Multi-scale habitat selection of land cover proportion by farmland birds in Ontario

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Modern agriculture is a central driver in species declines, and its harmonization with conservation is critical to achieving social and ecological sustainability. Due to agricultural land occupation and reduction of native vegetation covers, species like migratory birds use remaining habitats within agricultural landscapes to complete their life cycles. The consequent decrease in vital ecosystem functions linked to biodiversity (e.g., pollination, pest control) has prompted scientists and land managers to design strategies that benefit production and conservation. However, variation in species' perception of landscape fragmentation across agricultural areas makes difficult the delineation of favourable landscape attributes in agricultural systems. Species can interact with environmental factors at varying spatial and temporal scales, with highly context-dependent outcomes. Here, I aim to quantify farmland birds' selection of home range's location (i.e., Second order selection) based on the proportion of six land covers (Tame grass, Native grass, Trees, Shrubs, Developed) measured at five spatial scales of varying extent: 200m, 400m, 800m, 1600m and 3200m radii. I address the questions 1) Do farmland birds in Southern Ontario select land cover proportion in the local landscape as a habitat cue? 2) Do scales selected by farmland birds in the local landscape differ according to their degree of specialization? And 3) How is the distribution of farmland birds that use local-landscape cover proportion as a habitat cue in Ontario? Using bird occurrence data from North America's Breeding Birds Surveys (BBS) between 2014 and 2019 and landcover data from Ontario's Annual crop inventory (ACI), Resource Selection Functions (RSF) were built for farmland birds in Ontario. I applied a semioptimized modelling approach to determine the scales within farmland birds' perceived changes in land cover proportion and composition, making inferences on their plausible causes and management implications. Results indicate that multiple species select or avoid habitats using

landscape-level cues at varying scales below 800m and above 1600m radii. Farmland birds' multi-scale selection also seems to differ between generalists and specialists, with specialists selecting landcover proportion at smaller scales (i.e., >800m radii) and generalists at both smaller and large scales (<200m and >1600m radii). These patterns contrasted with species preferences indicated that selection for landcover proportion at scales below the 800m radius could be associated with patch-level attributes and above the 1600m radius with landscape-level attributes. Moreover, prediction surfaces built from species top models showed that highly selected locations for farmland generalists and specialists concentrated between Western and Central Ontario were larger grasslands and varying landscape composition favour specialist and generalist occurrence. However, the extension of areas where multiple species concur on their occurrence was low compared to groups' mean occurrence, implying that there is not an exclusive landscape structure that favours all species. In order to improve the availability of attractive habitats for farmland birds, I suggest that rather than defining a top landscape structure, scientists and managers need to work together to determine multiple landscape arrangements adjusted to the availability of relevant factors like grassland proportion.

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Dedication

This thesis is dedicated to my best friend and life partner, Jose, whose company and support during my studies gave me the strength to not give up despite adversity. I will be forever grateful to God for having you in my life.

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Chapter 1: Introduction

Historically, Southern Ontario has been a highly biodiverse region that, ironically, now has one of the lowest capacities to support wildlife populations (Environment and Climate Change Canada, 2019). As part of the Great-Lakes St.-Lawrence Forest ecozones, it is an important location for multiple migratory and resident species, but also, it is one of Canada's most productive agricultural areas, given its high soil fertility (Environment Canada 2014). Agricultural development in Southern Ontario since the 1920s has considerably reduced species habitats in exchange for increased livelihood production. As a result, drastic declines in biodiversity have altered the delivery of essential ecosystem services to agriculture (e.g. pollination, pest control and fodder production), affecting farmers' economy and natural resources stewardship (Ekroos et al. 2016). The detrimental effects of biodiversity loss threaten both productive and ecological systems functioning. Therefore, managing production and conservation trade-offs have become vital to building sustainable socio-ecological systems (Landis 2017).

Birds have been used as indicators of agriculture's ecological impacts due to their high sensitivity to land use changes and association with pest control and pollination. In North America, birds have exhibited accelerated declines (Stanton et al. 2018; NABCI 2019). For instance, grassland birds in Canada have shown a population decline of 57% since 1970 and require urgent conservation actions (NABCI 2019). Loss and fragmentation of native vegetation covers by agricultural processes is a primary cause of birds' and other organisms' declines (Fahrig 2003; Haddad et al. 2015; De Camargo et al. 2018; Gardiner et al. 2018). Ontario provincial government has implemented strategies to protect the remaining native covers of great ecological value while regulating surrounding agricultural uses, like the Natural heritage system (NHS) and the Greater Golden Horseshoe Greenbelt Plan (GGHG). However, native habitats for

open-country birds (i.e., species that rely on low or sparse vegetation covers) are extremely scarce in Ontario, making these species in dire need of alternative conservation actions to address threats like population isolation and climate change (Kremen and Merenlender 2018)

A potential strategy to support open-country birds' conservation in Ontario involves harmonizing conservation and production activities (Davis et al. 2013). As remaining habitats for open-country birds are scarce and primarily located within private lands (Lovett et al. 2003), some species are actively relying on agricultural covers as habitats to complete their life cycles and are considered by some as "farmland birds" (Kirk et al. 2020). Agroecosystems can still support sufficient habitat cover and congruency to allow farmland birds to use available resources and conditions. Nonetheless, agricultural covers possess attributes with counterproductive effects on species persistence, like landscape fragmentation. As a result of farming processes, native vegetation covers are reduced and subdivided. In contrast, productive covers (i.e., crops and pastures) increase with considerable variation in their size and distribution according to farmers' agricultural practices. Landscape ecology studies have found that patchlevel attributes (i.e. single covers size or shape) and landscape-level attributes (i.e. multiple covers configuration and composition) of both native and productive covers influence birds' habitat selection (Carvajal et al. 2018; Reiley and Benson 2019; Bueno and Peres 2019). However, species can exhibit varying, even contradictory, responses to landscape attributes in fragmented landscapes (Fletcher et al. 2018a; Fahrig et al. 2019). This stalls the proper characterization of species preferences in agricultural landscapes, suggesting the need for a better comprehension of species' perception of their habitats in agricultural landscapes (Miller-Rushing et al., 2019).

A key trait that can cause variation in species responses to landscape attributes is their interaction with environmental attributes across varying spatial and temporal scales (Wiens 1989). Species not only respond to changes in the quality of their immediate habitats but can be affected by the spatial characteristics of neighbouring habitats and non-habitat areas ('the landscape matrix') (Kremen and Merenlender 2018). Given the vast extent of agricultural regions, determining at what scales their attributes are influencing species habitats selection (also known as scales of effect) is vital for researchers to make proper inferences on species landscape responses and have accurate information to work with stakeholders in the development of management practices (Jackson and Fahrig 2015, McGarigal et al. 2016). This is especially notorious for birds, which can respond to landscape changes occurring at large distances from their breeding location (Whitaker and Warkentin 2010). Moreover, fragmentation effects are not comparable among agricultural regions as differences in habitat and matrix covers amounts might cause varying inter and intraspecific responses (Betts et al. 2006; Concepción and Díaz 2011). Species- and location-specific strategies are required but obtaining representative data to make accurate inferences about agricultural impacts on multiple species is logistically demanding and time-consuming. As a primary step to address these obstacles for farmland birds' research in Southern Ontario, my thesis addressed how birds may respond to ('select') differing amounts of land cover at different scales. I did this by developing Resource Selection Functions (RSF) for farmland bird species that are likely to be responsive indicators of agricultural impacts in Ontario (Kirk et al. 2020).

Chapter 2: Literature review

2.1. Conservation and Sustainability

Agriculture and its modernization have caused one of the most extended processes of ecosystem transformation. In exchange for higher crops and timber yields, ecosystems have been modified into highly intensive-use systems with simplified ecological and environmental attributes (Tscharntke et al. 2005). Improvements in livelihood production have allowed some countries to achieve stable food production. However, agriculture reduces the availability of resources and conditions required by species. When species populations and communities are drastically reduced, ecosystems lose their capacity to resist disturbances (Kay et al. 1999; Walker and Salt 2012) and might not provide essential services for livelihoods production like pollination, erosion control and fodder production. The loss of essential ecosystems and species processes can cause considerable yields reduction and costs increase, affecting livelihoods production in the long term (Cardinale et al. 2012; Duncan et al. 2015).

Regarding the agricultures-biodiversity dilemma, some researchers have suggested that some agriculture and biodiversity trade-offs can be managed by establishing "operational limits" between production and conservation purposes (Davis et al. 2013; Landis 2017). This implies improving our understanding of what conditions favour the persistence of ecosystem and species processes on agricultural systems and to what extent agricultural systems can be adjusted.

Despite agriculture's adverse effects on biodiversity, many species use or reside in agricultural systems (Boutin et al. 1999; Askins et al. 2007). From an ecological perspective, the key to agriculture and biodiversity harmonization relies on the potential of agricultural lands as supplementary species habitats. Conflicting findings on species interactions with agricultural transformation patterns arise from knowledge gaps on species habitat attributes within

agricultural lands. One of these aspects of the conflict is landscape fragmentation, one of agriculture's more significant impacts on wildlife habitats, which is highly variable across agricultural systems worldwide.

2.2. Wildlife habitats and landscape fragmentation.

Natural land covers are frequently reduced, divided, and isolated as agricultural land covers increase. Agricultural changes in vegetation patches attributes (e.g., size, isolation, shape) and landscape attributes (i.e. amount, heterogeneity, connectivity) affect wildlife habitats and key spatial dynamics through a complex process known as habitat fragmentation (Fischer and Lindenmayer 2007; Biswas and Wagner 2012). During this process, species habitats associated with vegetation cover decrease in size as they are subdivided into multiple habitat patches with distinct degrees of isolation (Haila 2002; Fahrig 2003). Habitat fragmentation often reduces species richness and species persistence through the reduction in habitat size (Haddad et al. 2017), edge contrast increase (Pfeifer et al. 2017) and connectivity loss (Horváth et al. 2019). Although fragmentation effects are pervasive at the patch scale, this can be contradicted by studies at the landscape scale, where habitat fragmentation does not always lead to biodiversity loss. Species richness increases or is stabilized in landscapes with high compositional diversity (Fahrig et al. 2011) and the use of networks of small habitat patches by threatened species (May et al. 2019). Contrasting findings on fragmentation effects have generated a debate about habitat fragmentation effects and their implications for promoting conservation on highly fragmented landscapes.

Based on species richness response to landscape fragmentation, one path may be to separate the effects of habitat heterogeneity or "Habitat fragmentation" from those of habitat amount or "Habitat loss" (Fahrig 2003; Hanski 2015). Decreases in habitat amount are inherently

pervasive to species persistence due to species-area relationships (Ribic et al. 2009). By comparison, changes in the configuration (i.e. covers spatial arrangement) and composition (i.e. covers diversity) of habitat components can positively or negatively affect species persistence through multiple mechanisms (Hanski and Ovaskainen 2000; Hanski 2015; Geertsema et al. 2016). For instance, while increasing patch isolation and edge contrast are detrimental to species richness due to connectivity loss and predation increase, covers diversity and subdivision can be beneficial through mechanisms like habitat complementation and risk spread (Fahrig 2017; Fahrig et al. 2019). These counteracting mechanisms derived from habitat fragmentation per se have led researchers to re-evaluate the conservation value of fragmented landscapes.

Large and undivided patches can be of higher conservation value if the assumption of equal or stronger pervasive effects of habitat fragmentation than habitat loss on biodiversity (Ewers and Didham 2005). However, if habitat fragmentation per se has weaker or more positive effects than habitat loss, it would be possible for a broader set of landscape settings to support species conservation according to their amount of habitat (Fahrig 2013). These are critical premises for conservation debates like the "Single Larger or Several Small" (SLOSS), which focuses on protected areas' establishment, or the land-sparing vs. land-sharing debate on agricultural landscape management (Fischer et al. 2013). Thus, understanding the influence of habitat loss and fragmentation per se has become vital for managing remaining natural land covers in fragmented landscapes. Multiple studies have assessed the relative influence of habitat fragmentation per se relative to habitat amount, but findings have shown highly variable and context-dependent patterns. For instance, studies on multiple taxa responses to fragmentation have found support for the dominance of habitat amount effects (Fahrig 2017; De Camargo et al. 2018), fragmentation per se (Haddad et al. 2015) and their combined effect (Cerezo et al. 2011;

Santana et al. 2017). Agreement on habitat loss and fragmentation per se relationships has not been reached (Fletcher et al. 2018a; Fahrig et al. 2019). However, researchers have identified multiple factors that interfere with assessing biodiversity responses to landscape fragmentation, including the omission of species and traits-specific responses to habitat fragmentation (Ewers and Didham 2005) and the scale-dependent nature of species habitat interactions (Whittaker et al. 2001; Jackson and Fahrig 2015).

Species' habitat diversity influences the debate surrounding landscape fragmentation's effects on biodiversity (Geertsema et al. 2016; Cong et al. 2016). Most of the theoretical background of landscape fragmentation research has relied on species richness and density measurements (i.e. pattern-based approaches) which might overlook species differences in habitat suitability (Jarzyna and Jetz 2016; Ke et al. 2018). Species are bound to exhibit variable responses to landscape fragmentation because of what constitutes suitable and accessible habitats for each of them (Fischer and Lindenmayer 2007). Habitat suitability is defined by a species' fundamental niche - the complete set of environmental and ecological factors that favour species growth based on unique functional traits and evolutive history (Vandermeer 1972; Soberón 2007). Conflicting responses to landscape fragmentation might emerge if niche differences are not accounted for in land cover studies. For example, an inappropriate distinction of patches and the surrounding dominant cover (also known as the matrix) might result in contradictory edge effects if species with low dispersal and energy use capabilities are contrasted with species that can use the matrix as a secondary habitat (Pfeifer et al. 2017).

In addition to niche identity, the scale-dependence of species habitats is a critical attribute that dictates fragmentation effects on biodiversity within species niche differentiation (Wiens 1989). A scale refers to the spatiotemporal limits where mechanisms or processes occur,

characterized by its extent (overall spatiotemporal range) and grain (finest spatiotemporal unit; Turner and Gardner 2015). As environmental factors are spatially and temporally structured, ecological processes defining species selection and use of available habitats can occur at different scales (Wiens 1989; Levin 1992; Whittaker et al. 2001). For instance, species might differ in the amount of space they occupy, how much they move or disperse, or within what time they reproduce (Addicott et al. 1987; Turner and Gardner 2015). Moreover, biodiversity patterns result from multiple ecological processes emerging from biotic organization levels (i.e., Individuals, populations, communities) that interact with environmental attributes at distinct scales. For example, while a species individual occupies a given amount of space, the population to which that individual belongs occupies a higher amount of space resulting from the aggregation of all individuals' territories. As environmental attributes like landscape structure vary non-linearly with scale, inferences on fragmentation effects must distinguish species responses to the same resource or condition at different scales to avoid inconsistencies (Whittaker et al. 2001).

Addressing interspecific niche differences is critical to interpret landscape fragmentation effects and provide accurate information to land managers (Dennis and Dyck 2003; Tscharntke et al. 2012). As landscape fragmentation alters multiple processes at multiple scales, linking landscape patterns with processes conditioning species responses is complex (Riva and Nielsen 2020). A deeper understanding of species' perception of fragmented landscapes and their variation can improve researchers' capacity to link observed abundance and distribution patterns to relevant ecological processes (Fischer et al. 2013; Ekroos et al. 2016). This requires studies focusing on one or few species processes and assessing the capacity of their approaches to habitat characterization to distinguish species scale-dependent responses to fragmented

landscape attributes. Habitat characterization approaches can vary according to what type of biodiversity attribute or "state variable" is used (e.g., Distribution, Abundance, Dispersal, Demography) and the assumed process dominating biodiversity patterns (i.e. Selection, Dispersal, Drift). Within selection-based approaches, habitat selection is a primary framework for assessing species' habitats and their attributes at varying scales.

2.3. Species habitat selection and scale patterning.

Habitat selection is a behavioural process widely used to characterize species' habitat attributes. It is defined by a species' active choice of locations to balance favourable and unfavourable conditions in areas where habitats are heterogeneously distributed with inhospitable spaces (Beyer et al. 2010). Based on this process, it can be assumed that locations with high-quality habitats will be disproportionally selected for low-quality ones. Researchers can use this assumption to compare used and unused (or available) locations defined from observed species patterns (i.e. distribution or abundance). When locations and their resources are used disproportionately to their availability, species use is said to be selective and interpreted as an indicator of those locations' environmental factors as potential habitat attributes (Manly et al. 2002). However, it is important to discern selection from use implications on species' overall success (i.e., fitness). Selection does not imply that species' use of locations and resources has positive outcomes (e.g., breeding success, population growth); more detailed studies on species population and community processes with more informative state variables are required (e.g., Natality/Mortality rates, Colonization/Extinction rates)(Boyce et al. 2016). Habitat selection studies using species distribution and abundance patterns are an initial source of information to unravel habitat attributes in the face of logistical limitations on species data.

Scale influence was quickly noticed from analytical considerations on environmental factors measurement within habitat selection studies (Mayor et al. 2009). Researchers' definition of used and available resources is conditional upon spatial and temporal limits because grain and extent changes can affect the heterogeneity of environmental attributes measured (Johnson 1980; Whittaker et al. 2001). If species do not respond continually to environmental changes across scales, these might be responding to regions or "domains" across the scale spectrum within limiting environmental factors are stable until a transition to other domains' factors is reached (Wiens 1989). Thus, identifying at what scales species are discerning resource availability is crucial for identifying selected environmental factors and avoiding analytical bias (Meyer and Thuiller 2006). Inspired by the hierarchy theory and the spatiotemporal structure of environmental factors and ecological patterns (Whittaker et al. 2001; Chase et al. 2018), researchers developed frameworks that organized species patterns according to their spatiotemporal attributes.

For wildlife studies of habitat selection, Johnson's (1980) orders of selection are the most widely adopted frameworks to study scaling patterns from a species perspective. This framework differentiates four spatial selection levels or "orders" according to behavioural differences in species territorial and dispersal patterns: Selection of geographical ranges (First order), Selection of home-ranges (Second order), Selection of feeding/nesting sites (Third Order) and Selection of feeding/nesting items (Fourth Order). Selection orders help recognize species' selection of habitat attributes at distinct scales, each potentially involving distinctive processes and selection outcomes that allow species to overcome limiting factors (Rettie and Messier 2000). However, selection orders do not explicitly define the precise scales to which species might select habitat attributes (Wheatley and Johnson 2009; Mayor et al. 2009). To avoid the arbitrary definition of

scales, Addicot (1987) suggested that selection scales must be delineated by the areas and times where ecological processes occur or "ecological neighbourhoods." Population and community processes along organisms' life cycle (e.g., foraging, breeding, competition) can alter an organism's perception of its environment, making species respond to environmental factors at multiple scales, even within the same selection order (Holland and Yang 2016). Therefore, Johson's selection orders are a standard guide to discriminating potential scales domains but require researchers to define relevant scales according to the spatiotemporal structure of both environmental and ecological processes.

Recognition that both environmental and ecological heterogeneity causes species to require multiple ecological neighbourhoods led to establishing the "multi-scale paradigm":

- 1. Selection processes can occur at multiple domains or levels at unique ranges of scales according to species and individuals' perceptions (Holland et al. 2004).
- 2. There is no correct scale to study species habitat selection as this might differ in each ecological and environmental context (Levin 1992).

One implication is that species responses to a habitat attribute might vary between selection orders as habitats' patchiness might vary across scales. Second, depending on relevant selection orders and species traits, the relative size and structure of habitat units might differ from what researchers observed as environmental units. A proper characterization of species-selected habitats requires defining relevant orders and their scales of effect (Meyer and Thuiller 2006; Jackson and Fahrig 2015). However, defining relevant scales of selection is complex for orders with highly variable boundaries and unknown limits like the geographic or home range

selection orders. This defines one of the main issues with scaling that habitat fragmentation studies need to address.

2.4. Home range habitat selection by birds

Within animals' hierarchical process of habitat selection, home range selection is likely influenced by landscape attributes at varying scales. A home range is defined as a stationary temporal area within which individuals travel across to perform activities like foraging, mating, and nesting (Rolando 2002). Many animals restrict their movement within a home range to satisfy energetic requirements and address competitive and reproductive pressures (i.e., inbreeding avoidance) (Sutherland et al. 2000; Börger et al. 2008). Animals' home range selection results from two phases: a prospective and settling stage. Animals disperse across accessible areas in search of suitable habitats, gathering information about habitat availability and quality based on direct factors (e.g., food availability, predators' presence) and indirect factors (e.g., Habitat type and structure). Then, based on gathered information, animals increase the time they spend in neighbouring locations with potentially good quality habitats, reducing their movement as they redirect energy and time from dispersal into other activities. Differences in animals' movement and interactions among their prospective and settling stages during their home range selection manifest in species responses to environmental factors at distinct scales.

Landscape structure can influence the location and size of animals' home ranges by modulating dispersal among locations and indirectly indicating habitat attributes like food availability and predation risk (Rolando 2002; Börger et al. 2008). For instance, some forest birds reduce their movement across forest gaps despite its energy-wise benefits, possibly linked to their perception of predation risk (Boesing et al. 2018). Due to the extent and variation of landscape fragmentation in agricultural regions, animals display diverse home range selection

patterns linked to changes in their access and perception of available habitats (Dale et al. 2006). Understanding how the location and size of animals' home ranges vary among fragmented landscapes is critical to identify where and how landscape structure can be managed to harmonize conservation and agriculture. For example, knowing at what spatial scales endangered species perceived critical changes in landscape structure might improve the coordination of landscape-level and patch-level strategies (Ekroos et al. 2016). However, delimiting the influence of landscape fragmentation is complex due to the plausible interaction of animals with multiple covers at varying scales, especially for highly mobile animals like birds.

Flying birds present unique attributes and challenges in the characterization of landscape fragmentation impacts on their home range selection. First, birds can interact with landscape attributes at large spatial extents within shorter periods of time compared to other organisms (Whitaker and Warkentin 2010). For instance, Dale et al. (2006) found that the Ortolan bunting, a widely distributed farmland bird in Europe, moved up to 43 km between singing and breeding territories. Large dispersal movement might imply that birds have considerably large perceptual ranges and could respond to landscape changes up to their maximum dispersal distance.

However, detection of relevant spatial scales of effect is highly dependent on the temporal boundaries within birds' selection processes are study (Börger et al. 2008; Whitaker and Warkentin 2010). Birds can interact with landscape attributes from a daily perspective according to the nature of their prospective movements (e.g., Soaring vs flapping) or larger according to their mapping memory (i.e., memorized information about habitat structure). Thus, birds can exhibit wide differences in their selection scale, and researchers' sampling capacity heavily limits their detection.

Second, birds can interact with multiple landscape attributes at varying scales within their breeding season (Whitaker and Warkentin 2010). Traditionally, it was considered that most birds would fairly limit their movement within their home range, and some species limit it further to their breeding or nesting territories (Rolando 2002). This perspective led some researchers to use single scales to delimit species landscape interactions during their home range selection.

However, studies on intra-seasonal movement have shown that birds can display highly variable movement patterns during their breeding season. For instance, (Williams and Boyle 2018) found that the Grasshopper sparrow, a grassland bird that breeds in U.S and Canada prairies, had interpatch movements reaching up to 9 km of distance from their breeding ground. Although less frequent than within-home range movements, larger dispersal movements during the breeding season have been associated with prospective foraging activities (possibly to explore new territories) and search for extra-pair copulations. This could imply that birds respond to habitat attributes at varying spatial scales above their home range, with potentially vital implications for their fitness (Miguet et al. 2016).

Improving our knowledge of the dynamic and variable nature of birds' (and likely other organisms') home ranges is key to comprehending the impacts of landscape fragmentation.

Researchers have found that birds can alter their movement and selection behaviours according to the landscape context (Olden et al. 2004; Chalfoun and Schmidt 2012; Schmidt et al. 2015), which could be involved with their response to multiple landscape attributes at varying scales.

Understanding this variation could contribute to developing management strategies which adjustable features according to species context-specific limitations (Hortal et al. 2015).

2.5. Research Objective and Questions

The objective of this thesis is to improve the understanding of farmland birds' habitat attributes by quantifying their selection for the proportion of six land covers (Tame grass, Native grass, Trees, Shrubs, Developed) at five scales with varying extents (12 ha, 50 ha, 200 ha, 800 ha and 3125 ha) associated with their local-landscape home range selection (i.e. second order of selection) in Southern Ontario. The research presented aims to answer the following questions:

- 1) Do farmland birds in Southern Ontario select land covers proportion in the local landscape as a habitat cue? And if they do, what land covers are these species selecting or avoiding? At what scales?
- 2) Do scales selected by farmland birds in the local landscape differ according to their degree of specialization? If they do, how do selected scales differ between specialists and generalists?
- 3) How are the habitats of farmland birds selecting land covers proportion at the local landscape distributed in Southern Ontario?

Understanding the environmental attributes making agroecosystems attractive for species as habitats is vital to help managers and stakeholders develop strategies that support both productive and conservation endeavours. Studies in avian species multi-scale selection in agroecosystems have shown that relevant scales of selection at the local-landscape levels are highly variable across agricultural regions, which can interfere with the detection and interpretation of habitat fragmentation effects. As a primary step to address these obstacles for farmland bird management in Southern Ontario, this research addresses important questions

about their local-landscape habitat selection using selection models, which can offer essential information to interpret the effects of agroecosystems fragmentation on avian species. This study will also contribute to delimiting the distribution of farmland bird habitats in Southern Ontario according to their resource selection functions (RSF) at the local landscape level, which can assist with planning conservation actions and future research.

Chapter 3: Methods

3.1. Study Area

The study area comprises the most developed portion of Ontario, which I limited using the boundaries of the Bird Conservation Region (BCR) number 13 (Figure 1). This region holds a critical ecozone known as the Great lakes mixed wood plains, which owns one-third of Canada's biodiversity, as well as 56% of Canada's most arable land (Epp and Caldwell 2018).

Furthermore, this area encompasses a total extension of 84700 km2 and holds one of Canada's fast-growing populations (Environment Canada 2014). In terms of land covers composition, the BCR13 is dominated by agricultural covers (60%), followed by natural covers (32 %) and developed covers (8%) (Environment Canada 2014). Agricultural covers in Southern Ontario consist primarily of Corn, Soybean, Hay, Oilseed, cereal grains, and seeded pastures. Natural covers consist of forest and grasslands relicts from the Great Lakes-St. Lawrence ecozones, a region with mixed wood forests, wetlands, and shrublands that connected the boreal forests with the southern deciduous forests (Dickinson and Royer 2014).

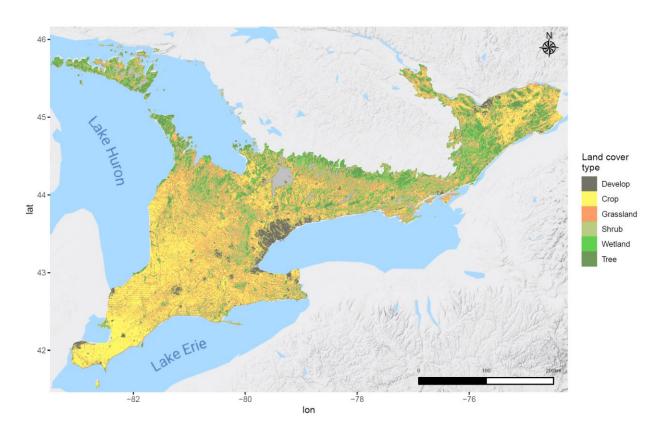


Figure 1. Landcover map of the BCR 13 of Canada. This map was created from the Agricultural Crop Inventory (AAFC) by reclassifying available covers into seven broader land covers.

The BCR13 possesses three characteristics that make it an ideal area for studying habitat selection patterns at the landscape level in farmland birds. Firstly, the Southern part of Ontario presents a temporally and spatially extended predominance of agricultural cover over natural covers (Blancher et al. 2009), with no significant changes in forested and agricultural cover proportion during the last 50 years (Pond 2009). Secondly, this region presents a gradient of natural covers fragmentation ideal for studying the influence of varying covers amounts at multiple scales (Pasher et al. 2013). For example, in terms of agriculture cover proportion, cropland area increases while tame pastures decrease from the North to the South (Ontario Partners in Flight 2008). Finally, its current levels of fragmentation have reduced the opportunities to establish large conservation areas and will not change significantly because of the importance of livelihood production (Enviroment Canada 2014). Thus, in agriculture-

dominated regions, farming policies and management actions on has a considerable impact on the avian biodiversity of the whole region.

3.2. Species occurrence data

Species associated with agricultural landscapes in Southern Ontario were defined based on the proposed list by Kirk et al. 2020. This list was developed using experts' opinions and scientific literature, then statistically classified into five potential guilds according to species preferences in agricultural habitat: row crop specialists (RCS), pastures specialists (PSS), farmstead specialists (FSS), farmland edge generalists (FEG). Occurrence datasets for these species were developed from the annual Breeding Bird Survey (BBS), extended roadside surveys conducted in North America since 1966 (Robbins et al. 1989). In these surveys, observers carry standardized 3-minute point counts along set routes. Each route comprises 50 stops with a separation distance of 800 m for a total length of 39.4 km. These data have been widely used to develop distribution models and assess species population trends (Sauer et al. 2017). BBS counts were retrieved using the File Transfer Protocol (FTP) site from the United States Geological Surveys (USGS), using the R function "fetch bbs data" from the package "bbsbayes."

Available BBS counts were filtered and georeferenced according to this study's taxonomic and geographic requirements. First, BBS counts were screened to the species listed as farmland birds and sampled between 2013-2019 within the BCR13 region. Then, the filtered BBS dataset was georeferenced using BBS coordinates at the stop level provided by the Canadian Wildlife Services (CWS). This was necessary as BBS counts from the USGS are georeferenced by each surveyed route centroid, reducing BBS data representation of species patterns at small landscape scales. Within the BCR 13, data for 2881 stops part of 58 distinct routes were obtained. However, some of these routes have changed during the period selected for

logistic and security reasons. Only stops whose locations have not changed during the study period were kept (Figure 2). A total of 54 farmland species were found to have count records on the BBS data set. All data filtering and georeferencing were done using the packages "tidyverse" and "sf" in the R software (R Core Team 2022).

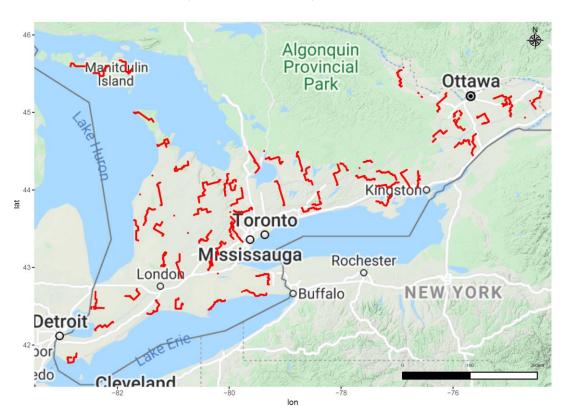


Figure 2. Map showing the surveyed routes by the BBS initiative between 2013 and 2019 in the BCR 13 of Canada. Each route is displayed in red. A total of 78 routes and 2881 stops were sampled between 2013 and 2019.

Next, species occurrence datasets were developed for each species by turning counts into presence/absence datasets. For each stop, species detected more than once between 2013 - 2019 were assigned a value of 1 (present) or 0 (absence) otherwise. Then, the detection ratio for each species was estimated by dividing their number of occurrences over the total number of stops surveyed. Only species detected in more than 5% of the stops were considered for developing species distribution models (Table 1).

Table 1. Estimated detection ratio for farmland bird species from the occurrence dataset generated using the BBS counts from 2013-2019 in the BCR13.

Common name	Species code	Latin name	Guild	Present	Absent	Detection
American Crow	AMCR	Corvus brachyrhynchos	FG	2506	375	0.87
American Goldfinch	AMGO	Spinus tristis	FG	1979	902	0.69
American Robin	AMRO	Turdus migratorius	FG	2751	130	0.95
Baltimore Oriole	BAOR	Icterus galbula	FG	916	1965	0.32
Barn Swallow	BARS	Hirundo rustica	FSS	1167	1714	0.41
Blue Jay	BLJA	Cyanocitta cristata	FG	1510	1371	0.52
Bobolink	BOBO	Dolichonyx oryzivorus	PSS	941	1940	0.33
Brown Thrasher	BRTH	Toxostoma rufum	FEG	741	2140	0.26
Brown-headed Cowbird	BRCO	Molothrus ater	FSS	1081	1800	0.38
Cedar Waxwing	CEDW	Bombycilla cedrorum	FG	1154	1727	0.4
Chipping Sparrow	CHSP	Spizella passerina	FEG	1941	940	0.67
Common Grackle	COGR	Quiscalus quiscula	FSS	2099	782	0.73
Common Yellowthroat	COYE	Geothlypis trichas	FEG	1640	1241	0.57
Eastern Bluebird	EABL	Sialia sialis	FEG	191	2690	0.07
Eastern Kingbird	EAKI	Tyrannus tyrannus	FEG	873	2008	0.3
Eastern Meadowlark	EAME	Sturnella magna	PSS	913	1968	0.32
Eastern Phoebe	EAPH	Sayornis phoebe	FEG	757	2124	0.26
Eastern Towhee	EATO	Pipilo erythrophthalmus	PSS	210	2671	0.07
European Starling	EUST	Sturnus vulgaris	FSS	1969	912	0.68
Field Sparrow	FISP	Spizella pusilla	FEG	436	2445	0.15
Great Crested Flycatcher	GCFL	Myiarchus crinitus	FEG	1051	1830	0.36
Horned Lark	HOLA	Eremophila alpestris	RCS	431	2450	0.15
House Sparrow	HOSP	Passer domesticus	FSS	685	2196	0.24
House Wren	HOWR	Troglodytes aedon	FSS	1350	1531	0.47
Indigo Bunting	INBU	Passerina cyanea	FEG	849	2032	0.29
Killdeer	KILL	Charadrius vociferus	RCS	1034	1847	0.36
Mallard	MALL	Anas platyrhynchos	FG	486	2395	0.17
Mourning Dove	MODO	Zenaida macroura	FSS	2237	644	0.78
Red-tailed Hawk	RTHA	Buteo jamaicensis	FG	188	2693	0.07
Red-winged Blackbird	RWBL	Agelaius phoeniceus	FEG	2417	464	0.84
Ring-billed Gull	RGBU	Larus delawarensis	FG	693	2188	0.24
Rock Pigeon	ROPI	Columba livia	FSS	520	2361	0.18
Savannah Sparrow	SASP	Passerculus sandwichensis	PSS	1336	1545	0.46
Song Sparrow	SOSP	Melospiza melodia	FEG	2595	286	0.9
Tree Swallow	TRES	Tachycineta bicolor	FSS	892	1989	0.31
Turkey Vulture	TUVU	Cathartes aura	FG	450	2431	0.16
Vesper Sparrow	VESP	Pooecetes gramineus	RCS	343	2538	0.12
Wild Turkey	WITU	Meleagris gallopavo	FG	542	2339	0.19

3.3. Landscape covariates

Covariates that reflected the proportion of each land cover surrounding each stop on the BBS routes were developed. Land cover data were obtained from the Annual Crop Inventory (ACI) created by Agriculture and Agri-Food Canada (AAFC, 2017-2019). The ACI data is a land-cover classification map provided as a raster layer with a 30x30m pixel resolution and 72 land-cover classes, derived from Landsat-8 optical imagery and RADARSAR-2 radar imagery from 2013 - 2019. This data was cropped to the extension of the BCR 13 and reclassified into broader cover classes frequently used to explore species responses to cover amounts (Table 2). As the proportion of cover in agricultural landscapes in Southern Ontario has not changed significantly during the last 50 years (Pond 2009), the measurement of landscape variables was fixed to 2016, assuming that summarization in that year is representative of land-cover composition during the study period. Land cover maps' reclassification, cropping and visualization were done using R packages "raster" and "rgdal."

Table 2. Table of land cover classes from the ACI data and their reclassified values corresponding to the landcover classes used in this study.

Land cover name	Description	ACI Class
Native grasses	Predominantly native grasses and other herbaceous vegetation, may include some shrubland cover.	110
Tames grasses	Periodically cultivated grasses. Includes tame grasses and other perennial crops such as alfalfa and clover grown alone or as mixtures for hay, pasture, or seed.	122
Grasslands	The combination of native and tame grasses	110, 122
Shrub	Predominantly woody vegetation of relatively low height (generally +/-2 Meters). May include grass or wetlands with woody vegetation, and regenerating forest.	50
Crop	Agricultural land, including annual and perennial crops, excluding grassland.	130 - 199

Tree	All treed areas comprising coniferous, broadleaf/deciduous, and mixed woodlands	200-230
Tree & Shrubs	The combination of shrub and tree	50, 200-230
Wetland	Land with a water table near/at/above the soil surface for enough time to promote wetland or aquatic processes (semi-permanent or permanent wetland vegetation, including fens, bogs, swamps, sloughs, marshes etc).	80
Developed	Land that predominantly built-up or developed, includes road surfaces, railway surfaces, buildings and paved surfaces, urban areas, etc.	34, 35

As species responses to landscape-level changes depended on the scale measured, the proportion of each cover classification was calculated using a focal site multi-scale approach (FSMS; Brennan et al. 2002). This approach uses windows of multiple sizes centred on a focal location to measure landscape attributes at various scales (Figure 3). Using each screened BBS stop as a focal location, covers proportions were computed using circular windows of the following radii: 200m (12 ha), 400m (50 ha), 800m (200 ha), 1600m (800 ha) and 3200m (3125 ha). These radii represent the potential scale at which species may select their habitat at the home-range level, and they were chosen based on previous studies' findings on the multi-scale habitat selection of birds (Shahan et al. 2017; Fedy et al. 2018; Lockhart and Koper 2018). All covariates (land covers proportion measured at a specific scale) were processed and standardized using R's package "exactextractr."

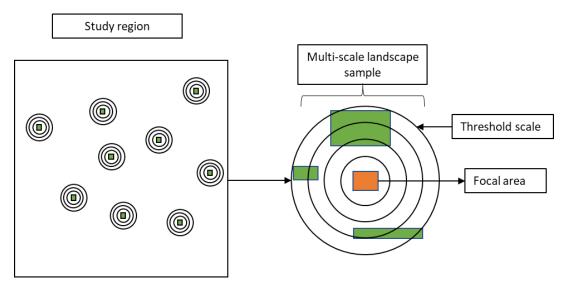


Figure 3. Example of a sampling unit on the focal site multi-scale approach. The focal areas correspond to the 30m pixels that concurred with the BBS stops' coordinates. Landscape metrics are measured using increasing windows sizes up to a threshold scale.

3.4. Resource selection functions

Occurrence and covariates data generated for farmland species within the BCR13 was used to develop resource selection functions. Resource units were defined according to the pixel size within habitat covariates were measured (30 x 30 m) and assigned use or unused based on species occurrence at sample points inside the study area. As BBS are censused during the breeding season and changes of land over amount during the study period are relatively low, a demographic and habitat pseudo-equilibrium were assumed. Thus, covariates selection was modelled using a generalized linear model (GLM) with a binomial link function for use/unused habitat units. All models were built using the "glm" function from the "stats" package in R.

3.4.1. Models' development and selection

Assuming that species interaction with landscapes covariates is stronger at specific scales (Miguet et al. 2016), each covariate selection was assessed independently through univariate

regression to identify the scale of effect (Pasher et al. 2013). All univariate models included an intercept-only model and were compared using Akaike's Information Criterion (AIC, (Burnham and Anderson 2002). When the intercept-only model outperformed a univariate model, the corresponding covariable was discarded. Then, each univariate model left was compared, and the scale of effect for each land cover was selected according to the univariate model with the lowest AIC value. Correlation levels between selected covariates were examined using Pearson's correlation index to avoid collinearity between remaining covariates. When two covariates exhibit a high correlation (r > |0.65|), the covariate with the lowest AIC was preserved for the development of subsequent models.

Using the top covariates by land cover, multivariate models were developed for each specie to predict the probability of use of sampled locations using the function "TrainGlm" from the package "enmSDM" (Morelli et al. 2020). All possible model combinations from each species' top covariates were considered, and top models were selected based on the AIC values < 2. Models' composition was explored among farmland birds by averaging all coefficients' effects in a heatmap and comparing each variable's marginal effects. Then, according to the covariates included in each species, prediction surfaces were developed for the BCR 13 region by creating a raster map for each covariate. Each species' probability of selection was predicted across the BCR13 using its matching set of raster covariates maps to identify the distribution of each farmland bird's suitable habitats in Southern Ontario.

3.4.2. Models and predictions validation

The performance of species top models was evaluated for each species using two validation approaches, the Receiver Operating Characteristic (ROC) and the Boyce validation index (i.e. k-fold validation) (Boyce et al. 2002). First, the specificity and sensitivity of models' predictions

were estimated at different classification thresholds to draw a ROC curve, and the Area Under the Curve (AUC) was interpreted as an estimate of each model's predictive power. Next, species occurrence datasets were partitioned into five random subsets (folds), and top models were iteratively fitted to training fold sets (i.e. 80% of the data). An RSF prediction surface was generated for each fitted model, and the area adjusted frequency of five RSF bins was calculated for the validation set (i.e. 20% of the data). These bins were created arbitrarily by dividing predicted probability values on equidistance probabilities ranges. Spearman rank correlation was calculated between each bin mid-value and area-adjusted frequencies, and the average Spearman correlation of fitted models was used to indicate the reliability of their predictions. A good model was considered to have AUC values above 60% and correlation values above 60% (Boyce et al. 2002; Fedy et al. 2018).

After identifying valid models, their RSF surfaces were assessed in search of the possibility of autocorrelation. Two methods were used to describe valid models' spatial patterns: Models' residuals mapping (Fedy et al. 2018) and Moran's I correlograms (Fletcher and Fortin 2018). Residuals' mapping is a qualitative approach to detect geographic patterns on models' prediction. Models residual were obtained from each model and plotted over the BCR 13 using R's package "ggplot" and the library "ggmap." On the other hand, Moran I correlograms is a quantitative approach that estimates Moran's I coefficients between sampled points pair as a function of increasing distances classes corresponding to the evaluated scales. Models' capacity to deal with spatial autocorrelation was assessed by comparing across-scales Moran's I estimations between species' intercept-only and top models' residuals. Correlograms were built using the R package "spdep" as illustrated by Fletcher and Fortin (Chapter 6, 2018).

Lastly, prediction surfaces built from validated models were combined to generate raster maps displaying each species' most important habitats within the BCR 13. An average RSF value was estimated for each pixel across the study area to examine species habitat selection as one guild. Also, a finer map was built by summarizing binary surfaces (0-1) of the habitat units with probability values belonging to the top 25% (Highest probability bin) for each species.

Chapter 4: Results

A total of 2881 point-count belonging to 71 BBS routes were used to analyze the multi-scale habitat selection of farmland birds recorded within the BCR 13 in Ontario. Models were built for a total of 38 species with enough detections (> 0.05) based on Kirk et al. 2020 suggested list of farmland birds (Table 1). On average, 150 model combinations were generated for each species, and only one was selected as the top model based on their Δ AICc values. Other models with an Δ AICc < 2 are listed in Appendix 1. Based on Spearman rank correlations and AUC values, top models' performance varied considerably among species (Figure 4). All models exhibited AUC values above 50%, but Spearman correlation values had a larger variation with a lowest average value of -0.74 (Eastern bluebird) and a highest of 1 (Eastern Meadowlark).

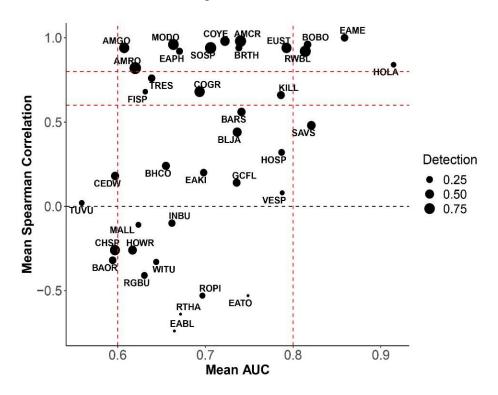


Figure 4. Plot contrasting each model mean Spearman correlation (Boyce Index) and Area Under de Curve (AUC) estimates. Each model performance was estimated according to its location with respect to each metric performance threshold, shown by dashed red lines. Only models above the performance threshold for both metrics were deemed valid. Species migratory status in Ontario and Population changes in Canada since 1970 are also shown in the table below. Species codes are shown in Table 1.

4.1. Model validation and spatial autocorrelation.

Models' performance was assessed using AUC and Spearman correlation values estimated through K-fold cross-validations. According to the selection criteria (AUC & Spear. Corr > 0.6), 17 species had good accuracy and were deemed as valid models, while 21 had all their models below the established criteria and, therefore, were deemed non-valid. Species with valid models are likely to select their habitats using land cover proportion at the local scale. Two valid models (FISP and TRES) were excluded because of the wide confidence intervals of their estimated AUC and Spear. Correlation values (Appendix 2 & 3). Therefore, a total of 15 models corresponded to species that likely selected land cover proportion at the local scales and were considered for further analysis. Among these species, 7 out of 15 were farmland specialists according to Kirk et al. classification (Table 3). Their detection at point-count locations varied from 15% to >70%, with the Horned Lark having the lowest detection and the American Crow the highest. This group included both migratory and year-round species, and species that have species little to larger decreases in their population size since 1970 (NABCI 2019).

Table 3. Farmland species from the BCR13 with valid models based on the Boyce Index correlation and AUC values. All species guilds suggested by Kirk et al. were included. Specialist guilds are highlighted in bold (Pasture specialist – PSS, Farmland Stead Specialist – FSS and Row Crop Specialist - RCS). Species migratory status in Ontario and Population changes in Canada since 1970 are also shown in the table below.

Common name	Code	Guild	$\overline{r_s}$	r _s CI	AUC	AUC CI	Mig. Stat.	Pop. change
American Crow	AMCR	FG	0.98	0.9-1	0.74	0.65-0.8	Year-round	Little change
American Goldfinch	AMGO	FG	0.94	0.8-1	0.61	0.58-0.67	Year-round	Little change
American Robin	AMRO	FG	0.82	0.7-0.9	0.62	0.51-0.82	Year-round	Little change
Bobolink	BOBO	PSS	0.96	0.9-1	0.82	0.74-0.87	Migratory	Large decrease
Brown Thrasher	BRTH	FEG	0.94	0.9-1	0.74	0.68-0.8	Migratory	Moderate decrease
Common Grackle	COGR	FSS	0.68	0.6-0.7	0.69	0.65-0.74	Year-round	Little change
Common Yellowthroat	COYE	FEG	0.98	0.9-1	0.72	0.66-0.76	Migratory	Moderate decrease
Eastern Meadowlark	EAME	PSS	1	1-1	0.86	0.78-0.89	Migratory	Large decrease
Eastern Phoebe	EAPH	FEG	0.92	0.7-1	0.67	0.62-0.71	Migratory	Little change
European Starling	EUST	FSS	0.94	0.9-1	0.79	0.76-0.86	Year-round	Large decrease
Horned Lark	HOLA	RCS	0.84	0.7-1	0.91	0.87-0.94	Year-round	Large decrease
Killdeer	KILL	RCS	0.66	0.6-0.7	0.79	0.74-0.82	Migratory	Large decrease
Mourning Dove	MODO	FSS	0.96	0.9-1	0.66	0.59-0.75	Year-round	Moderate increase
Red-winged Blackbird	RWBL	FEG	0.92	0.9-1	0.81	0.75-0.86	Migratory	Little change
Song Sparrow	SOSP	FEG	0.94	0.9-1	0.71	0.59-0.79	Year-round	Moderate decrease

With respect to models' levels of spatial autocorrelation, bubbles maps and correlograms displayed varying patterns among species (Appendix 1). Most models' residuals were randomly distributed on most species bubble maps. The absence of spatial patterns in models' residuals is a qualitative indicator of the absence of spatial correlation after the models' prediction. However, Moran's I correlograms show varying positive values of autocorrelation among species. This suggests that developed models are probably capturing exogenous factors influencing species distribution (i.e. environmental gradients) but that finer exogenous processes or endogenous processes are also influencing species distribution.

Across-scale Moran's I estimations varied among species, but all models displayed values above the zone of null spatial autocorrelation based on generated confidence interval from

normal approximations (Appendix 1). This indicates that all models presented significant autocorrelation values. Interestingly, most of the highest Moran's I values occurred at the 800m at 1600m scales, contrary to the expectation of the highest scale (i.e. 3200 m radii) exhibiting higher autocorrelation due to studied landscapes overlap (Table 4). The contrast between models and raw residuals (i.e. intercept only model) indicated differences in models' capacity to explain spatial data dependence. Some models were consistently better than the raw model, which can be interpreted as an indicator of how relevant models' covariates are to explain observed species' spatial patterns.

Table 4. Summary of validated models spatial correlograms based on Moran's I estimation. Mean Moran's I was estimated by averaging all scale values. The distance to the nearest confidence interval (CI) represents the distance of each scale Moran's I estimate from the zone of null spatial correlation. Bolded values correspond to those scales where spatial autocorrelation was stronger. Intercept and top models' differences in Moran's I estimations indicate top models' contribution to explaining spatial patterns relative to only-intercept models.

Negative values indicate those cases where the top models' contribution was higher than the intercept-only model.

							Difference between intercept					
			Distance to nearest CI				and top models					
		Mean	0.8	1.6	2.4	3.2	4	0.8	1.6	2.4	3.2	4
Code	Guild	Moran's I	km	km	km	km	km	km	km	km	km	km
AMCR	FG	0.28	0.19	0.28	0.27	0.26	0.2	-0.09	-0.06	-0.04	-0.04	-0.07
AMGO	FG	0.27	0.25	0.26	0.2	0.2	0.21	0	0	-0.01	0	0.01
AMRO	FG	0.23	0.27	0.17	0.25	0.02	0.23	0.12	0.06	0.11	-0.06	0.1
вово	PSS	0.13	0.1	0.13	0.08	0.08	0.09	-0.11	-0.08	-0.05	-0.04	-0.05
BRTH	FEG	0.12	0.1	0.09	0.11	0.06	0.04	-0.08	-0.12	-0.11	-0.11	-0.1
COGR	FSS	0.19	0.18	0.2	0.14	0.14	0.13	-0.03	-0.04	-0.04	-0.03	-0.03
COYE	FEG	0.19	0.14	0.22	0.16	0.12	0.14	-0.07	-0.08	-0.09	-0.08	-0.07
EAME	PSS	0.14	0.18	0.14	0.06	0.09	0.07	-0.15	-0.13	-0.15	-0.13	-0.13
EAPH	FEG	0.07	0.03	0.04	0	0.06	0.04	-0.06	-0.07	-0.07	-0.05	-0.05
EUST	FSS	0.16	0.15	0.12	0.12	0.08	0.11	-0.09	-0.08	-0.06	-0.06	-0.05
HOLA	RCS	0.14	0.11	0.08	0.11	0.13	0.08	-0.19	-0.29	-0.2	-0.19	-0.18
KILL	RCS	0.12	0.09	0.1	0.1	0.05	0.08	-0.1	-0.14	-0.12	-0.13	-0.12
MODO	FSS	0.24	0.19	0.22	0.21	0.2	0.21	-0.01	-0.02	0	0	0.01
RWBL	FEG	0.25	0.29	0.29	0.22	0.13	0.15	-0.03	-0.01	-0.03	-0.08	-0.04
SOSP	FEG	0.27	0.29	0.27	0.16	0.28	0.16	0.09	0.06	0.02	0.11	0.04

4.2. General models composition

From 135 univariate comparisons (15 species x 9 covariates), the intercept-only model outperformed eight models, leaving a total of 127 comparisons. Of these, the smallest and largest scales (200m and 3200m radii) were each selected 44 times (0.34%) as a covariate top scale, followed by the second smallest scale (400 m radius, 19%). However, by ranking each model's cover-scale combination based on AICc values, the top scale was 400 m radius for 7 out of 15 species models (47%) and 3200 m radius for 5 out of 15 (33%). High correlations among selected covariates occurred between combined and single land covers (i.e., grassland and tame grass) and between crop and tree-shrubs land proportions, with positive and negative correlation values, respectively. Other significant correlations (14 out of 19 pairs) were from covariates measured at the same scale (e.g. Tame-grass 200m vs Tame-grass 400m).

Top multi-scale models for each species included each covariate at its top scale (i.e. lowest AICc value) according to univariate comparisons (Table 5). Models' covariates varied considerably across selected species, and all but one top model (Hornet lark) included covariates at multiple scales (Appendix 1). Other valid models for the Hornet lark with an AICc < 2 included covariates at varying scales, but their coefficients' confidence intervals included zero. Most of the covariates included in the top models occurred at the smallest scale (200m radius, n = 23), followed by the largest scale (3200m radius, n = 21) and the 400m radius scale (n = 15). Overall, patterns of scale selection suggest that farmland birds use land cover proportion in the local landscape as a habitat cue at both small (≥ 400 m) and large scales (< 1600m).

Regarding land covers selection, covariates' standardized coefficients from multi-scale models suggest consistent effects across scales and few neutral values (i.e. $\beta = 0$). From the nine

land covers measured, six displayed positive coefficients and three negative coefficients across scales (Figure 6). Frequently include variables in the top models were developed (n = 13), grassland (n = 10), crop (n = 10), wetland (n = 8), shrub (n = 8) and tree (n = 7). No land cover was included in all top models (Table 5). Develop, grassland and shrub covers had a stable directionality (i.e. only positive o negative coefficients across scales). Tree, crop, and wetland covers exhibited directionality change at the smallest (Wetland) and the largest (tree and crop) scale. Grassland was the most selected cover while tree and developed were the most avoided. Overall, land covers selection patterns suggest that grassland proportion is a key habitat cue disregarding its alteration and that crop, shrub and wetland covers tend to favour locations' selection by farmland birds in the local landscape.

Table 5. List of valid top models (i.e., resources selection functions) for farmland birds that selected land cover proportion as a habitat cue during their home range selection in the BCR 13 in Ontario, Canada. Species predicted relative occurrence was interpreted as the probability of use of a location according to relevant land covers' proportion for each species.

Guild	Species code	Model
FEG	BRTH	use ~ 1 + Crop_3200m + Develop_3200m + Native_grass_200m + Shrub_800m + Tree_200m
FEG	COYE	use ~ 1 + Crop_1600m + Develop_3200m + Grassland_1600m + Shrub_3200m + Wetland_400m
FEG	ЕАРН	use ~ 1 + Grassland_200m + Tree_shrubs_3200m
FEG	RWBL	use ~ 1 + Crop_800m + Develop_200m + Grassland_200m + Native_grass_3200m + Shrub_200m + Tree_shrubs_400m
FEG	SOSP	use ~ 1 + Crop_200m + Develop_200m + Grassland_200m + Native_grass_200m + Tree_200m + Wetland_1600m
FG	AMCR	use ~ 1 + Crop_3200m + Develop_400m + Grassland_3200m + Shrub_1600m
FG	AMGO	use ~ 1 + Develop_800m + Shrub_3200m + Tame_grass_3200m
FG	AMRO	use ~ 1 + Develop_200m + Grassland_3200m + Native_grass_3200m + Tree_3200m + Wetland_3200m
FSS	COGR	use ~ 1 + Crop_1600m + Develop_400m + Grassland_200m + Tree_shrubs_400m + Wetland_3200m
FSS	EUST	use ~ 1 + Crop_400m + Develop_200m + Native_grass_200m + Shrub_200m + Tame_grass_400m + Tree_400m + Wetland_200m
FSS	MODO	use ~ 1 + Develop_200m + Grassland_3200m + Tree_3200m + Wetland_1600m
PSS	ВОВО	use ~ 1 + Develop_200m + Shrub_200m + Tame_grass_400m + Tree_200m + Wetland_200m
PSS	EAME	use ~ 1 + Crop_3200m + Develop_3200m + Grassland_400m + Shrub_3200m + Tree_200m
RCS	HOLA	use ~ 1 + Crop_400m
RCS	KILL	use ~ 1 + Crop_400m + Develop_400m + Grassland_3200m + Tree_shrubs_400m + Wetland_400m

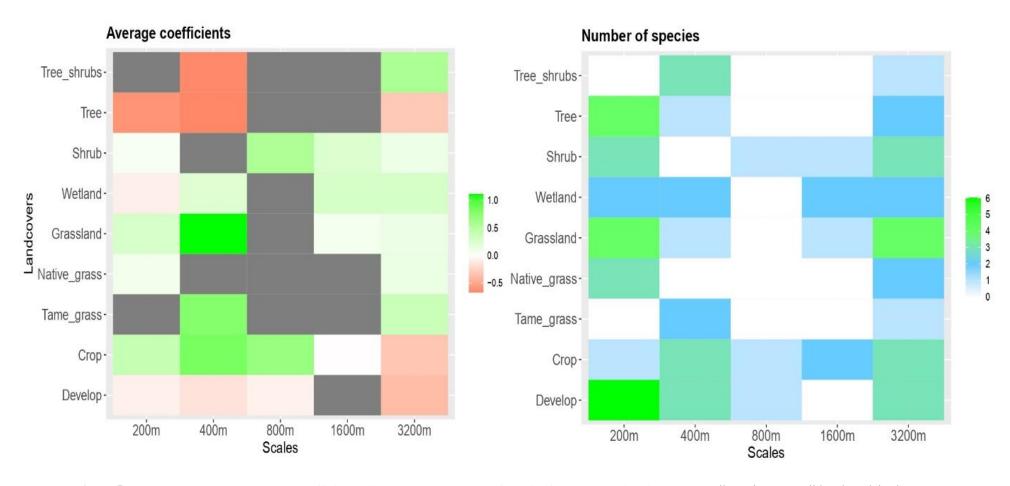


Figure 5. Heat map showing the average coefficient estimate and the number of species for each covariate included on all species' top validated model. The number of species indicates how many a covariate (landcover x scale combination) was included in a species' top model. If a variable was not included in a model, it was assigned a missing value.

4.3. Models' composition and species specialization degree.

According to farmland birds' specialization level, plausible differences in their overall model composition and potential association with species known ecology were noted. Contrasting the number of times each scale was included in a model (Figure 6) shows that specialists' models mainly included covariates measured below the 800m scale. On the other hand, generalists' models included covariates at the smallest and largest scales (200m and 3200m radii). These patterns suggest that farmland specialists who perceive local landscape attributes are primarily constrained by landscape changes at smaller window sizes than farmland generalists when defining their breeding habitats' location. Regarding land cover composition (Figure 7), generalists displayed a higher selection for shrubland, and wetland covers, while specialists displayed a higher selection for developing and crop covers. These patterns support the division of farmland birds into generalists and specialists suggested by Kirk et al. 2020. Therefore, models' composition and species ecology are explored further within generalists' and specialists' species and their respective guild level subdivisions.

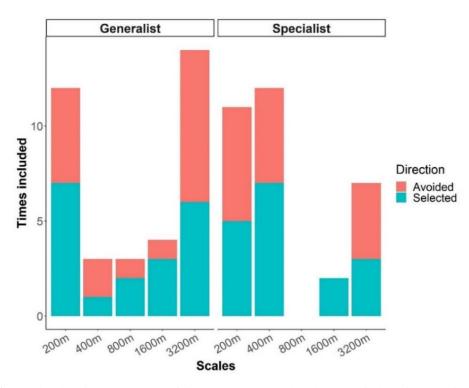


Figure 6. Bar plot showing the number of times each measured scale (I.e., window size) was included in a validated model between farmland generalists and specialists.

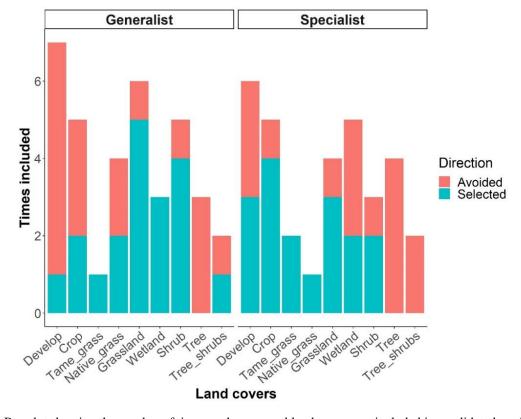


Figure 7. Bar plot showing the number of times each measured land cover was included in a validated model between farmland generalists and specialists.

4.3.1. Generalists' selection patterns

Regarding generalist farmland birds, covariates' coefficients from univariate models were stable across scales with only slight changes in their slope (Figure 8). For example, most generalists' slope for Wetland and Tree related covers became more positive as scale extent increased, while develop and crop covers became more negative. Nonetheless, few species displayed changes in the sign (+/-) of their covariates' coefficient values. Notably: The Brown Thrasher (Tree coefficients became positive above 800m radius), the Red-Winged Blackbird (Develop coefficients became positive at 3200m radius), the American Goldfinch (Shrub coefficients became negative above 200 m radius) and the American Robin (Wetland became positive above 400m radius). Only shrub and develop covers' coefficients from univariate models were consistently selected or avoided across scales

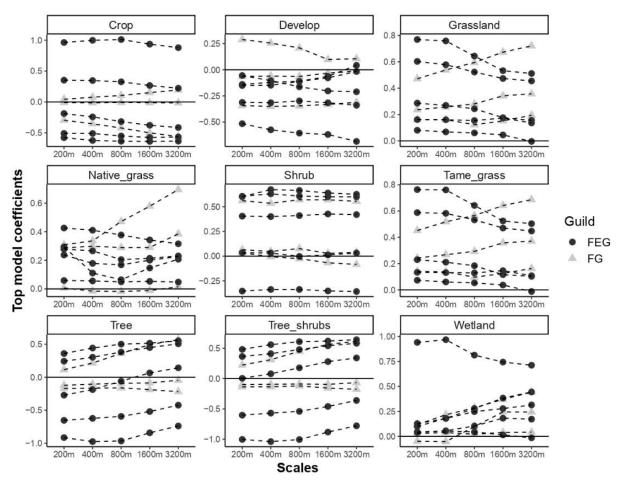


Figure 8. Cross-scale coefficient estimates from each land cover's univariate models for farmland generalist species with validated models. Sharp changes in coefficient values are a primary indicator of cross-scale interactions. Line type indicates species' guild-level classification.

In terms of how Generalist guilds' models varied, the divergence has higher on selected scales rather than on selected covers. Most farmland generalists and edge generalists selected grass-related covers except for the American Robin and the Song Sparrow, and most farmland generalists and edge generalists had a common avoidance of developed covers except for the American Robin (Figure 9). On the other hand, farmland generalists primarily selected land covers at the largest scales, while farmland edge generalists selected land covers proportion at both the lowest and largest scales. Covariates selected at scales below <800m and >1600m radii had a strong influence on generalists' selection (Table 6), but farmland generalist had more weak interactions with land cover proportion compared to farmland edge generalists

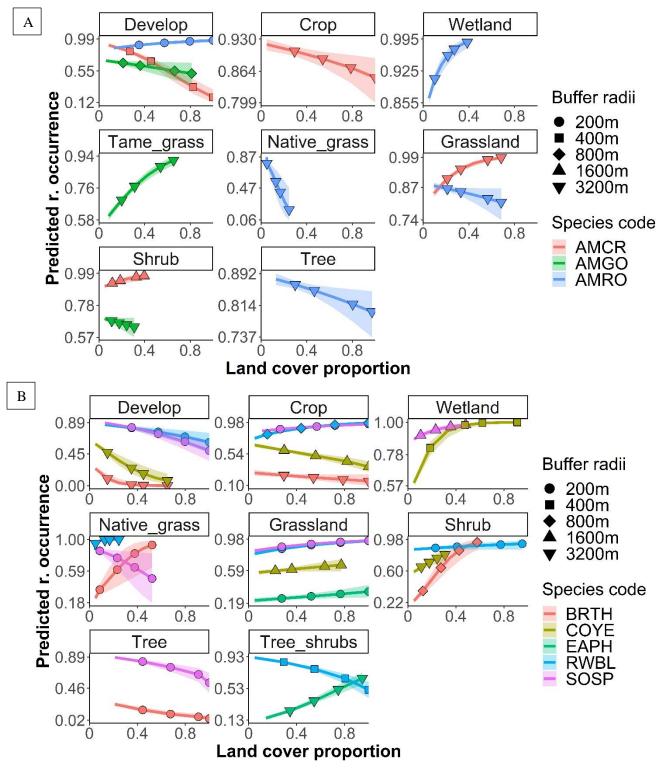


Figure 9. Marginal predicted effects of landcover proportion on the home range selection of A) farmland generalist and B) farmland edge generalist birds. Plots represent each species' occurrence probability as a response to each of the covariates included in their top model. Each line colour corresponds to one species, and points shapes correspond to the scale at which each predictor was selected or avoided.

Table 6. Covariables strength for generalist guilds' models based on the slope of each covariable marginal effect. Classification bins were assigned by dividing all slope is three quantiles: Weak ~ 0 - 0.33, Moderate ~ 0.33 - 0.66 and Strong ~ 0.6 - 0.99.

Code	Guild	Covariate	Slope	Effect Strength
AMCR	FG	Develop_400m	-0.68696	Strong
AMCR	FG	Crop_3200m	-0.06522	Weak
AMCR	FG	Shrub_1600m	0.227557	Weak
AMCR	FG	Grassland_3200m	0.324891	Moderate
AMGO	FG	Develop_800m	-0.2297	Weak
AMGO	FG	Shrub_3200m	-0.203	Weak
AMGO	FG	Tame_grass_3200m	0.601701	Strong
AMRO	FG	Native_grass_3200m	-2.66846	Strong
AMRO	FG	Grassland_3200m	-0.10763	Weak
AMRO	FG	Tree_3200m	-0.09141	Weak
AMRO	FG	Develop_200m	0.146168	Weak
AMRO	FG	Wetland_3200m	0.458496	Moderate
BRTH	FEG	Develop_3200m	-0.67615	Strong
BRTH	FEG	Tree_200m	-0.2579	Moderate
BRTH	FEG	Crop_3200m	-0.1222	Weak
BRTH	FEG	Shrub_800m	1.316942	Strong
BRTH	FEG	Native_grass_200m	1.328418	Strong
COYE	FEG	Develop_3200m	-0.89764	Strong
COYE	FEG	Crop_1600m	-0.28142	Moderate
COYE	FEG	Grassland_1600m	0.134764	Weak
COYE	FEG	Wetland_400m	0.686053	Strong
COYE	FEG	Shrub_3200m	0.837636	Strong
EAPH	FEG	Grassland_200m	0.108207	Weak
EAPH	FEG	Tree_shrubs_3200m	0.563183	Strong
RWBL	FEG	Tree_shrubs_400m	-0.34256	Moderate
RWBL	FEG	Develop_200m	-0.25602	Moderate
RWBL	FEG	Shrub_200m	0.079232	Weak
RWBL	FEG	Grassland_200m	0.192167	Weak
RWBL	FEG	Crop_800m	0.253473	Weak
RWBL	FEG	Native_grass_3200m	1.227446	Strong
SOSP	FEG	Native_grass_200m	-0.71952	Strong
SOSP	FEG	Develop_200m	-0.39088	Moderate
SOSP	FEG	Tree_200m	-0.33437	Moderate
SOSP	FEG	Crop_200m	0.114898	Weak
SOSP	FEG	Grassland_200m	0.150371	Weak
SOSP	FEG	Wetland_1600m	0.261302	Moderate

4.3.2. Specialists' selection patterns

Farmland specialist guilds displayed distinctive patterns in their coefficient's stability and multivariate models' composition. First, there were both stable and unsteady univariate coefficients across scales (Figure 10). Crop and grassland-related covariates were stable across scales for all specialist species, and coefficient values corresponding to each guild were clearly separated except on native grass. In contrast, coefficient values for wetland and tree-related cover were less stable and dissimilar. RCS displayed negative coefficient values for wetland and tree-related covers but an increasing positive slope toward larger scales. FSS displayed negative coefficient values for tree-related and wetland covers except for the Morning Dove, in which coefficient values for wetland covers were positive and stable across scales. PSS showed sign changes (negative to positive) on coefficient values above 1600 m radius for wetland and tree-related cover proportions. Lastly, develop cover coefficients exhibited the most discordant patterns between guilds: FSS exhibited positive selection values, but its slope became negative as the scale increased; RCS showed negative coefficients values, but its slope became positive as the scale increased, and PSS showed a stable avoidance.

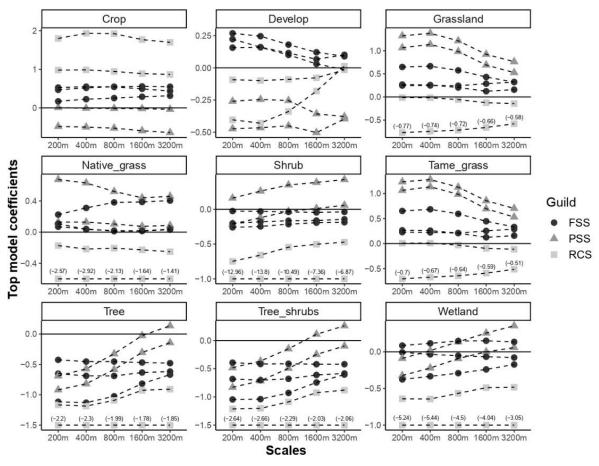


Figure 10. Cross-scale coefficient estimates from each land cover's univariate models for farmland specialist species with validated models. Sharp changes in coefficient values are a primary indicator of cross-scale interactions. Line type indicates species' guild-level classification.

Next, regarding multivariate models for specialist species, all shared a strong avoidance of Tree covers and a strong selection for their cover of preference: PSS for grassland, FSS for develop and RCS for crops covers (Figure 11, Table 7). Stronger selection tendencies occurred mostly at small scales for specialist guilds, between 200 m and 400 m radii. Nevertheless, some species exhibited selection to other variables at higher scales, both positive and negative. For example, the Eastern Meadowlark (PSS) selection for develop and crop covers, the Morning Dove (FSS) selection for grassland and trees covers, and the Killdeer (RCS) selection toward grassland covers.

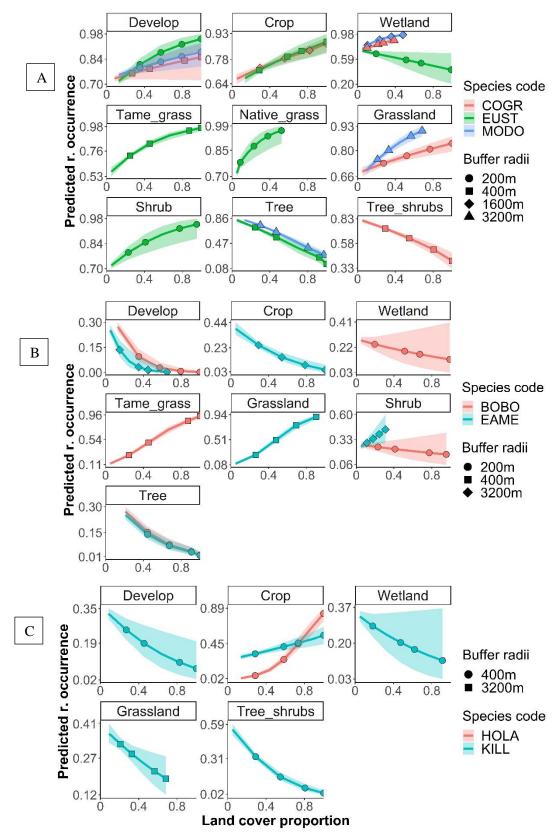


Figure 11. Marginal predicted effects of landcover proportion on the home range selection of: A) Farmstead specialists, B) Pasture specialists and C) Row crop specialists. Plots represent each species' occurrence probability as a response to each predictor of each species' top model. Each line colour corresponds to one species, and points shapes correspond to the scale each predictor was selected or avoided.

Table 7. Covariables strength for specialist guilds' models based on the slope of each covariable marginal effect. Classification bins were assigned by dividing all slope is three quantiles: Weak ~ 0 - 0.33, Moderate ~ 0.33 - 0.66 and Strong ~ 0.6 - 0.99.

Code	Guild	Covariate	Slope	Effect Strength	
вово	PSS	Develop_200m	-0.51236	Strong	
ВОВО	PSS	Tree_200m	-0.3586	Moderate	
BOBO	PSS	Wetland_200m	-0.15745	Weak	
ВОВО	PSS	Shrub_200m	-0.11805	Weak	
BOBO	PSS	Tame_grass_400m	0.708397	Strong	
COGR	FSS	Tree_shrubs_400m	-0.36587	Moderate	
COGR	FSS	Develop_400m	0.13439	Weak	
COGR	FSS	Grassland_200m	0.162842	Weak	
COGR	FSS	Crop_1600m	0.2068	Weak	
COGR	FSS	Wetland_3200m	0.475205	Moderate	
EAME	PSS	Develop_3200m	-0.59664	Strong	
EAME	PSS	Crop_3200m	-0.40287	Moderate	
EAME	PSS	Tree_200m	-0.33674	Moderate	
EAME	PSS	Shrub_3200m	0.684785	Strong	
EAME	PSS	Grassland_400m	0.814173	Strong	
EUST	FSS	Tree_400m	-0.55866	Strong	
EUST	FSS	Wetland_200m	-0.29923	Moderate	
EUST	FSS	Crop_400m	0.248399	Weak	
EUST	FSS	Shrub_200m	0.290307	Moderate	
EUST	FSS	Develop_200m	0.313152	Moderate	
EUST	FSS	Tame_grass_400m	0.443572	Moderate	
EUST	FSS	Native_grass_200m	0.547388	Strong	
HOLA	RCS	Crop_400m	0.777666	Strong	
KILL	RCS	Tree_shrubs_400m	-0.56361	Strong	
KILL	RCS	Grassland_3200m	-0.32107	Moderate	
KILL	RCS	Develop_400m	-0.30572	Moderate	
KILL	RCS	Wetland_400m	-0.25359	Weak	
KILL	RCS	Crop_400m	0.293172	Moderate	
MODO	FSS	Tree_3200m	-0.59656	Strong	
MODO	FSS	Develop_200m	0.154526	Weak	
MODO	FSS	Grassland_3200m	0.393616	Moderate	
MODO	FSS	Wetland_1600m	0.572987	Strong	

4.4. Prediction surfaces

Prediction surfaces were generated for all selected farmland birds by estimating their top models' RSF values over Southern Ontario (Appendix 1). Then, combined surfaces were obtained by estimating mean RSF values and top-bin counts among species classified as farmland generalists and specialists (Figure 12 - 15).

The consistency of summarized predictions surfaces to identify habitat availability across Southern Ontario varied between farmland generalists and specialists. Mean RSF values showed an increasing habitat availability from the east to the west for farmland generalists (Figure 12). However, combined top bins displayed a homogeneous distribution of best habitats for farmland generalists. Aside from small areas in the west, mostly groups of 2 to 4 generalist species coincided in their best habitats distribution across Southern Ontario (Figure 13). These patterns suggest that farmland generalists might select similar habitat attributes in the local landscape (e.g., slight avoidance of one-cover dominated areas), but it does not seem to limit the distribution of their best habitats in Southern Ontario considerably.

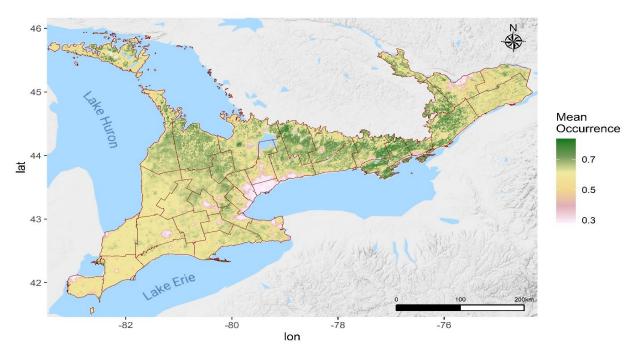


Figure 12. Mean predicted occurrence values from resource selection functions for eight species of farmland generalists in the BCR13 of Canada. Each pixel value was calculated using all farmland generalist's occurrence values. Areas with high use estimates represent locations that most species find suitable from a landscape perspective.

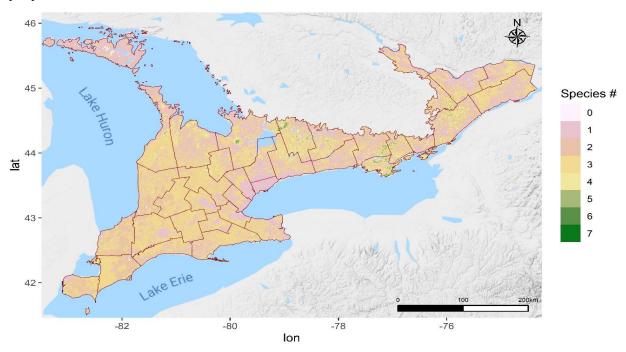


Figure 13. Number of farmland generalists' species with top-bin habitat units in each pixel according to their resource selection predictions across the BCR13 of Canada. Each species value represents how many species perceived that location as a top habitat unit (i.e., RSF values > 75%). Areas with high frequencies represent locations with high suitability for multiple species.

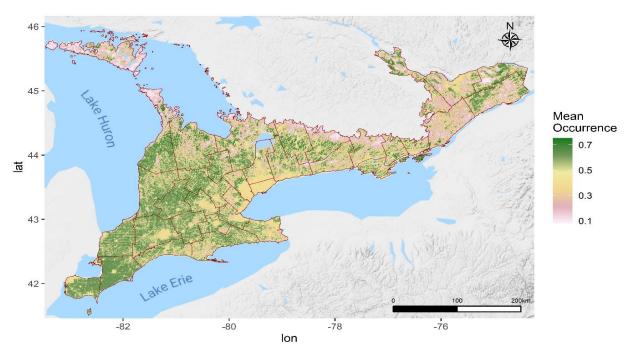


Figure 14. Figure 14. Mean predicted occurrence values from resource selection functions for seven species of farmland specialists in the BCR13 of Canada. Each pixel value was calculated using all farmland generalist's occurrence values. Areas with high use estimates represent locations that most species find suitable from a landscape perspective.

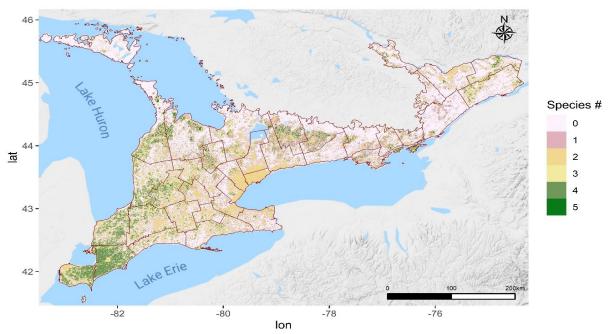


Figure 15. Number of farmland specialist species with top-bin habitat units in each pixel according to their resource selection predictions across the BCR13 of Canada. Each species value represents how many species perceived that location as a top habitat unit (i.e., RSF values > 75%). Areas with high frequencies represent locations with high suitability for multiple species.

In contrast, a consistent influence of land-cover proportion in farmland specialists' habitat distribution was observed on their summarized prediction surfaces. Mean RSF values showed that farmland specialists' habitats were less available in the east, but their higher RSF values were located between the west and central regions (Figure 14). Moreover, combined top bins displayed a narrower distribution for farmland specialists, as groups of 4 to 5 specialist species coincided in their best habitats distribution in more restricted areas (Figure 15). These patterns suggest that the distribution of specialists' best habitats is remarkably limited by land cover proportion in the local landscape compared to farmland generalists.

According to Southern Ontario's census subdivisions, generalists and specialists coincided and differed in various counties and municipalities with high habitat availability. According to the locations with top bin RSF values, Kawartha lakes municipality has the highest habitat availability for generalists, while Bruce County has the highest habitat availability for specialists (Figure 16). However, by adding locations which RSF values above the fourth bin values (i.e., moderate and top-quality habitats), Grey county and Chatham-Kent municipality had the highest habitat availability for generalists and specialists. Counties and municipalities where high habitat availability for generalists and specialists coincided included Grey county, Kawartha lakes municipality, Dufferin county and Simcoe county.

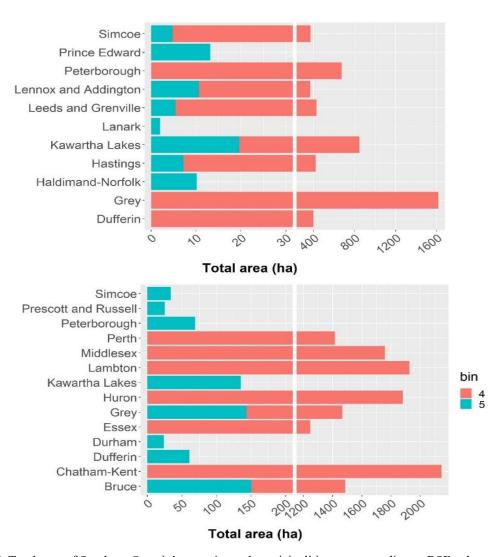


Figure 16. Total area of Southern Ontario's counties and municipalities corresponding to RSF values associated with moderate and top-quality habitats (i.e., bins 4 and 5 respectively) for A) farmland generalists and B) farmland specialists.

Differences in what counties had the highest availability of top-quality (i.e., RSF values within the fifth bin) and moderate plus top-quality habitats (i.e. RSF values above the fourth bin) for farmland birds respond to habitat availability patterns at the guild level (Figure 17). For instance, Kawartha lakes municipality was the only location where both farmland generalist and farmland edge generalist coincided, but Grey county had a considerably large habitat availability for farmland generalist only. As the habitat availability for farmland edge generalists was so low compared to farmland generalists, the addition of moderate-quality habitats to availability estimates overshadowed their preferences. Similarly, the higher habitat availability for Row crop

specialists when adding moderate-quality habitats made Chatham-Kent municipality predominate over counties with higher top-quality habitat availability for farmland stead and pasture specialists, like Bruce and Grey counties. Overall, farmland birds' top-habitats availability across Southern Ontario can be divided into three zones: The west zone preferred by Row crop specialists; the west-central zone preferred by farmland generalists, farmland stead and pasture specialist; and the east zone preferred by farmland edge generalists.

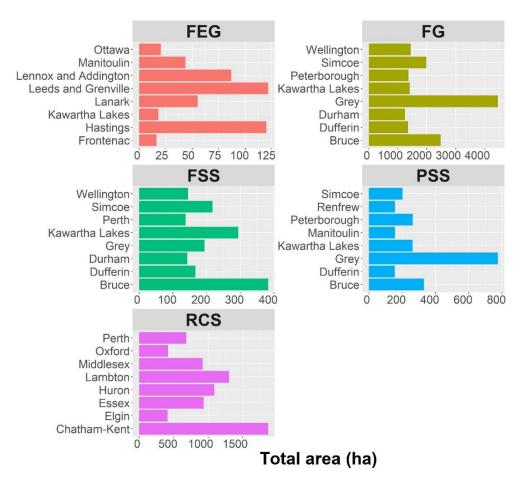


Figure 17. Total area of Southern Ontario's counties and municipalities corresponding to RSF values associated with top-quality habitats (i.e., RSF bins 5) for farmland edge generalists (FEG), farmland generalist (FG), farmland stead specialists (FSS), pasture specialists (PSS) and row crop specialists (RCS).

Chapter 5: Discussion

5.1. Overall achievements and findings

Understanding species' perception of available resources and conditions in human-transformed landscapes has become critical to weighing decisions on how to reconcile land use allocation for agricultural production and ecological conservation. My study narrowed that question to assessing one group (farmland birds) and their potential use of multi-scale land cover proportion as a habitat cue in agricultural landscapes in Southern Ontario. Resource Selection Functions (RSF) were developed using data from the Breeding Bird Survey (BBS; 2014-2019) that were available for 32 species that had been proposed as farmland bioindicators (Kirk et al. 2020).

The analysis using these RSFs showed three major patterns:

- 1) Farmland bird species showed selection for local-landscape cover proportion at two distinct scales of ≤800 m and ≥1600m radii; most farmland bird species interacted with the local-landscape covers at two or higher number of scales.
- 2) Most farmland specialists primarily selected land cover proportion at scales <800m radii compared to farmland generalists, which selected cover mostly at the smallest and larger scales (200m and 3200m radii). These differences are likely linked to patterns of guild-level cover usage and regional habitat availability.
- 3) Farmland birds' occurrence increased from Southern to Western Ontario and from Central to Easter Ontario, probably caused by higher availability of grassland cover (from a patch-level perspective) and cover heterogeneity (from a landscape-level perspective) in Western and Eastern Ontario, favourable for most farmland generalist and specialist birds.

These findings highlight the importance of conducting multi-scale studies to discern bird species' response to landscape attributes in agricultural landscapes. Below, I elaborate on the evidence and implications of the three patterns listed in addressing my research questions.

5.2. Farmland birds' multi-scale selection for land cover proportions

The performance of developed RSF was interpreted as an empirical indicator of farmland birds' selection of land cover proportion at varying extents above their breeding territories (i.e., first selection order). According to the validation criteria (acceptable: AUC > 0.6, Spearman's ρ > 0.6), 15 out of 32 species were predicted by RSF with acceptable accuracy, suggesting these species use land cover proportion in the local landscape as a habitat cue (Figure 4). I had anticipated that developed RSF models would accurately predict more area-sensitive species than area-insensitive species. My results showed that the relative occurrence of some area-sensitive species was indeed accurately predicted by land cover proportion (e.g., Eastern Meadowlark, Bobolink) but others were not (e.g., Savanna Sparrow, Vesper Sparrow; Ribic et al. 2009). This outcome indicates that area sensitivity might not always reflect at the landscape level or that used cover classification or species data were not adequate to characterize some species' habitat selection patterns (See Challenges and Next Steps).

Surprisingly, the relative occurrence of multiple area-insensitive species was accurately predicted (e.g., American Crow, European Starling). This outcome might suggest that cover composition differences across Ontario are high enough to influence area-insensitive species. However, certainty about area-insensitive species responses to cover composition is reduced for those species that have high detection values (i.e., >80% of the sampled stops). Models of species with high detection could have a lower capacity to discern between false unused locations (i.e., use by species but the species not recorded by the surveyor) and true unused

locations. Nonetheless, the fact that only half of the birds considered farmland indicators were accurately predicted reflects the variation and distinctiveness of each species – and perhaps each individual bird's - selection to land cover proportion can be in the local landscape. This underscores and supports the need to better understand species (or even individual) responses and selection to land covers at different scales. There are some valuable trends and statistically valid outcomes across the broader categorization of species responses to land cover on one scale (e.g., De Camargo et al. 2018; Frei et al. 2018), but there is enough variation in those responses to warrant caution about over-generalization when making land-use decisions about how species will respond to efforts for conservation or agricultural production

Farmland birds with valid models selected all open land covers and avoided trees and developed covers. Most species selected grassland covers (both native and tame), likely because of their higher offer of nesting and foraging resources with less intervention and predation risks, followed by shrubs and crops (Figure 5). Tree avoidance by most species was expected, given the low tolerance of most farmland birds to tree intrusion near their breeding grounds (Cunningham and Johnson 2019). Accordingly, coefficient estimates for grassland and tree were the highest among other selected or avoided land covers. These relationships are consistent with expectations of birds that primarily rely on open country covers, implying that the valid models capture the relevant variation from farmland birds' habitat preferences. At first glance, it could be assumed that all farmland birds are benefited from mixtures of managed covers (crops and old fields) and open native covers (native grasslands, shrubs, and wetlands) with reduced presence of forest and urban covers. However, varying strength in their responses (i.e., coefficient values) indicates that habitat selection patterns are more diverse at the species level.

Most validated models consisted of covariables measured at two or more scales. This finding agrees with other studies that reported higher performance of multi-scale models than single-scale models (McGarigal et al. 2016). Moreover, scales below 800 m and above 1600m radii were frequently selected by farmland birds. This division suggests that both patch-level and landscape-level habitat attributes are relevant for farmland birds with relative area sensitivity in Southern Ontario. Previous studies have reported farmland birds' association or selection to land cover proportion at scales either ≤ 800 m (Ribic and Sample 2001; Cunningham and Johnson 2006; Herse et al. 2018, 2020) or ≥ 2400 m (Shahan et al. 2017; Fedy et al. 2018; Lockhart and Koper 2018). However, findings in the selection scale are highly variable among agricultural regions, with studies detecting habitat attributes influence on farmland birds only at small scales (e.g., Ribic & Sample 2001), only at large scales (e.g., Fedy et al. 2018) or both (e.g., Cunningham & Johnson 2006).

Scale and landcover relationships were not homogeneous among farmland birds. All land covers were associated with farmland birds' occurrence at both small and large scales.

Furthermore, some covers showed an opposite selection among farmland birds across scales. For instance, the influence of trees and crops became weaker with increasing scales and changed direction at 3600m radius (Figure 5). This discrepancy in selection scales can have multiple causes, including scale-dependent interactions, species traits variation or landscape context differences (Miguet et al. 2016). Hence, implications of farmland birds' divergent scale selection should be interpreted based on species' habitat preferences and availability within the study area.

5.3. Multi-scale selection patterns among farmland generalists and specialists

Models' comparison based on Kirk et al. definition of specialism and functional groups among farmland birds revealed distinct multi-scale selection patterns. According to their level of

specialization, farmland specialists' models included more covariates at smaller scales ($\leq 800 \text{ m}$) than generalists (Figure 6). This pattern might imply that specialists use more habitat cues at the patch level than at the landscape level compared to generalists. Within plausible causes of generalists' and specialists' discrepancy on selection scales, differences in dispersal capacity have been suggested as a prominent cause (Brennan et al. 2002; Dale et al. 2006). Martin and Fahrig (2018) proposed that specialists are likely influenced by habitat attributes at larger scales than generalists based on the proportional relationship between specialization and dispersal in temperate migratory birds. Observed patterns in Southern Ontario contradict this hypothesis; however, this disagreement could result from the dynamism of scale selection according to the ecological neighbourhood concept. The relative spatial extent of ecological neighbourhoods is usually defined by species movement, and it could vary with changes in species' movement patterns associated with specific activities or phenological states (Addicott et al. 1987; Fletcher et al. 2018b). Scale selection patterns in this study may result from farmland birds' selection to cover proportion during their breeding season, which might differ in magnitude from their selection during migration. Therefore, seasonal variation in species behaviours might be essential in detecting divergent intraspecific selection scales.

Divergence in scale selection between farmland specialists and generalists' birds during the breeding seasons had mixed agreement with previous studies findings. Multi-scale studies on species classified as farmland generalists have reported responses to landscape attributes (including landscape proportion) at scales ≥ 1600m (Forcey et al. 2015; Shahan et al. 2017; Fedy et al. 2018; Paton et al. 2019) or absence of association with landscape attributes (Durán 2009). Also, farmland generalists' responses to land cover proportion were sometimes weak or exceeded by other landscape attributes like configurational or compositional heterogeneity (e.g.,

American goldfinch in Shahan et al. 2017). In contrast, findings on farmland specialists' selection scales were more inconsistent than generalists. Multi-scale studies have reported farmland specialist response to land cover proportion at scales <800m (Ribic and Sample 2001; Guttery et al. 2017; Herse et al. 2020), at scales <1600m (Fedy et al. 2018; Lockhart and Koper 2018) or not occurring at any scale (Bakker et al. 2002). Selection scales can vary for multiple reasons, including interspecific and intraspecific variations on traits defining species' spatial resource perception (Delattre et al. 2013; Thornton and Fletcher 2013; Fletcher et al. 2018b), regional differences in environmental conditions (Cady et al. 2021) or differences on species data quality (e.g. detection rates). However, based on the differences between generalists' and specialists' multi-scale selection and their variation across studies, three potential ecological factors can be suggested: Habitat breadth, area sensitivity and habitat availability.

Instead of dispersal capacity, habitat breadth and area sensitivity might primarily mediate the divergence on local-landscape selection scales among the studied farmland birds.

Generalists' weak selection or avoidance of breeding covers at scales >1600m could derive from their low area sensitivity and capacity to use multiple covers. Species favouring the presence of multiple covers over one cover might be selecting larger scales as cover heterogeneity increases with scale. This hypothesis might also explain why some farmland generalists avoid land covers they use when these become dominant. In contrast, specialists' strong selection of their preferred breeding cover at scales <800m while avoiding trees and other covers at similar scales could derive from their area sensitivity or low tolerance to the intrusion of non-breeding covers. Area sensitivity has been reported for species like the Eastern Meadowlark, Bobolink, and Hornet Lark (Ribic et al. 2009), and low tolerance to tree intrusion has been reported for various species classified as specialists in this study (Cunningham and Johnson 2019). From these habitat

interactions, specialists might select their preferred covers at smaller scales as these get scarcer and sparse at larger scales. Therefore, regional landscape attributes likely define scale and specialism inverse relationship.

Regional variation in habitat amount might affect movement distances (and possibly selection scales) as dispersal mortality varies with habitat availability across local landscapes (Flather and Bevers 2002; Delattre et al. 2013). Farmland specialists might use selection scales < 800m due to the low regional proportion of their breeding cover in Southern Ontario. Partial comparisons of study areas' cover proportion among reviewed studies support habitat amount influence on intraspecific variation among some farmland specialists' selection scales. For instance, pasture specialists like the Bobolink and the Eastern meadowlark showed variation in scale selection that aligned with apparent differences in grassland proportion. These species selected grassland covers at smaller scales in regions with low average grassland amounts like Southern Ontario ($\bar{x} = 0.24 \pm 0.20$ for grassland % at 400m) than in regions with higher grassland amounts like easter Manitoba ($\bar{x} = 0.4$ for Grass% at 3200m; Duran 2009, Lockart et al. 2018) or South Dakota ($\bar{x} = 0.45 \pm 0.01$ for Grass% at 400m; Bakker et al. 2002). However, farmland specialists' selection at scales <800m can also occur in regions with high habitat amount. For instance, Herse et al. (2020) found that the Grasshopper sparrow (a pasture specialist in Ontario) selected grassland proportion at 400m in the Flint Hills ecoregion in Kansas, which possesses approximately 80% of reaming tallgrass prairies in North America (\bar{x} = 0.6 for Grass% at 400m). While there is some evidence that regional habitat amount might influence farmland specialists' selection scales in Southern Ontario, other factors might lead to similar patterns (e.g. species traits or additional landscape attributes).

5.4. Distinctive patterns among functional groups

Aside from overall differences between farmland generalists and specialists, functional groups displayed distinctive interspecific and intraspecific patterns. Farmland generalists and edge generalists differed considerably on their selection scales. While farmland generalists showed an overall weak association with diverse cover amounts at 3200 m radius, some edge generalists selected land covers at combinations of scales <800 m and >1600 m radii. This distinction in selection scales by Farmland edge generalists could be associated with the differential use of covers composing edges within their breeding territories (Perkins et al. 2003). For example, species like the BRTH and the EAPH breed in wooded areas but feed on open areas like grasslands; the former was selected at scales above 1600m scale radius and the latter at 200m radius. Similarly, the Common Yellowthroat can use wetlands and shrublands for breeding and foraging activities but prefers to be near wet areas. This species selected wetland at the 400m extent and shrubs and grassland at the 1600m scale. These selection patterns suggest that selection scales might vary with species' resource usage aside from their local availability.

Variation in scale selection and effects' strength within pasture and row crop specialists could be associated with critical intraspecific differences. Pasture specialists differed in selecting secondary covers' proportions like crops and shrubs (Table 7). The Eastern Meadowlark avoided crops at large scales (3200m), while the Bobolink did not show any association with crops.

Bobolink's lack of association with crop covers might be a consequence of this study's broad crop classification, as studies have documented Bobolink's capacity to nest and raise successful nestling in some crops (McCracken et al. 2013; Fromberger et al. 2020). Similarly, Bobolink avoided shrubs at 400 m radius while the Eastern Meadowlark selected them at 3200 m radius. However, both species are known to use sparse shrubs as perches; thus, these patterns might be

displaying apparent differences in these species' sensitivity to shrubs' encroachment (McCracken et al. 2013). Concerning Row Crop Specialists', the Killdeer avoidance and the Horned lark's mixed response to grasslands could be associated with the availability of suitable local vegetation conditions. These species prefer bare or low vegetation covers, and these conditions availability during summer is likely higher in crop-dominated areas with fallow, tilled or soy fields than in pastures (OMAFRA 2017). Overall, variation in scale selection and effects strength among specialist species could indicate potential differences in their sensitivity to secondary covers.

On the other hand, similarities among some farmstead specialists and edge generalists suggest a distinctive response to local-landscape attributes. Selection for diverse covers at scales < 400m was shared between the Song Sparrow and the Red-winged blackbirds, classified as edge generalists, and the Common grackle and the European Starling, classified as farmstead specialists (Figures 9 & 11). All four species are widespread in agricultural areas, with high similarities with generalists given their wide habitat breadth. This pattern denotes that land cover selection at small scales might not always be related to area sensitivity as in pasture and row crop specialist cases. Alternatively, based on these species' ecology and multi-scale studies challenges, two factors can be suggested as causes of the observed pattern: breeding behaviour and habitat mischaracterization. A common characteristic among these four species that could impact their selection scales is their aggregation during nesting. The Common grackle, European Starling and Song Sparrow tend to gather in colonies and nest nearby, while the Red-winged blackbird is polygynous (1 male and various females in one territory)(Selander 1965; Picman et al. 1988; Templeton et al. 2012). These nesting behaviours may favour patch-level attributes rather than landscape-level attributes as groups will be attracted to more suitable patches

(Valente et al. 2021). Another possibility is that data and scope limitations cause selection toward the smallest scale. Land cover data obtained from the AICC has a resolution of 30mx30m, which overlook small human structures used by farmstead specialists. Also, habitat selection at the smallest scale (200m) could be an artifact of species selection to attributes at higher selection orders rather than local-landscape attributes (Pasher et al. 2013). Selection to the smallest scale should be cautiously approached as it could indicate either selection for small local landscapes or non-selection to local-landscape attributes.

Lastly, cross-scale validation of selected covers' effects revealed some potential scaledependent interaction within some functional groups. Two general patterns were noticed: decreases in land cover effects as scale increases and changes in effects directionality with scale increase (Figures 8 & 9). As the scale increased, grassland selection became weaker for most edge generalists and specialist species. Similarly, selection for develop cover by farmstead specialists and avoidance by row-crop specialists became weaker at larger scales. These patterns were expected as grassland and develop covers contribution to the landscape decreases with scale, diminishing area-related effects. Separately, pasture specialists and one edge generalist exhibited directionality change in their interaction with some covers. The Eastern Meadowlark and the Brown Thrasher avoided Trees at small scales but selected them at larger scales. Also, the Bobolink interaction with wetlands changed from avoidance to selection at larger scales, and the avoidance of trees reduced drastically. All three cover proportions increased with scales, suggesting that these changes in effect directionality might result from species responses to other attributes aside from cover proportion. For instance, Eastern Meadowlark avoids dense forests but uses sparse trees as perches to sing for mating, territorial or alarm purposes (McCracken et al. 2013). This agrees with findings of grassland species not showing strong avoidance of tree

cover at larger landscape scales (de Zwaan et al. 2022). It is possible that across fragmented regions (like Southern Ontario), other metrics like covers continuity or clumping decrease cause large scales to capture a fraction of these species' interactions with other metrics aside from habitat amount.

5.5. Distribution of farmland birds' suitable habitats in Southern Ontario

While farmland birds' suitable habitats extended all over Ontario's agricultural region, contrasting patterns between farmland generalists and specialists highlight key factors shaping their distribution. Generalist species' mean occurrence and top habitats were larger across Ontario than those from specialists' species. This pattern is a natural result of the intraspecific differences in land cover preferences among farmland generalists and specialists. However, locations classified as top habitats were principally located in two areas for both groups: Western-central Ontario and Eastern Ontario. Both areas differ from Southern Ontario in their more significant proportion of pastures and trees, the former benefitting farmstead and pasture specialists while the latter benefitting edge generalists. Important conservation projects like Ontario's greenbelt and Farm stewardship programs probably have a considerable incidence on the observed conservation value of Western and Central Ontario. Other studies highlighted these areas as critical areas for the conservation not only of farmland birds but as well forest birds, given their high cover heterogeneity (de Zwaan et al. 2022). Heterogeneity of natural and productive covers is likely to favour farmland birds' richness (Redlich et al. 2018), but distinct processes define habitat suitability for farmland generalists and specialists.

The continuity and number of locations predicted as top habitats among specialist and generalist species align with their typical response to composition and proportion changes in the local landscape. Relative habitat suitability for farmland generalists and edge specialists agreed

on the importance of areas with higher cover heterogeneity. However, most edge generalists preferred continuous areas with a higher proportion of grassland and woody covers than crop and developed covers (i.e., Kawartha lakers and Grey counties). On the other hand, despite the apparent homogeneous distribution of farmland specialists across agricultural areas, they exhibited uninterrupted and interrupted suitable areas (e.g., Southern vs Western Ontario) caused by the divergent cover preferences among specialist guilds. While heterogeneous areas like those within Bruce, Dufferin and Grey County may congregate all farmland birds' guilds, maintaining suitable habitats for all may not be feasible, and prioritization must be required (See Management implications). Alternative strategies could involve developing management plans that align with the gradual changes in farmland birds' communities in Ontario as covers transition from forest, pastures and crops from Northeast to Southern Ontario.

Chapter 6: Management implications

Multi-scale selection by farmland birds provides key insights on relevant local-landscape cues that could improve researchers' inferences and guidance over effective farmers' and institution management strategies. Firstly, selected scales are a primary indicator of the spatial extent within which some species are more sensitive to changes in land cover proportion. For instance, pasture specialist sensitivity to changes at 400 m support management measures that maintain relatively continuous grasslands with extensions >50ha, aligning with previous findings of larger fields ≥30 ha exhibiting higher Bobolink densities (Bollinger and Gavin 1992) and Eastern Meadowlark (Renfrew and Ribic 2008). However, species selection for land cover proportion at either scale <800m or > 1600m radii cannot be generalized to linear relationships with land cover proportion. The diverse responses of farmland birds to land cover proportion in terms of their effects' strength and selection scales possibly indicate the influence of other landscape attributes. For example, generalists' weak responses to multiple landcover at scales either <800m or >1600m radii could arise from these species' selection for heterogeneous landscapes. I suggest that only strong responses to land cover proportion observed in this study (Table 6-7) could translate to benefits of cover increases on species persistence at their selected scales. Weak responses might translate into non-linear responses to land cover increase which limits between beneficial and prejudicial effects need to be assessed by examining their interaction with other landscape metrics at selected scales.

Secondly, variation in selected scales by farmland birds suggests the need for distinct levels of management to deal with agriculture impacts on biodiversity at multiple scales.

Agriculture impacts frequently exceed the area of influence of single stakeholders. For instance, since the average farm size in Ontario is approximately 100 ha, individual farmers' management

could be insufficient to counteract landscape fragmentation effects at scales >1600m radii (~803 ha). The reconciliation of agricultural activities requires action by multiple stakeholders according to the relationship between their area of influence and species scales of responses. Therefore, farm management and coordinated management between farmers and local and provincial authorities should be promoted to deal with multi-scale fragmentation effects. This would likely increase farm management benefits to species maintenance as ecological processes occurring at different scales would be supported (Ekroos et al. 2016). However, conflicting management approaches could arise because of distinct and sometimes opposite responses to land cover proportion among species (i.e., guild-level differences) and within species (i.e., Scaledependent interactions). For instance, Martin et al. (2020) found that positive effects of crop diversity decreased with scale for multiple taxa, possibly because at smaller scales (<250-400m radii), increases in crop diversity lets to area reduction that affects species use of single crop covers. It is necessary to design management strategies that take advantage of the landscape context differences under each management unit (e.g., agricultural subdivisions) and prioritize distinct landscape arrangements with varying land cover proportions and heterogeneity.

It is important to note that the success of management strategies derived from species responses at the landscape levels is likely to increase if lower-level habitat attributes are accounted for. As a result of agriculture's replacement of native covers for row crops and forage pastures, landscape-level cues could be decoupled from habitat quality and misinform animals (Schlaepfer et al. 2002). Farmland birds are exposed to multiple threats, including increased exposure to pesticides and habitat disruptions (Boutin et al. 1999). For example, Bobolinks population growth and nesting success in used hay fields and forage pastures are strongly associated with harvest times and cattle stocking rate (Fromberger et al. 2020). From a landscape

perspective, suitable habitats for the Bobolink could become ecological traps due to an early harvest and high cattle stocking rates. Therefore, increases in landscape-level cues for farmland birds had to be accompanied by stable or enhanced habitat quality at finer spatial levels.

Multi-scale selection patterns displayed by species with validated models offer important insights into the consistency of Ontario's farmland bird indicator (OFBI) as a tool to assess agricultural impacts. Each guild displayed distinctive patterns either in their cover or scale selection that aligned with each species' ecology. This supports the application of OFBI as a tool that could allow the assessment and identification of diverse impacts of agricultural management on biodiversity. Nevertheless, conflicting selection patterns within farmland edge generalists and farmstead specialists suggest the need for further characterization of these farmland birds' habitats. Farmland specialists were expected to be defined by a strong response to a specific managed cover (Cover, Crop, or Developed), but farmstead specialists exhibited a wide habitat breadth and similarities with some edge generalists (i.e., Red-winged blackbird and Song Sparrow). This inconvenience with the characterization of farmstead specialists could be caused by the potential spatial dependency of this species' specialism. Ecological specialization is conditioned not only to the set of resources used by species but also to the spatial and temporal scale within which they are evaluated (Devictor et al. 2010). Species using farm buildings might exhibit selection for these structures within their territories (i.e., 3rd order selection) but not at the home range level where local landscape attributes could be more relevant. Alternatively, it is also possible that the observed use of buildings by farmland birds is a context-dependent response to regional fluctuations in local environmental conditions. Defining specialization among farmland birds (as any other group) requires further research on species responses at different scales and environmental contexts.

Chapter 7: Challenges and next steps

Species distribution models developed from empirical data are powerful tools to make inferences about species' relationship with their environment. Through the development of resource selection functions, I found relevant patterns of farmland birds' multi-scale selection that could contribute to the design of management plans that reconcile production and conservation purposes. However, empirical models do not represent causal ecological processes but rather approximations of plausible species responses based on data correlation. These approximations are constrained by models' assumptions and specifications, which understanding can help to identify sources of uncertainty that need to be addressed. Particularly for resource selection functions developed in this study, I identify two areas that require further research to consolidate my findings on Farmland birds' multi-scale habitat selection in the local landscape: landcover classification and model structure fit to species responses.

First, all species distribution models are subjected to environmental attributes defined by the study area and the research objectives. Including all potential environmental and ecological factors influencing species habitat selection is a difficult task; hence, most species distribution models aim to characterize subsets of species habitat attributes (i.e., Realized niche) that could inform management decisions within the study area (Hirzel and Le Lay 2008). In landscape ecology, researchers might limit the complexity of landscape attributes by defining a thematic resolution (e.g., land cover classification schemes) and defining spatiotemporal boundaries on their environmental data.

 The number of land cover classes can impact the capacity of landscape metrics to capture relevant ecological responses (Bailey et al. 2007). For instance, land cover classes based on one classification criteria may lead researchers to overlook species responses to other environmental attributes within the grouped landforms. In my study, using the type of human intervention as a criterion, I classified multiple crop types and human structures within the land cover classes "crop" and "developed." Other studies have reported farmland birds' distinct response to finer classes related to these covers (i.e., annual vs perennial crops; Martin et al. 2020), raising the possibility of relevant habitat responses being overlooked. For instance, the Bobolink is known to be capable of nesting successfully on crops like rye and wheat (McCracken et al. 2013). This response was not detected on the RSF developed for Ontario agricultural region using only one Crop classification (Figure 2.8), suggesting the need to evaluate other thematic resolutions. However, increasing the thematic resolution does not guarantee improvements in models' accuracy as, at the extent of Ontario, multiple cover types are considerably unrepresented (i.e., mean across scales proportion < 0.1%). Therefore, I suggest that the next studies could compare different thematic resolutions and assess their impact on the predictive capacity of RSF at smaller management units (i.e., Agricultural census subdivisions). It is necessary to examine other land covers thematic resolution and grain sizes, as this may alter the quantification of species scales of effect (Jackson and Fahrig 2015).

- Inferences from empirical studies are limited by the attributes of both ecological and environmental data.
 - Occurrence data used in this study might have influenced observed selection patterns according to their detectability. For example, species detected in less than 10% of the sample stops displayed models with a low performance, likely because of a lack of information. Also, high detectability might have affected models' reliability due to a lack of contrast among sample locations. Therefore, collecting

- data for species with lower detectability is required to reassess their responses to land cover proportion, while using a more informative state variable (e.g. abundance) might improve inferences of highly detected species.
- Spatiotemporal boundaries might reduce the variation of environmental conditions, reducing the observed species' niche breadth. This could have happened in some farmland bird responses to native grassland and wetlands, as these covers are scarce (e.g., Native grasslands) or possibly underrepresented (e.g., Wetlands). For instance, native grasses proportion did not strongly influence PSS as in other guilds not specialized in pastures like FEG or FSS. It is not advisable to extrapolate my result to other agricultural regions, as landscape context in terms of cover proportion and composition likely influence farmland birds' multi-scale selection patterns. Similarly, it is also possible that species selection patterns vary across seasons or more extensive periods. Examining seasonal variation due to species behavioural changes was out of the scope of this research as I focused on habitat selection during the breeding season. Yearly variation in farmland birds' multi-scale selection was assumed to be low as Ontario land cover composition changes have been relatively low since 1970 (Pond 2009). However, increasing the replacement of perennial crops for annual crops might critically affect farmland birds' habitat selection in row-cropsdominated areas in the long term. My study offers a standpoint for contrasting patterns occurring at finer extents and identifying potential deviations from the regional trend.

Second, SDMs' capacity to represent species responses to their environment is delimited by a trade-off between structural complexity and explanatory power (Elith and Leathwick 2009). A high number of variables and complex structures (e.g., non-linear terms, nested variables) could increase models' accuracy when representing species responses. However, higher model complexity increases the required computing power for parameter estimation and might reduce models' prediction capacity due to overfitting. Researchers balance this trade-off according to their research objectives and data attributes (Thuiller et al. 2013). I applied a standard modelling approach (i.e., GLM with linear additive terms) as an exploratory approach to understanding the implications of multi-scale selection in species modelling and land management. This allowed me to assess multiple models' combinations for multiple species to a wide extent (i.e., Ontario's agricultural region) and generated prediction surfaces useful for management purposes. However, there are two aspects of ecological data that were not analyzed in-depth, but that developed models in this study can illustrate: non-linear relationships, scale-dependent relationships, and spatial dependence.

• Assuming linear and additive effects of land cover proportion in farmland birds allowed an intuitive interpretation of variable effects. However, farmland birds' responses to land cover proportions that were weak or not completely consistent with species ecology could be a sign of non-linear relationships. For instance, the Eastern meadowlark's positive response to Shrub proportion at 3200m radii is unlikely to persist in Shrub dominated landscapes, as this species uses areas dominated by grassland rather than any other cover. Non-linear responses to some land cover proportion by farmland birds may be partially captured with multi-scale modelling, but this requires a more in-depth assessment. Non-linear relationship to land

- cover proportions obeys not only differences in species multi-scale perception but also ecological factors exogenous to species traits (e.g., environmental gradients).
- While the scales at which each land cover has a stronger effect were detected, this does not mean that species selection for a land cover only occurs at these scales. Highly mobile species likely use habitat cues across scales as they move in search of suitable locations (Meyer and Thuiller 2006). This assumption implies that species habitat selection might be conditional among scales (i.e., higher scales influence lower scales selection) and that selected scales reported in this study represent thresholds within habitat selection is stronger. Acknowledging the spatially hierarchical and conditional nature of habitat selection is critical when species responses to land cover proportion are scale-dependent. I assessed the consistency of each land cover effect across all evaluated scales and found that the direction of some species' responses changed with scale (i.e., Eastern Meadowlark and Shrubs). I did not account for plausible conditional effects of landscape proportion at varying scales as I aimed to identify relevant scales as a first step to informing more complex multi-scale analysis. Reported selected scales can be used as a reference for techniques like hierarchical modelling, which can use collinear and nested data (Lipsey et al. 2017).
- Spatial dependency is a common attribute in ecological data that can affect the estimation of confidence intervals from models' coefficients (Fletcher and Fortin 2018). Addressing spatial dependence is difficult given the multiple sources it originates, from endogenous processes like conspecific attraction to exogenous factors like the spatial aggregation of resources.

 Moreover, spatial dependence on models' residuals may occur from missing variables not included in this study. Techniques to account for spatial dependence have been developed (e.g., Data thinning and Spatial Species Distribution Models). However, applying these

techniques does not guarantee a reduction in spatial dependence (Zuckerberg et al. 2012) and might require complex modelling structures, which misspecification could lead to wrong inferences (Dormann et al. 2007). I explored the contribution of land cover proportion in explaining the spatial correlation between sampled sites as a primary input to develop more complex models to deal with the remaining spatial dependence

Chapter 8: Conclusions

This study quantified farmland birds' use of land cover proportion at varying scales as a habitat cue in Southern Ontario. My results indicate that some farmland birds use local landscape cues at varying scales, potentially due to species processes like migration, foraging and nesting occurring at distinct scales. For species with unacceptable models, it is still early to say if they do not use habitat cues in their local landscape, for other data and models' structures needs to be tested. Farmland birds with validated avoided highly developed areas (i.e., cities) and dense forest areas while selecting agricultural and native covers. However, the scales at which these covers were avoided or selected varied considerably among species, with most selecting land covers proportion at mixed scales between ≤800 m and ≥1600m radii. Variation in scale selection reflects the complexity of farmland bird habitat selection in the local landscape and suggests that management strategies aiming to reconcile production and conversation requires the coordination of stakeholders with a distinct area of influence.

Distinctive patterns of multi-scale habitat selection were found in farmland birds considered bioindicators in Ontario by Kirk et al. (2020). Generalists displayed weak to moderate associations to multiple cover proportions at similar scales, while specialists had a stronger selection to one cover proportion at smaller scales than other selected covers. This variation in generalist and specialists scale selection is possibly caused by differences in species' habitat breadth and area sensitivity during the breeding season. Guild-level patterns of local-landscape habitat selection were associated with inter and intraspecific differences in foraging, nesting, and tolerance to matrix attributes. However, the consistency of these species' traits and related responses varied with scale and landscape context. A regional variation in landscape attributes like land covers' proportion and heterogeneity may cause species to exhibit varying habitat

selection behaviours (Betts et al. 2006; Hadley and Betts 2016). This variability in farmland birds' responses to agricultural landscape composition implies that generalization is difficult and that the design of management policies that benefits all species will be complex.

The distribution of farmland birds based on land cover proportion indicated that top habitat locations increased toward North Ontario for farmland generalists and western-central Ontario for farmland specialists. Heterogeneous landscapes that include all cover seem to favour habitat generalist occurrence. Specialists' occurrence was favoured by grassland and row crop gradients with parse trees near Ontario's green belt. Farmland birds' distribution patterns indicate that large-scale landscapes (>1600m radii) with high cover heterogeneity favours all farmland birds, but management at smaller scales requires different management strategies according to what productive cover is dominant (row crops vs tame grasslands). I suggest future research to assess changes in farmland birds' responses to local-landscape habitat cues in Ontario across gradients of land cover amount and heterogeneity at multiple scales according to reported selected scales in this study. This could help research to improve their inferences on landscape fragmentation effects and inform management decisions by identifying diverse landscape arrangements with varying production and conservation potential.

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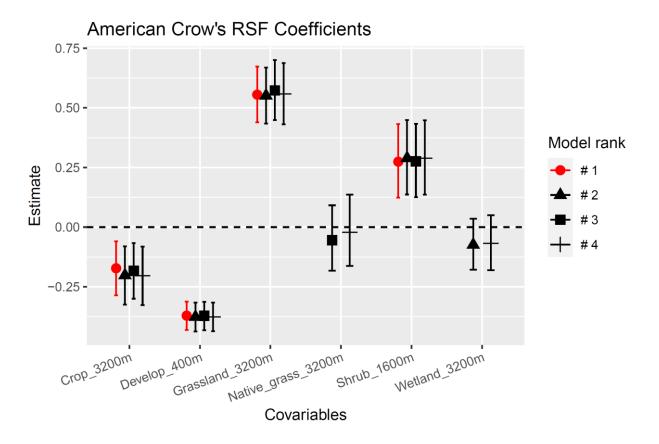
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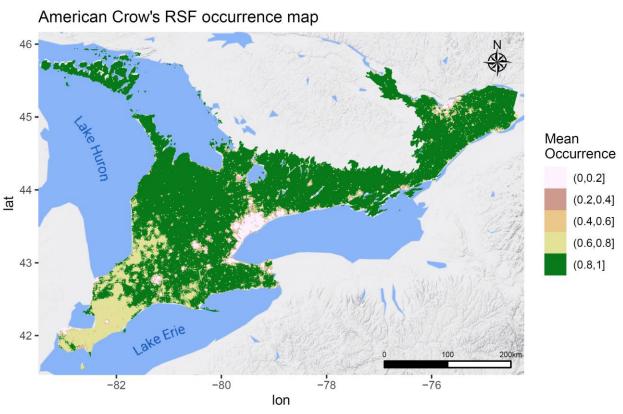
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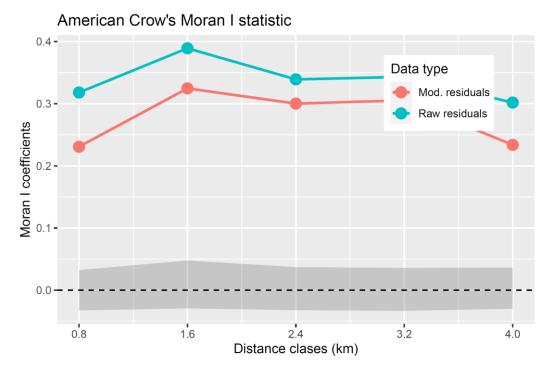
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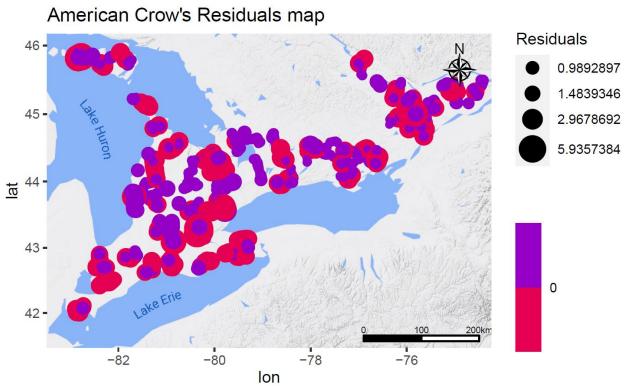
Appendixes

Appendix 1. Species-specific models result. Four figures are presented for each species with validated models: a) A panel with the standardized beta-coefficients and their standard errors for all variables included in each species' resource selection functions with delta-AIC > 2. b) A map representing the relative predicted occurrence probability across the BCR 13 of Canada; c) A spatial correlogram based on Moran I coefficients estimated at each studied scales using the residuals of each species top model; and d) A bubble plot of model residuals for each species top model across the BCR 13 of Canada.

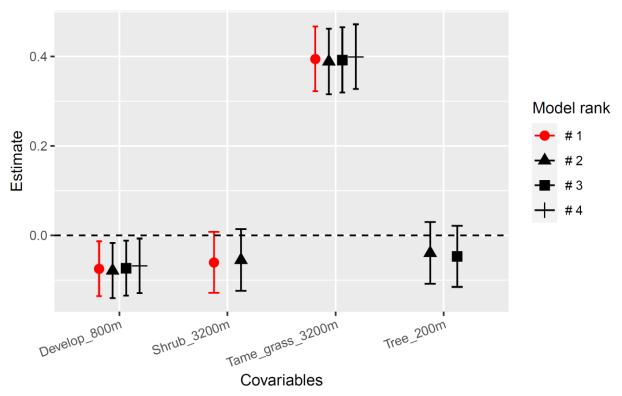




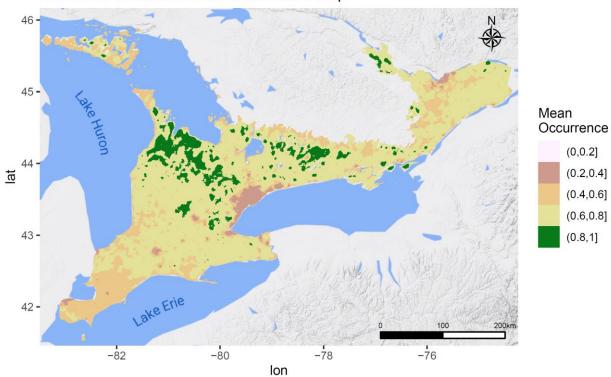




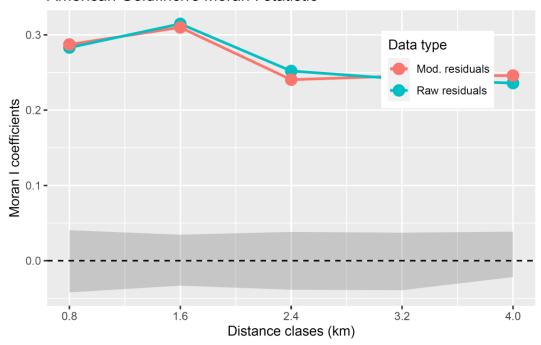
American Goldfinch's RSF Coefficients



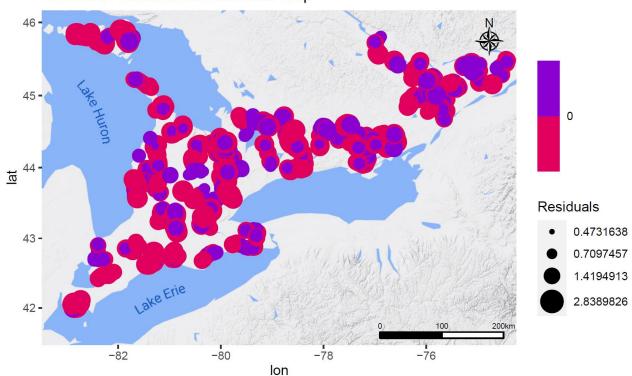
American Goldfinch's RSF occurrence map



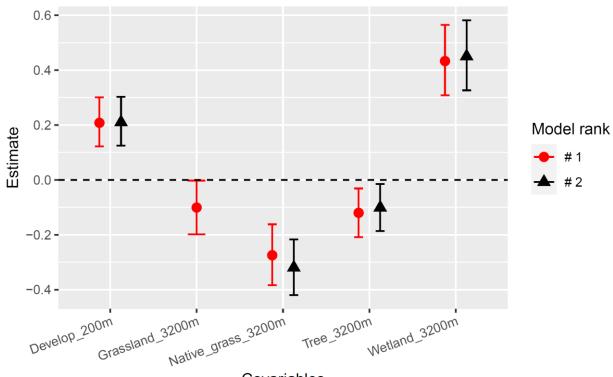
American Goldfinch's Moran I statistic



American Goldfinch's Residuals map

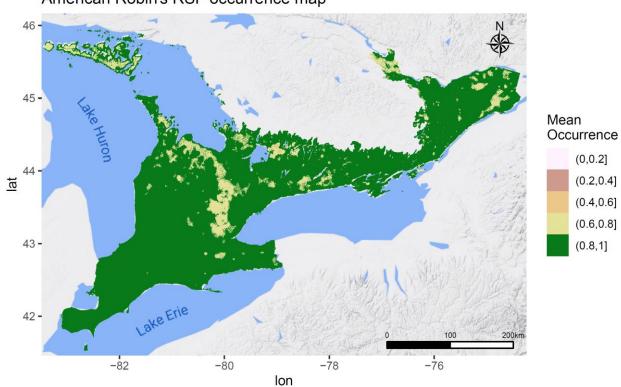


American Robin's RSF Coefficients

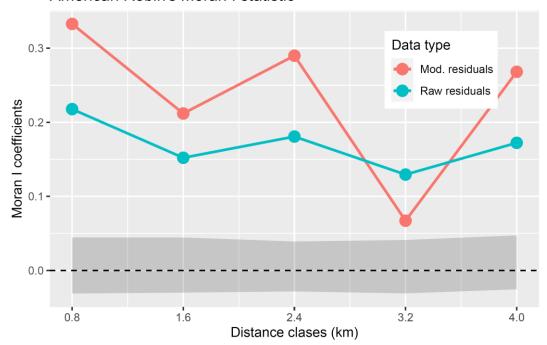


Covariables

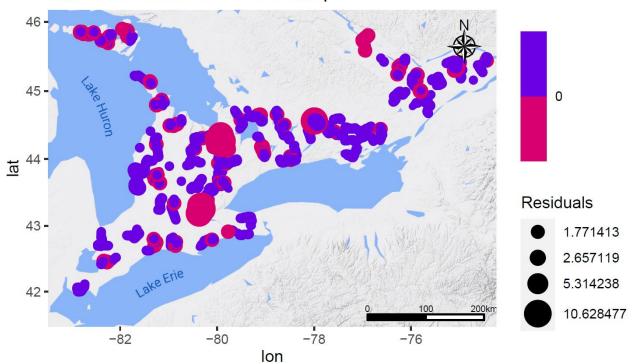
American Robin's RSF occurrence map



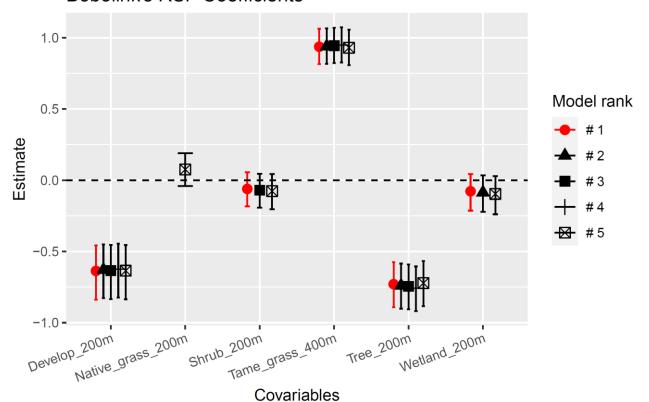
American Robin's Moran I statistic



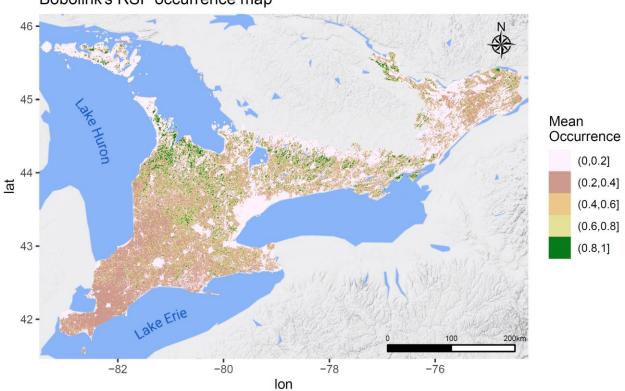
American Robin's Residuals map

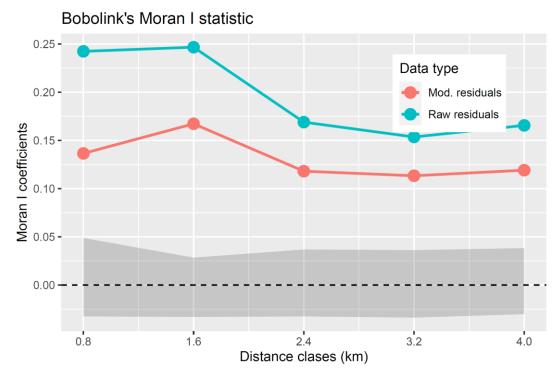


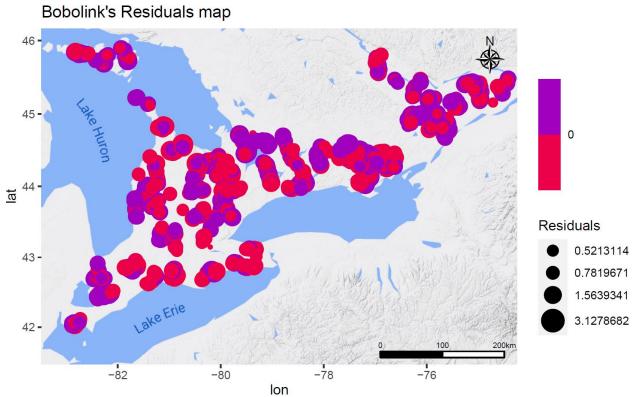
Bobolink's RSF Coefficients



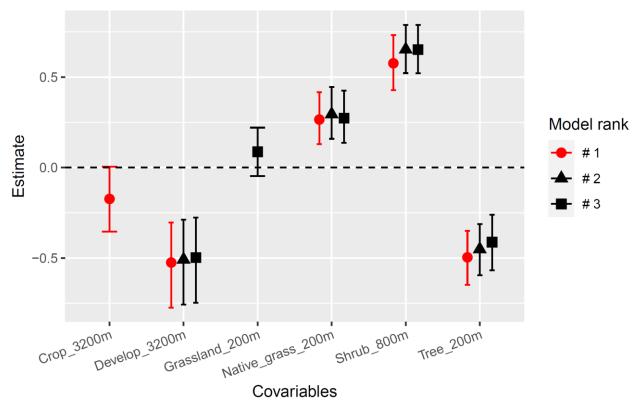
Bobolink's RSF occurrence map



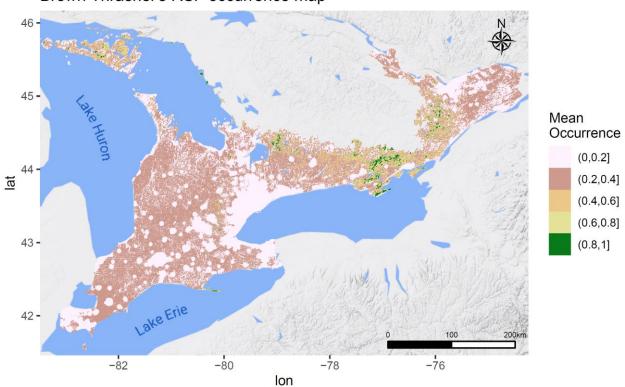




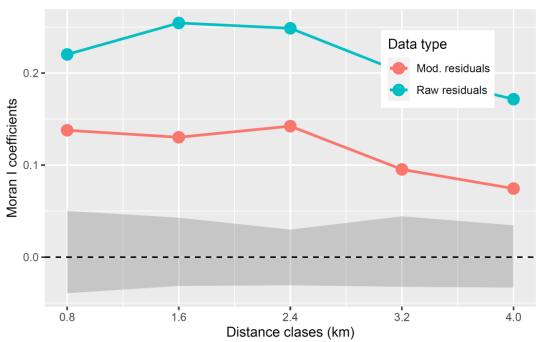
Brown Thrasher's RSF Coefficients



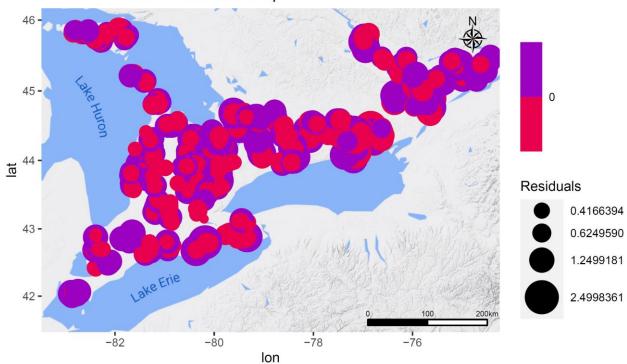
Brown Thrasher's RSF occurrence map



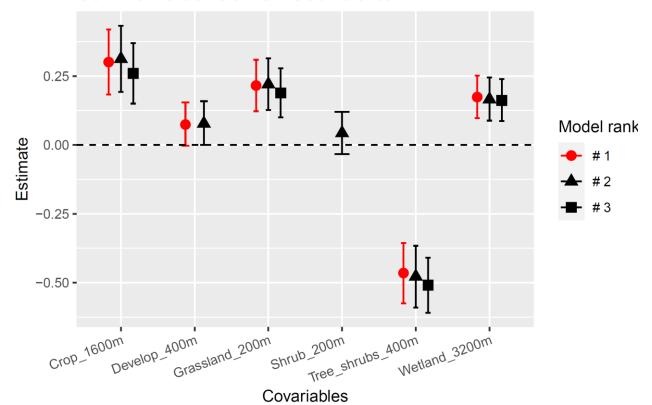
Brown Thrasher's Moran I statistic



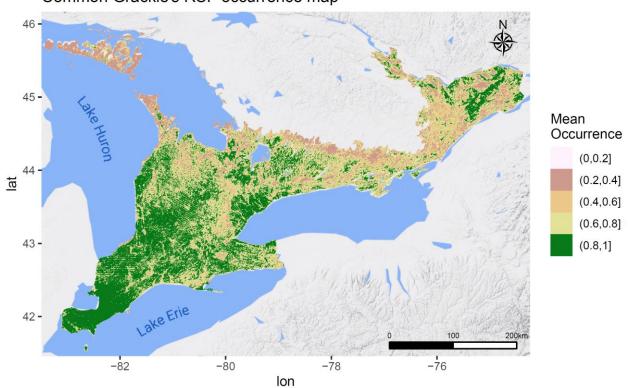
Brown Thrasher's Residuals map



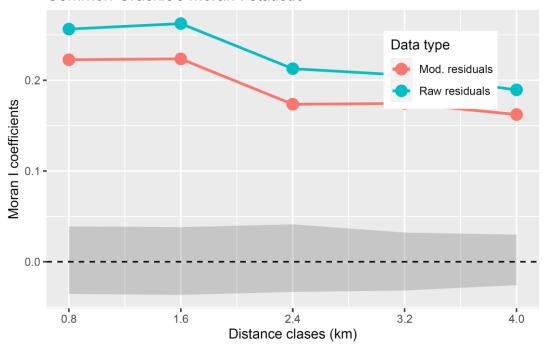
Common Grackle's RSF Coefficients



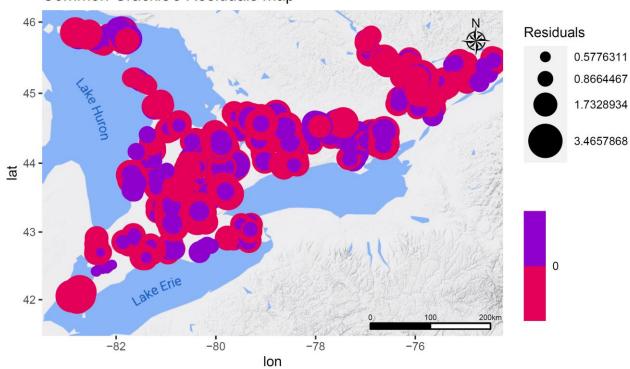
Common Grackle's RSF occurrence map



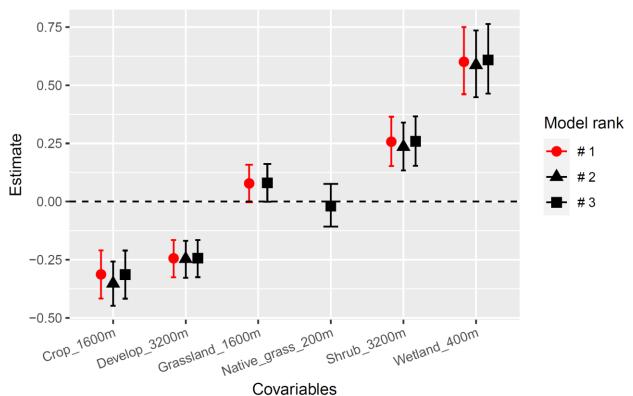
Common Grackle's Moran I statistic



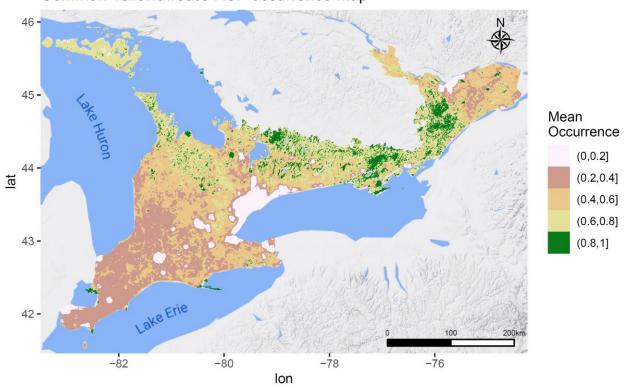
Common Grackle's Residuals map



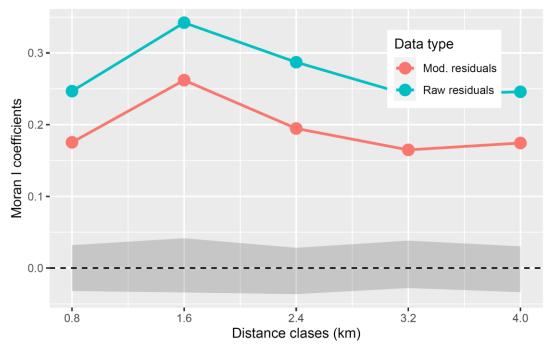
Common Yellowthroat's RSF Coefficients



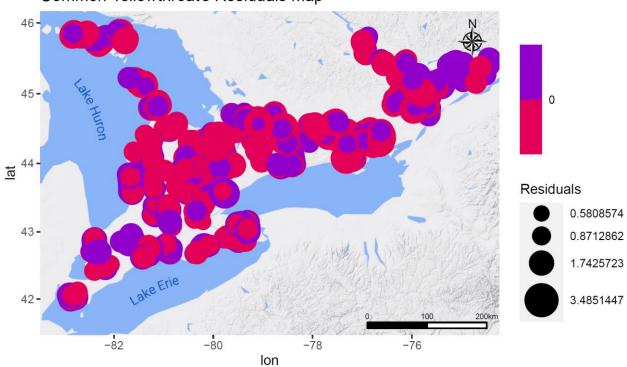
Common Yellowthroat's RSF occurrence map



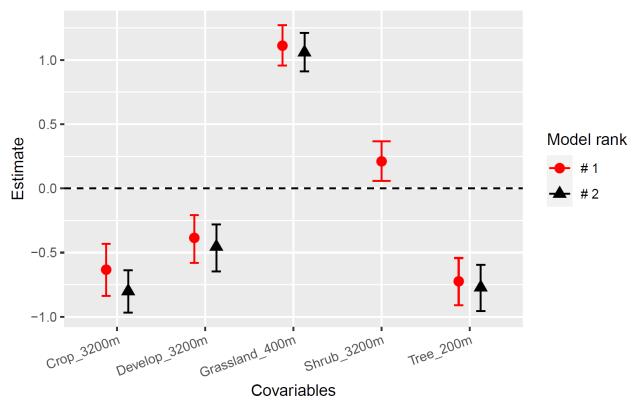
Common Yellowthroat's Moran I statistic



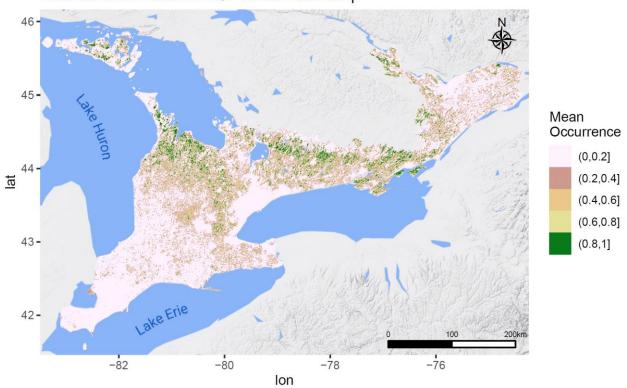
Common Yellowthroat's Residuals map



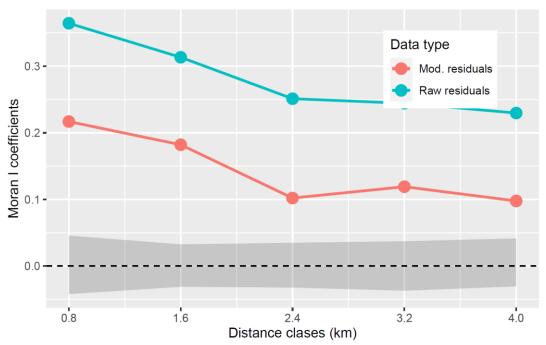
Eastern Meadowlark's RSF Coefficients



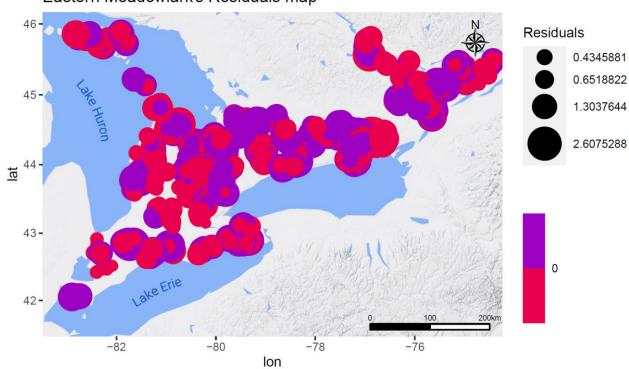
Eastern Meadowlark's RSF occurrence map



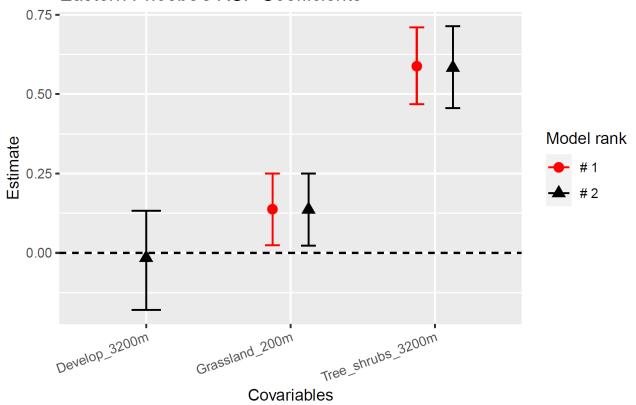
Eastern Meadowlark's Moran I statistic



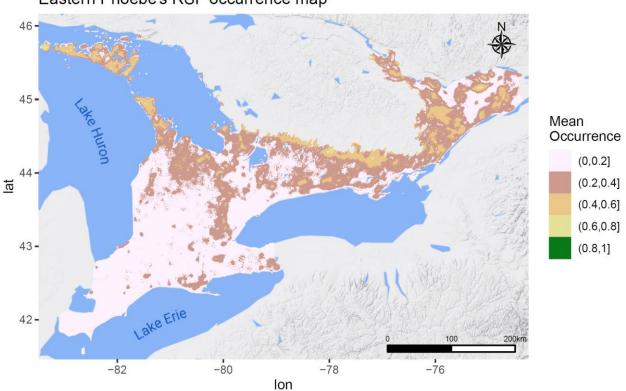
Eastern Meadowlark's Residuals map

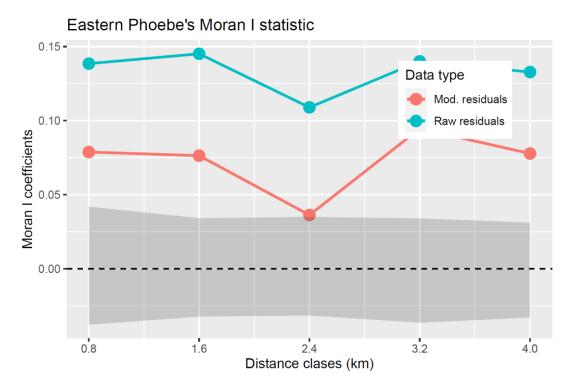


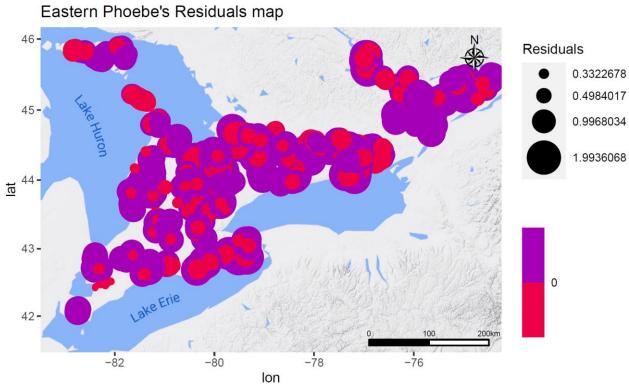
Eastern Phoebe's RSF Coefficients



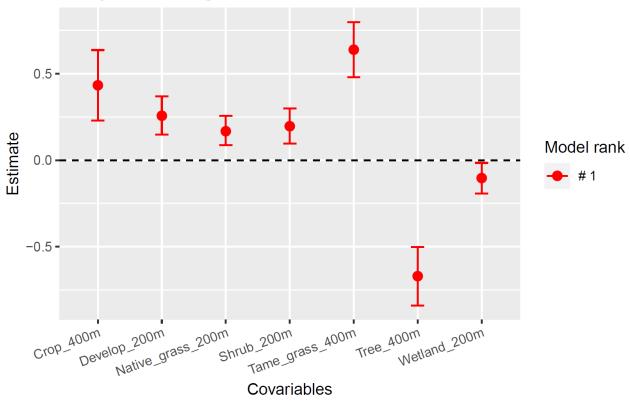
Eastern Phoebe's RSF occurrence map



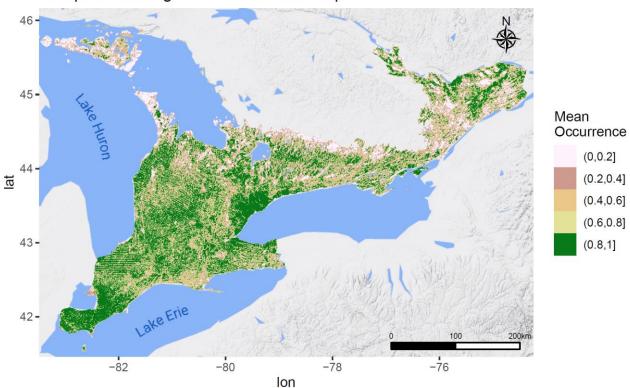


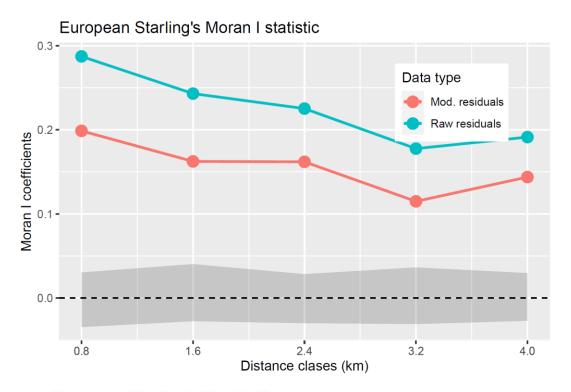


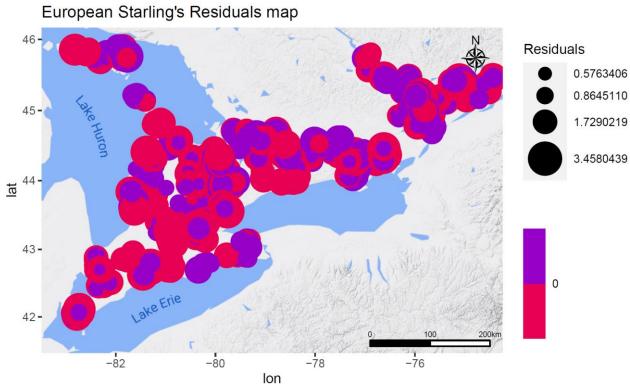
European Starling's RSF Coefficients



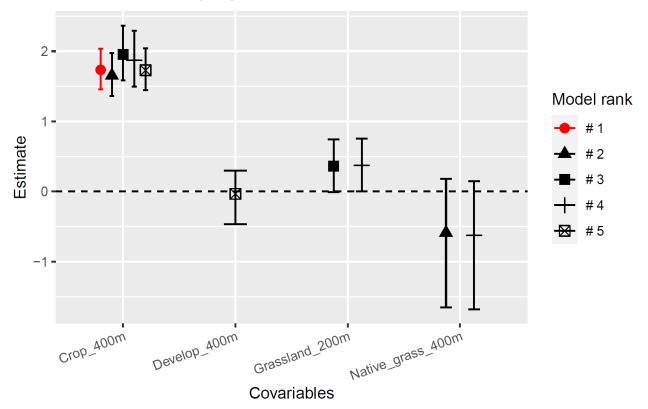
European Starling's RSF occurrence map



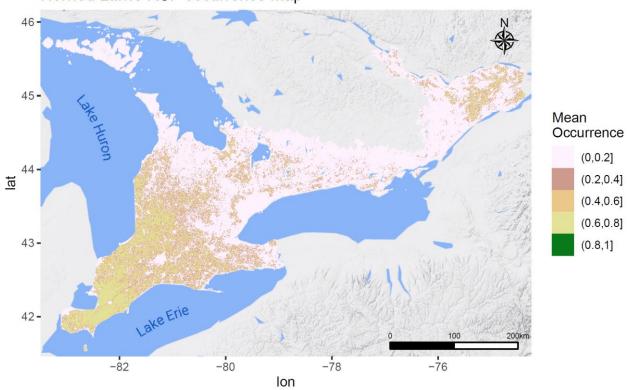


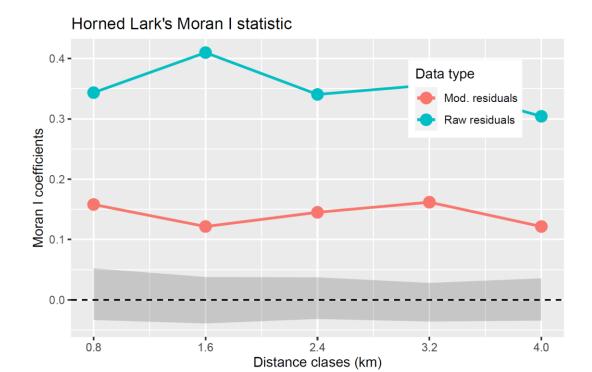


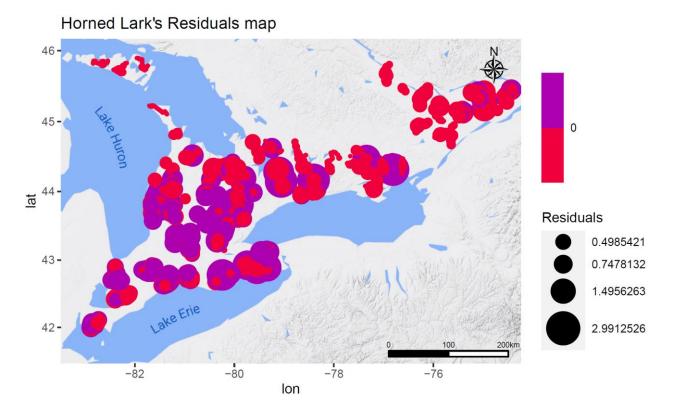
Horned Lark's RSF Coefficients



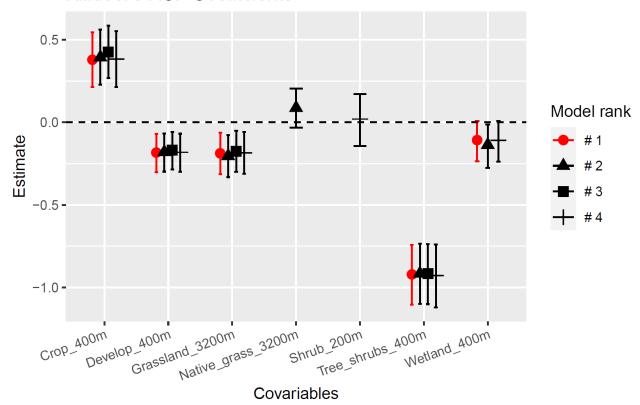
Horned Lark's RSF occurrence map



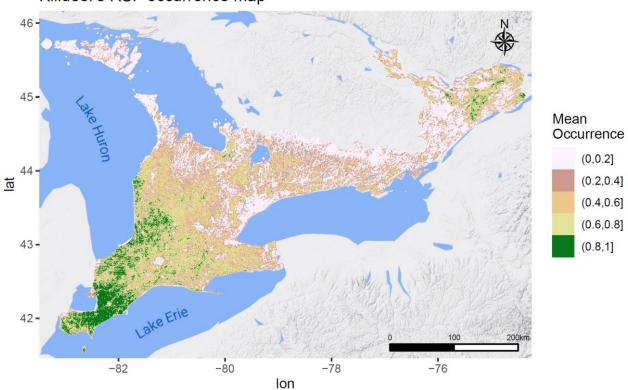


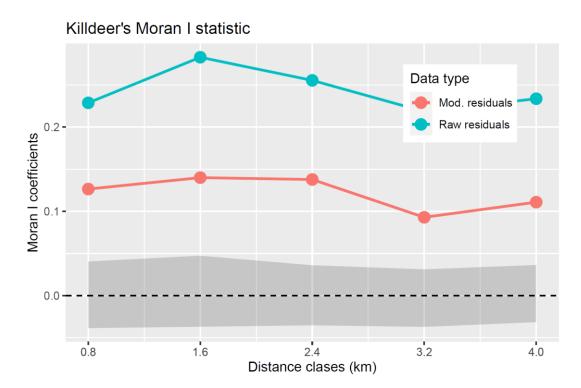


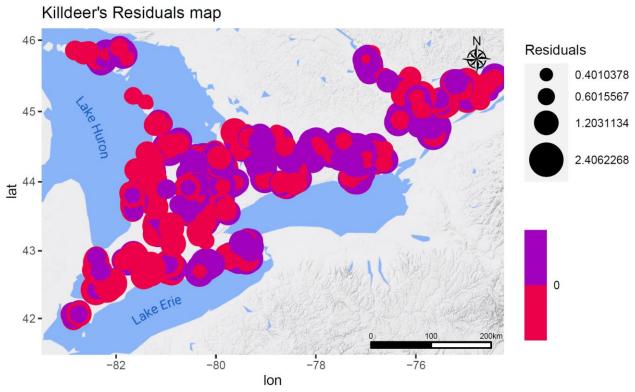
Killdeer's RSF Coefficients



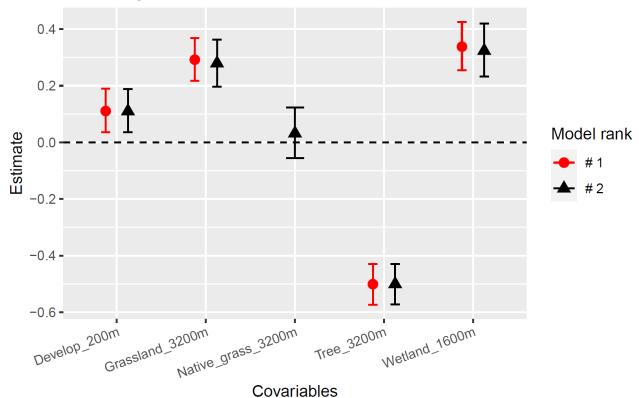
Killdeer's RSF occurrence map



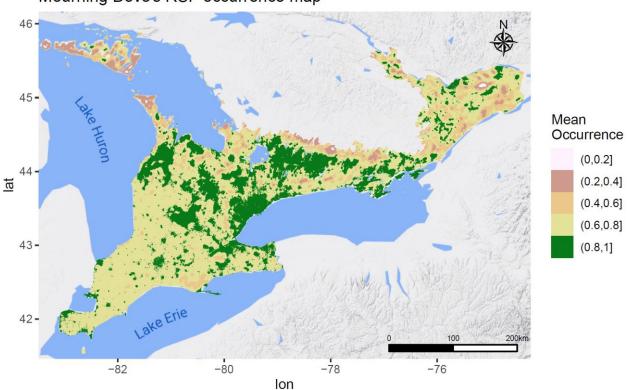


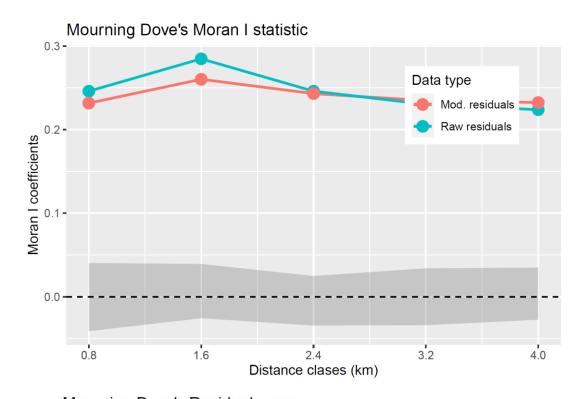


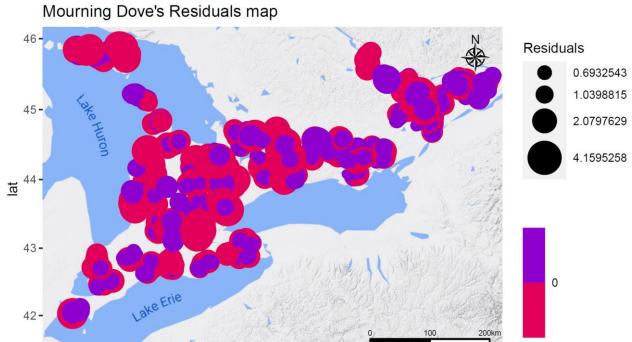
Mourning Dove's RSF Coefficients



Mourning Dove's RSF occurrence map







-78

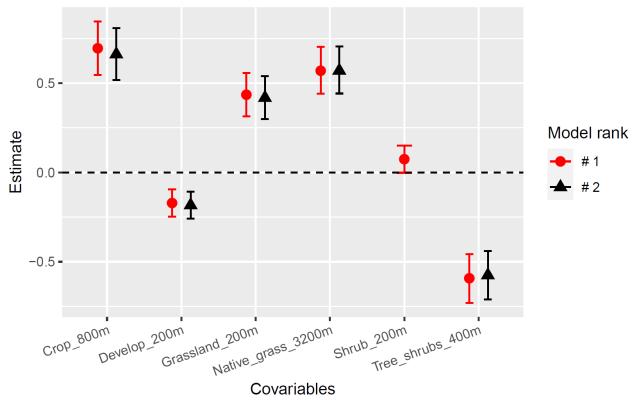
lon

-82

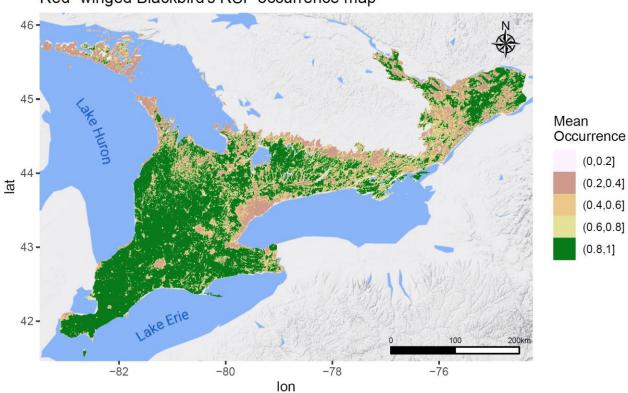
-80

-76

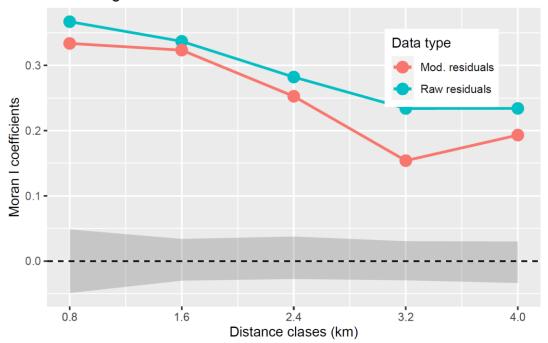
Red-winged Blackbird's RSF Coefficients



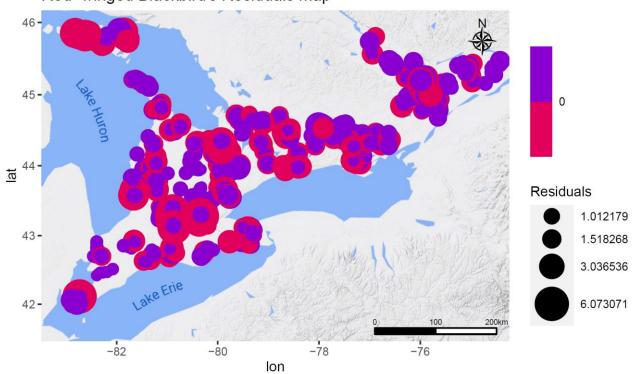
Red-winged Blackbird's RSF occurrence map



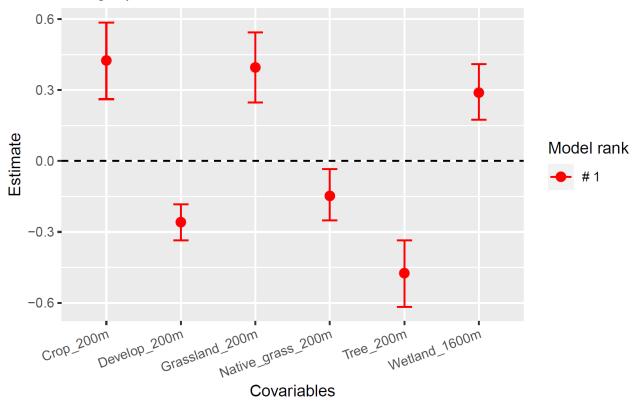
Red-winged Blackbird's Moran I statistic



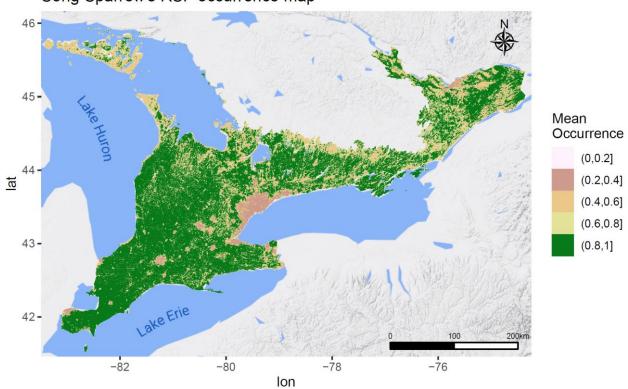
Red-winged Blackbird's Residuals map



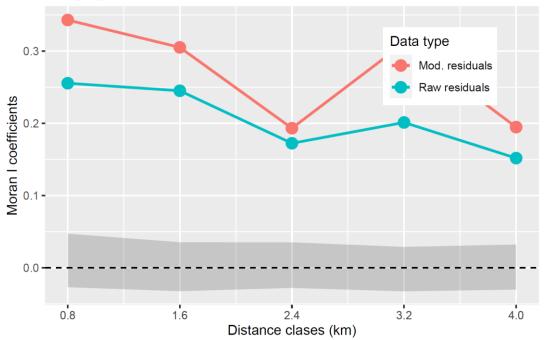
Song Sparrow's RSF Coefficients



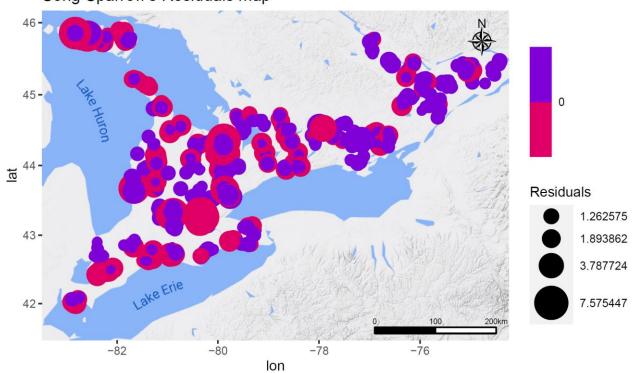
Song Sparrow's RSF occurrence map



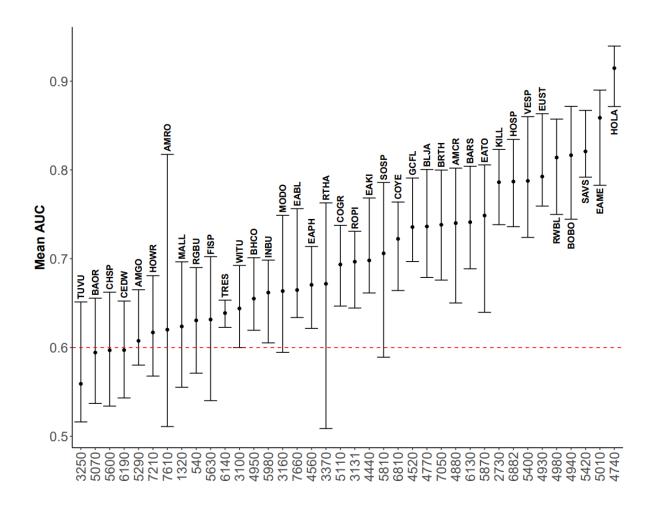
Song Sparrow's Moran I statistic



Song Sparrow's Residuals map



Appendix 2. Estimated area under the ROC curve (AUC) values and their standard error for each species' multivariate top model (i.e., Lowest AICc values).



Appendix 3. Estimated mean Spearman correlation values and its standard error for each species' multivariate top model (i.e., Lowest AICc values).

