriculture gradient resulted in strong similarity among transects with similar proportions of surrounding agriculture, it is important to note that communities were never more dissimilar than expected by chance, regardless of the amount of agriculture in their respective landscapes. This suggests only a partial turnover of the community with more extensive agriculture. Specifically, as the extent of agriculture increased, we observed a decline in insectivorous, foliage-gleaning, small-bodied Neotropical migrants, which accounted for nearly a third of all species and represented a greater proportion of the avian community in more heavily forested landscapes. In contrast, there was less variation across the agricultural gradient on average for larger-bodied species, short-distance migrant and resident guilds, granivores, omnivores and ground gleaners. Several abundant short-distance migrants or residents were present across all or nearly all transects indicating a broad tolerance to the degree of openness

created by agriculture (e.g. American robin *Turdus migratorius*—100% of transects, American crow *Corvus brachyrynchos*—100%, chipping sparrow *Spizella passerina*—98%, song sparrow *Melospiza melodia*—98%, black-capped chickadee *Poecile atricapillus*—97%). The presence of these species in our study likely explains why communities were always more similar than expected by chance, even when their surrounding landscapes differed strongly in amount of forest and agricultural land cover.

Earlier studies have shown the variability among species within forest bird communities in their response to differing extent of forest loss and the degree of patch isolation created by it (Lynch and Whigham 1984; van Dorp and Opdam 1987; Suarez-Rubio et al. 2013). Our results are similar to a recent analysis using eBird data in eastern North America showing that in comparison with resident and short-distance migrants, Neotropical migrants show the strongest associations with forest cover and the least variation in land cover diversity during the breeding period (Zuckerberg et al. 2016). Also similar to our results, Schmiegelow et al. (1997) and Hobson and Bayne (2000) found that in boreal western Canada, Neotropical migrants were most abundant in contiguous forest, while short-distance migrants were more generalist in habitat use and less affected by forest loss. The stronger association of long-distance migrants with high-forest landscapes on the breeding grounds contrasts with patterns observed in the Neotropics where long-distance migrants are often common in semi-open and disturbed habitats compared to many resident species, which are more sensitive to disturbance (Petit et al. 1995; Zuckerberg et al. 2016).

Compared to short-distance migrants and residents, the Neotropical migrant guild represents a species rich group with low functional diversity. The vast majority of species in this guild are small foliage- or ground-gleaning insectivores with 75% of the species in the group and 35% of all species in the study represented by only three families with a Neotropical origin (Parulidae, Tyrannidae and Vireonidae). In contrast to Neotropical migrants, the short-distance migrant and resident guilds are more functionally diverse with fewer species per family and lower taxonomic relatedness among most species. This greater functional and taxonomic diversity combined with the generalist nature of several species (described above) results in a more even representation of short-distant migrant and

resident species across the forest-to-agriculture gradient with a decline in abundance only apparent in agriculture-dominant landscapes. Because short-distance migrants and residents remain within North America year round, a possibility for this pattern is that a greater flexibility in diet and habitat use allows them to use multiple resources even when the insect base is low or unavailable in winter. The majority of these species are granivores, herbivores or omnivores but also forage on insects when available.

The fact that insectivorous Neotropical migrants are species rich and respond most negatively to agriculture has both an ecological and a practical implication for our results. Ecologically, the high species richness of insectivorous Neotropical migrants resulted in a pattern where functional diversity declined more slowly than species richness as the amount of agriculture increased. Where as species richness declined with any increase in agriculture, functional diversity did not decline until the amount of agriculture in the landscape exceeded approximately 40%. Moreover, functional diversity was higher in landscapes with 10–30% agriculture than it was in landscapes with < 10% agriculture. An important caveat to this result is that the measure of functional diversity is dependent on how species are assigned to guilds and there are likely finer-scale differences in the functional roles for the foliage-gleaning, insectivorous Neotropical migrants in our study region. As an example, some Parulidae are specialists of spruce budworm and have an important role in regulating budworm abundance (Crawford and Jennings 1989); their loss from the landscape may not be equally compensated by other foliage-gleaning insectivores in this functional group. A practical implication of the high Neotropical migrant species richness is that it makes it challenging to separate which guild association most influenced the observed change in community composition. In other words, because such a high proportion of foliage gleaners and insectivores are from the Neotropical migrant guild, it is difficult to conclude on the independent effects of forest loss for agriculture on each guild independently. Further studies could examine guild level responses to agriculture with a balanced sample of species from the different migratory guilds to test how diet and foraging strata influence susceptibility to the expansion of agriculture.

While we observed a decline in foliage-gleaning insectivorous Neotropical migrants in landscapes comprised of more agricultural land cover, it is possible that this result is further amplified by the influence of wintering ground habitat loss. Populations of many Neotropical migrants have declined in recent decades and growing evidence suggests that for many species, the cause of the decline is habitat loss on the non-breeding grounds (Jones et al. 2004; Kramer et al. 2018; Wilson et al. 2018b). Proportionately greater non-breeding-ground habitat loss could result in a broad surplus of breeding-ground habitat such that populations occupy the most favorable conditions in an area (i.e. highly forested sites) even if they might use more open agricultural landscapes when population abundances are greater. This effect would also contribute to the pattern that we observed.

From a conservation perspective, we found the lowest similarity in the forest bird communities and the highest functional diversity in landscapes with 10–30% agriculture rather than those with < 10% agriculture. Our results suggest that this is because the 10–30% range allows for species that are found in continuous forest as well as those that favour partially open landscapes. Community homogenization with a drop in functional diversity and strong declines in species richness occurred when agriculture represented more than half of the land cover, with insectivorous, foliage-gleaning Neotropical migrants in particular showing the most negative response to increasing agriculture. Of the three migratory guilds, Neotropical migrants are undergoing the strongest long-term population declines (NABCI 2012). Maintaining landscape-scale forest cover above 50% and ideally above the 70% range combined with conservation initiatives on the non-breeding grounds would help support this guild. The retention of linear woody habitats (e.g. riparian strips and hedge rows, Wilson et al. 2017) and reforestation on abandoned land are two planning strategies to promote greater landscape level forest cover in the more agriculturally intensive parts of the study region.

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