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Is habitat conversion likely to impede the ability of bird species to track changing climate?

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Abstract

As climate changes, species' ranges may shift poleward. However, habitat loss in intervening areas has been hypothesized potentially to impede the movements of these species. Populations near range margins offer opportunities to study how marginal species have reacted to habitat loss. We examined the presence/absence of bird species in landscapes that were historically mainly forested (natural land covers) in Southern Ontario, Canada. We used logistic regression to determine each bird species' probability of occupancy (p_{occ}) as a function of natural cover in 991 landscapes, each 100-km². We distinguished three groups of species: i) southerly species whose northern range limits fall in the study area (n=37), ii) northerly species whose southern range limits fall in the study area (n=35), and iii) mid-range species (n=106). We compared p_{occ} for these three groups of species in six different habitat guilds. We found that species near their southern range edges are *less* likely to occur in landscapes where forest amount is reduced, while species near their northern range edge are *more* likely to occur in landscapes with reduced forest. This result is independent of habitat guild. Our results are inconsistent with the hypothesis in the climate change literature proposing that loss of natural land cover near poleward range margins would inhibit range expansion in response to climatic warming. Rather, we hypothesize that, at southern range edges, the dual stresses of climatic warming and forest conversion both reduce species' ability to occupy a landscape. However, near northern (potentially expanding) range edges, partially disturbed landscapes are more readily invaded than undisturbed landscapes.

Highlights

- The study of species near their range edges may offer clues to whether habitat conversions due to human activities are imposing barriers to species tracking warming climates.
- Southerly species living at their northern edge, and northerly species near their southern edge, have responded differently to land cover conversions.
- Species at their southern range edge are *less* likely to occur in landscapes where forest amount is reduced, while species near their northern range edge are *more* likely to occur in landscapes with reduced forest.
- We propose that warming climate and forest conversion both reduce many species' abilities to occupy landscapes at their southern range edges. In contrast, near northern range edges, which are potentially expanding, partially disturbed landscapes are more readily invaded than undisturbed forested landscapes.

Keywords: Birds, land-cover conversion, probability of occupancy, range limits, southern Ontario, warming climate.

Introduction

Many climate change studies have suggested that habitat loss and fragmentation threaten to pose a barrier to shifting species' ranges, as ranges shift to track warmer temperatures (van de Pol et al. 2010,

Mantyka-Pringle et al. 2012, Oliver et al. 2015). At species' poleward range edges, warmer temperatures may provide new habitat opportunities (Thomas et al. 1999b, Lennon et al. 2002, Oliver et al. 2012). If populations near northern range limits have been limited by their cold tolerance, then climatic warming should

potentially lead to larger population sizes and range expansion (Davies et al. 2006). However, as species' ranges expand poleward (Parmesan et al. 2003), a lack of undisturbed habitat could, in principle, prevent species from occupying newly climatically suitable areas (Sieving et al. 1996, Travis 2003, Opdam et al. 2004, Lawler et al. 2013, 2014; Robillard et al. 2015). For example, in a recent study with European birds, Oliver et al. (2017) showed that greater land use intensity exacerbates the decline of species adapted to cold places (northerly species) and prevents increases in abundances of species adapted to warmer places (southerly species). Melles et al. (2011) showed that range expansion of the Hooded Warbler (*Wilsonia citrina*) is primarily driven by trends of warmer temperatures in southern Ontario, Canada. The authors speculated, however, that habitat connectivity might slow the species' range expansion.

Alternatively, species colonizing novel areas may actually do better in partially disturbed environments. The reasons are several. Such areas may have reduced "biotic resistance" (Guo et al. 2012, González-Moreno et al. 2015). Human-modified landscapes can be highly productive and have high structural complexity (Swanson et al. 2011). Some bird species prefer open habitats, while others prefer forest (Cadman et al. 2007). Thus, mixtures of land cover types offer a greater diversity of potential habitats than does uniform natural land cover (De Camargo et al. 2015). Desrochers et al. (2011) found that avian species richness in 100-km² landscapes in Ontario, Canada, is a peaked function of the ratio of natural to human-dominated land covers. Their result suggested that natural land cover conversion and fragmentation may not pose a barrier to shifting species' ranges in landscapes with more than ~40% natural cover.

Marginal populations may offer a good opportunity to test whether species respond differently to land cover conversion at northern, versus southern, limits of their ranges. Overall, smaller population size and lower genetic variability in edge-populations could increase extinction proneness (e.g., "central-marginal" hypothesis, Eckert et al. 2008). Conversion of natural land covers to human-dominated land covers could harm marginal populations through spatial isolation, habitat fragmentation, or heterogeneity that reduces gene flow (Eckert et al. 2008). Near their southern range edges, northerly populations might be more prone to extinction due to climate conditions that exceed individual species' tolerances (Kirkpatrick & Barton 1997, Hampe & Petit 2005, Anderson et al. 2009, Sunday et al. 2012), which ultimately determine limits of a species' niche (Brown 1984, Parmesan et al. 2005). For instance, bird populations in protected areas of Finland have experienced increased population densities at the (leading) northern edge of species' ranges and decreased density at the (trailing) southern edge (Virkkala et al. 2011, 2014). Northwards range shifts of bird species in eastern North America appear to be driven mainly by climatic variables, and southern-edge boundaries are moving northwards faster than the northern-edge limits (Zuckerberg et al. 2009).

In this study, we test the following hypothesis: at their northern range limits, southerly avian species are generally *more* likely to occupy landscapes in which moderate amounts of natural land cover have been converted to human-dominated land cover. Near their southern range limits, northerly avian species are generally *less* likely to occupy landscapes with significant amounts of human-dominated land cover. We refer to "natural land cover", rather than "habitat", because habitat is species-specific. Our focus in this study is the overall response of avian species to anthropogenic land modification; species richness clearly depends upon the amount of natural land cover in an area (Pereira et al. 2006, Fahrig 2013). However, we also test our hypothesis with several avian habitat guilds. We speculated that moderate disturbance of natural land cover makes landscapes more favourable for species whose ranges are expanding into an area and less favourable for species that are already established in the area. Our hypothesis, if supported, implies that natural habitat conversion does not in fact inhibit species' ability to track changing climate.

Most studies of northern and southern range edges have considered a fixed set of species in different geographic regions. Here, we use a complementary approach: we examined a single region in which a large number of both northern and southern range limits occur. This approach has the advantage that it avoids the confounding effects of environmental variables other than land cover that may also differ between southern-edge and northern-edge boundaries. This approach has the disadvantage that we examine different sets of species at southern, versus northern, range boundaries.

Methods

Overview

We address the questions above using a "natural experiment". We examine a large region which was largely covered by natural land covers prior to European settlement. Subsequently, in landscapes across the region, varying proportions of natural land covers were converted to human-dominated land covers. We assume that the amount of natural land cover in landscapes has remained relatively stable for the last 50–100 years (Warwick 1980, Elliott 1998). We examine the probability of occurrence of avian species in landscapes that differ in natural cover. We assume that bird assemblages are more or less at equilibrium with respect to land cover in the landscapes where they occur.

Study Area and land cover

Our study area covers southern Ontario, Canada (41°–44° N and 84°–74° W, an area of ~200,000 km², see Fig. 1). Prior to European settlement, southern Ontario was covered mainly by forest and wetlands (Warwick 1980, Puric-Mladenovic 2011). Open habitats resulted from fires, beaver activity, and natural alvars (sparsely treed wetland environment on limestone). Indigenous people also created clearings for shifting

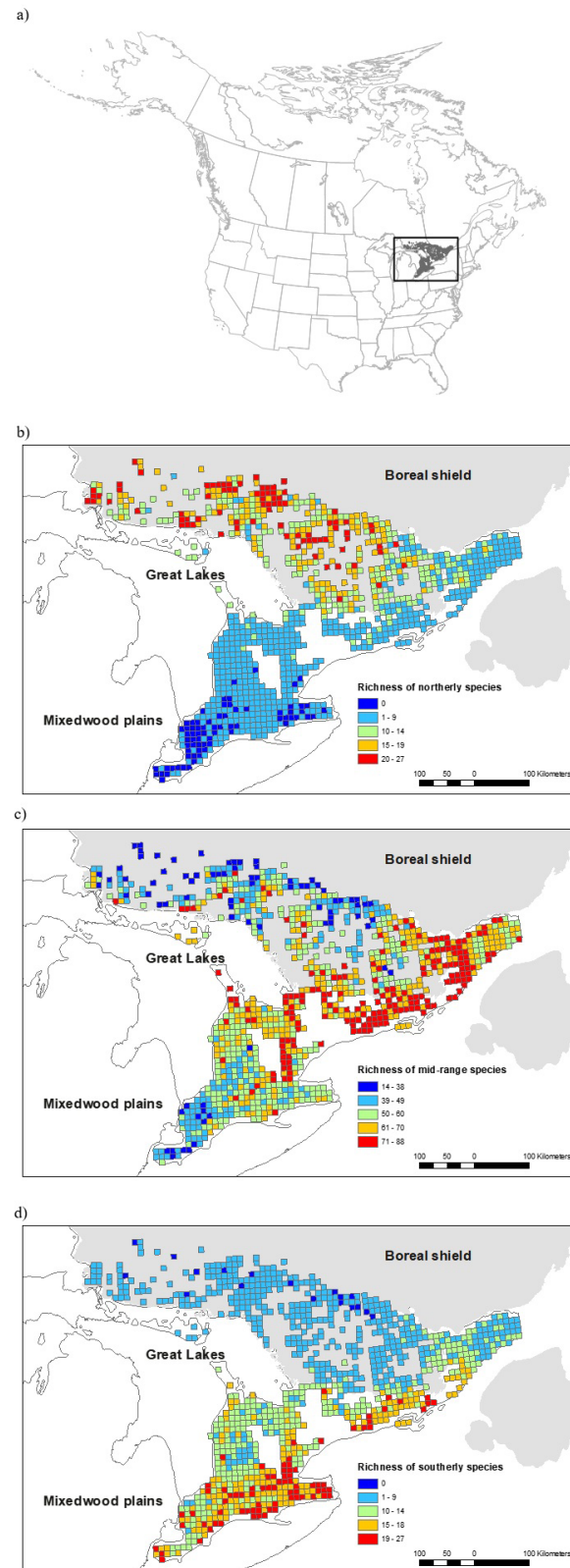


Figure 1. a) Study area in southern Ontario, Canada (shaded in grey in the map of North America). b) The number of northerly species (i.e., those whose southern range margin falls within the study area). c) The number of mid-range species (those whose ranges completely overlap the study area). d) The number of southerly species (those whose northern range margin falls within the study area). b-d, The pale grey background represents the conifer-dominated Boreal Shield ecozone. Unshaded background represents the Mixed Wood Plains ecozone, with a high proportion of deciduous trees. Uncoloured quadrats did not meet the inclusion criteria for the study (most often, insufficient sampling effort). The projection is Lambert conformal conic.

agriculture (Elliott 1998, Belshaw 2015). European colonization brought extensive logging and land clearing for farming in the 18th – 19th centuries (Warwick 1980). By the early 20th century, intensive logging had finished (Elliott 1998), and by the mid-20th century, government programs promoted afforestation, selective harvesting, and silviculture on private woodlots in southern Ontario (Perera, A.H., Euler, D.L. and Thompson 2000). As a result of decreased agriculture and forestry, the amount of forest cover has been relatively stable for the last 70 years¹. However, fire suppression and selective harvesting have favoured deciduous species at the expense of conifers in remaining forest, both within the study area and further north (Jackson et al. 2000)

We determined the proportions of different land covers within 100-km² UTM (Universal Transverse Mercator) quadrats (hereafter, landscapes) covering the study area. Remotely sensed land cover data were obtained from the Ontario Provincial Scale Land Cover data set produced by the Ontario Ministry of Natural Resources (2002) from Landsat 7 Thematic Mapper² scenes captured primarily in the 1990s (resampled to a 30-m resolution). Land cover had been classified into 28 land cover classes. We grouped these classes into two broad categories: “human-dominated” land covers and “natural” covers. Human-dominated land covers include seven classes, including recent cutovers, mine tailings, quarries, bedrock outcrops, settlement and developed land, pasture and abandoned field, and cropland. Within human-dominated covers, 76% is cropland (row crops, hay, or open soil), while the rest (24%) corresponds mainly to recent cutovers, mining, urban areas, and pastures. Natural land covers (those with relatively little recent anthropogenic disturbance) include nine classes of forest cover, including older forest clear-cuts and forest fires, and seven classes of wetlands. Forests constitute 97% of the total area in the natural category. We excluded water and unclassified land cover in the calculation of % natural area. Five other classes in the original land-cover classification did not occur in the study area. The current landscapes in the region vary from entirely natural to entirely human-dominated land covers.

Bird species distributions

We used bird species distributions in southern Ontario (Canada) reported in the 2005 Atlas of the Breeding Birds of Ontario (ABBO) (Fig. 1b-d, Cadman et al. 2009). The ABBO reports the presence or absence of breeding bird species in the 100-km² UTM quadrats in southern Ontario. Volunteer ornithologists searched each ABBO landscape as thoroughly as possible for evidence of breeding birds over a five-year period, 2000–2005. We excluded the data from the northern parts of the province where the ABBO quadrats were much larger (10⁴ km²) and sampling intensity was much lower. We also excluded wedge-shaped UTM

quadrats and quadrats overlapping the Great Lakes that were >10% water to minimize variation in area among landscapes.

Sampling effort positively influences species detection, and sampling intensity varies considerably among landscapes. We excluded landscapes with the most extreme observer effort (<20 or >600 hours) (Cadman et al. 2007) because these points had disproportionately high leverage in our models. We then used sampling effort in the remaining quadrats as a covariate in our models. These sampling effort criteria included a total of 202 species (Table S1). Next, we eliminated 18 species that occurred in <3% or >90% of the quadrats (i.e., they are quite rare or nearly ubiquitous) because the probability of occupancy of these species is essentially independent of environmental variables (Jiménez-Valverde et al. 2008). We also eliminated six species for which logistic regression models did not converge. These selection criteria left 178 bird species in 991 landscapes (see the complete list of included and excluded species in Table S1.1, Appendix S1).

In each landscape, we tallied total species richness, as well as richness in six guilds defined by preferred habitat, as characterized in Cadman et al. (2009). We distinguished six categories. Edge species: specialist species more commonly found close to forest edges than in the interior forest (n=16 species). Interior-edge species: species found throughout forested land cover (n=27). Interior species: specialist species totally dependent on forest interior to nest and/or to feed (n=33). Open Habitat species: species commonly found in grasslands, disturbed woodlands, scrub or hills / mountains (n=45). Urban species: species adapted to live in cities, nesting in buildings, backyards, light posts, among others (n=8). Wetland species: specialist species found close to lakes or ponds, shorelines, marshes, rivers, or streams (n=49) (see Table S1.1, Appendix S1).

Geographic range groups

We divided the 178 species into three geographic groups using BirdLife International range maps³ (see Fig. S1.1, Appendix S1). The first group, which we shall call “northerly species”, consists of species with ranges whose southern edge falls within our study area and the range extends farther north (n=35, Fig. 1). The second group, “southerly species”, includes species whose ranges reach their northern limit in the study area and the range extends farther south (n=37, Fig. 1). The third group, “mid-range species”, includes species whose ranges extend over the entire study area (n=106 species, Fig. 1, Table S1.1, Fig. S1.1, Appendix S1). Ranges maps are known to be somewhat approximate (Herkt et al. 2017); however, we found reasonably good correspondence between the BirdLife range maps and the field observations of birds in the

1 Retrieved from: <http://www.drpaulkeddy.com/pdffiles/Cathy%20Keddy--1993--A%20Forest%20History%20of%20Eastern%20Ontario.pdf>. Date of access: 1st July 2019.

2 Retrieved from: <https://landsat.gsfc.nasa.gov/the-thematic-mapper/>. Date of access: 25th Sept 2018.

3 Retrieved from: www.birdlife.org. Date of access: 25th Sept 2018.

North American Breeding Bird Survey data (S. Venne, unpublished).

Many northerly species in southern Ontario are mainly associated with the coniferous boreal forests of the Laurentian Shield (gray area in Fig. 1b), while many southerly species are associated with the mixed-wood forests bordering the Great Lakes (Fig. 1d). However, the distributions of these species' groups are not strictly limited to the biomes where they are most common, and there is no distinct boundary between the two (Fig. 1).

Statistical Analysis

First, we modelled individual species' probability of occurrence (p_{occ}) in each ABBO landscapes as a function of the proportion of natural cover. We considered a species to be present in a landscape if there was confirmed or probable evidence of breeding in the landscape. We considered a species as being absent from a landscape if evidence of breeding was lacking and if that landscape fell within 20 km of an occupied landscape. Otherwise, the quadrat was considered out-of-range, and it was excluded from analysis for that species. This limits the data to occupied quadrats and neighbouring unoccupied quadrats. Land cover can vary dramatically from one 100-km² landscape to the next, whereas unoccupied landscapes farther away may be unoccupied for a varied of other reasons: unsuitable climate, dispersal barriers, historical factors, etc. Note that this exclusion criterion does not yield a paired study design; rather, it is intended to ensure that the distributions of environmental variables other than land cover are similar in occupied and unoccupied quadrats (in order to minimize collinearity).

We related the probability that a species will occupy a given landscape, p_{occ} , to varying proportions of natural cover using logistic regression models in which the species' presence and absence is fitted as a quadratic function of natural area (A) and log-transformed sampling effort ($\log_{10} Effort$) within landscapes in the study area, as follows:

$$\ln(p_{occ} / (1 - p_{occ})) = \alpha + \beta_1 A + \beta_2 A^2 + \beta_3 \log_{10} Effort \quad (1)$$

with a logit link. We used the quadratic term in the logistic model because it allows maximal occupancy to occur in landscapes with intermediate proportions of natural cover. The quadratic model better describes the shape of the relationship between species' probability of occurrence and area for about half of the species, in comparison to models that included only the linear term ($\Delta AIC \leq 2$); α , β_1 , β_2 and β_3 represent the fitted coefficients.

Bird species' sensitivity to low amount of natural land cover

The main goal of this study is to test whether the sensitivity of bird populations to the amount of natural (versus human-dominated) land cover differs between northerly species and southerly species. To do this, for each species we calculated the predicted probability of

occurrence \hat{p}_{occ} in low densities of natural cover versus \hat{p}_{occ} in fully natural landscapes from the fitted logistic models. Then, we calculated each species' sensitivity (Ω_i) to a given proportion of natural land cover i below 100% as the log of the ratio of predicted probability of occurrence \hat{p}_{occ} within landscapes with reduced natural cover (e.g., 15% natural cover), relative to the probability of occurrence with 100% natural cover:

$$\Omega_i = \log_{10} \left(\frac{\hat{p}_{occ}(A_i)}{\hat{p}_{occ}(A_{100})} \right) \quad (2)$$

where $\hat{p}_{occ}(A_i)$ is the predicted probability of occurrence of a species in a landscape with i % natural cover, calculated from 5%, to 95%, and $\hat{p}_{occ}(A_{100})$ is the predicted probability of occupancy at 100% natural cover. For this calculation, we held sampling effort constant at its median value. Values of $\Omega_i < 0$ indicate that the species has a lower probability of occurrence when the natural cover is lower than 100%. Values of $\Omega_i > 0$ mean that \hat{p}_{occ} is greater with reduced natural cover.

Do northerly and southerly species respond differently to low natural cover?

To answer this question, we used two-way ANOVA to test whether the $\bar{\Omega}_i$ (i.e., mean ratio of \hat{p}_{occ} at i % to 100% natural cover) calculated for each group of species (northerly, southerly, and mid-range species) differ from each other and from zero. The objective here is to compare how different groups of species respond to the amount of natural cover in the landscape. Below, we present the results for $\bar{\Omega}_{15\%}$, and in Appendix S1 we show results for $\bar{\Omega}_{25\%}$, $\bar{\Omega}_{50\%}$, and $\bar{\Omega}_{75\%}$ (Fig. S1.2. Fig. S1.3 shows the distributions of Ω among species. Fifteen percent natural cover is arbitrary, but higher values of Ω yield qualitatively similar results. Several authors have suggested that forest cover below $\approx 25\%$ may represent an extinction threshold for many species (Andr n 1994, Fahrig 2003, Rybicki et al. 2013).

It is possible that $\Omega_{15\%}$ may differ among species with different habitat requirements. For example, low natural cover, which is mainly forest, should more adversely affect forest birds than open-habitat species. We therefore summarized $\bar{\Omega}_{15\%}$ for the six different habitat groups. For each group, we tested whether $\bar{\Omega}_{15\%}$ depends upon whether species are northerly, mid-range, or southerly.

Finally, the proportion of a species' range that falls within the study area varies among species. In principle, most of the range of a small-ranged species could fall within the study area, while only a very small portion of a very widespread species may do so. In practice, very few species that breed in Ontario are small ranged. However, we tested whether the variance in $\Omega_{15\%}$ among species was collinear with the fraction of a species' range that falls within the study area. Statistical analyses were performed in the R statistical programming environment (R Development Core Team, 2019).

Results

In landscapes where moderate proportions of natural cover have been converted to human-dominated covers (assuming ≈100% natural cover before European settlement) there are relatively few species whose probability of occupancy is much reduced (Fig. 2a). In fact, 66% of all species showed $\Omega_i > 0$ in landscapes with moderate amount of natural cover conversion (e.g., 50%), meaning that they are more likely to occur in partly disturbed landscapes than in undisturbed natural cover (Fig. 2b).

However, at lower levels of forest cover (e.g., below 25%), the probability of occupancy does decline substantially for all guilds, except for urban species (Fig. 2a). Most forest-interior species were sensitive to landscapes with low forest cover, but perhaps surprisingly, 30% of interior-edge species did not have a lower probability of occurrence at 15% forest cover, relative to 100% (Fig. 2a). In landscapes with very little forest, even open-habitat species and wetland species are less likely to occur than at 100% natural cover (Fig. 2a).

The effect of extensive conversion of natural land cover to human-dominated covers varies strongly among the three geographic groups of species, and among species guilds (Table 1 & 2). At low proportions of natural covers (e.g., 15%), northerly species had on average significantly reduced probability of occurrence

(Fig. 3) in the study region, whereas southerly species had on average significantly greater probability of occurrence than in landscapes with 100% natural cover (Fig. 3). For mid-range species, the mean ratio of the predicted probability of occupancy at 15% forest cover, relative to 100% forest cover ($\bar{\Omega}_{15\%}$), differs among habitat guilds, but, overall, the mean is close to zero. For these species, reduction of natural cover from 100% to 15% had predictable effects on their probability of occupancy: lower probability for forest-associated guilds and higher probability for open habitat-associated guilds. Similar results were obtained using different proportions of natural land covers (e.g., $\bar{\Omega}_{25\%}$, $\bar{\Omega}_{50\%}$ and $\bar{\Omega}_{75\%}$) (Fig. S1-2).

Probability of occupancy at low forest cover ($\bar{\Omega}_{15\%}$) was not significantly correlated with the proportion of species' ranges that fall within the study area ($r^2=0.003$, $p>0.05$). The differences in $\bar{\Omega}_{15\%}$ among habitat guilds were also uncorrelated with the fraction of species' ranges that fall within the study area.

Discussion

In southern Ontario, species that are at their northern limits have a higher probability of occurrence in landscapes with reduced forest cover, while species that are at their southern limits have lower probability of occurrence when forest cover is lower (Fig. 3). Like elsewhere, southern Ontario is experiencing warmer

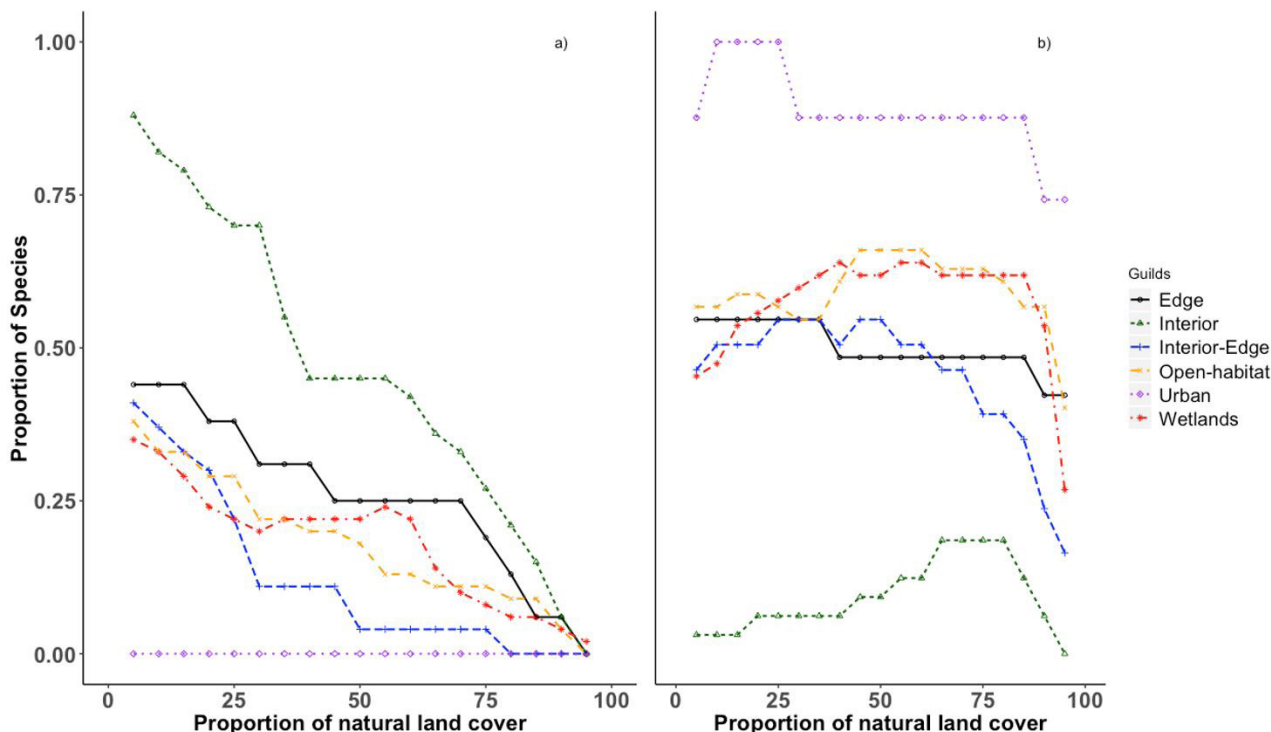


Figure 2. The proportion of bird species in six habitat guilds for which the predicted probability of occurrence ($\hat{\rho}_{occ}$) is a) $>25\%$ lower or b) $>25\%$ higher than $\hat{\rho}_{occ}$ in landscapes with 100% natural land cover. This ratio is shown as a function of the percentage of natural land cover within landscapes of southern Ontario, Canada. It is evident, for example, that reduced natural cover has a dramatically negative effect on forest-interior birds. Total number of species = 178, edge-species = 16; interior-edge =27; interior =33; open-habitats =45; urban=8; wetlands=49.

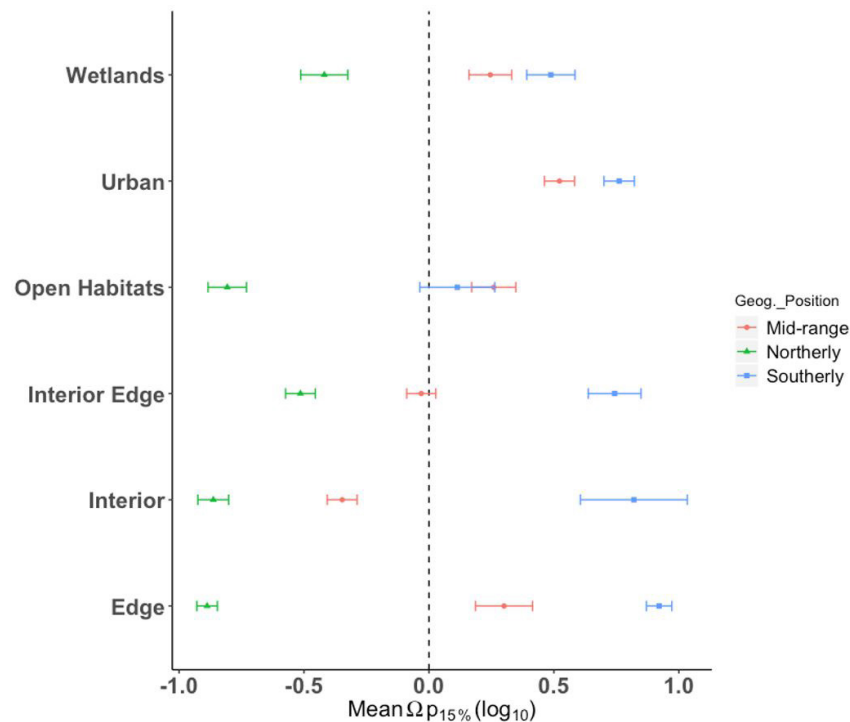


Figure 3. The ratio of the probability of occupancy at 15% natural cover in the landscape ($\bar{\Omega}_{i15\%}$), relative to the probability of occupancy at 100% forest cover, within landscapes of southern Ontario, Canada. This ratio is shown for three geographic range groups (mid-range-, northerly-, and southerly- species) divided into six habitat guilds (i.e., mean ratio of \hat{p}_{occ} at 15% to 100% natural cover). Bars represent standard errors.

temperatures due to climate change (Varrin et al. 2007, Zuckerberg et al. 2009, Melles et al. 2011, McDonald et al. 2012). The literature often suggests that in northern hemisphere mid-latitudes, northern-edge populations should therefore expand their range limits northwards, while southern-edge populations potentially retract (Parmesan et al. 1999, 2003, Thomas et al. 1999a, Brommer 2004, Chen et al. 2011, Coristine et al. 2015), and that anthropogenic habitat modification could pose additional challenges for these marginal species (Opdam et al. 2004, Oliver et al. 2009, 2014, Melles et al. 2011). The literature also suggests that habitat loss and fragmentation could block the expansion of ranges of marginal species northwards as temperatures increase (Warren et al. 2001, Opdam et al. 2004, Manning et al. 2009, Mantyka-Pringle et al. 2012, Oliver et al. 2015, 2017). For example, habitat loss may have impeded habitat-specialist butterflies to track warmer temperatures in the UK (Warren et al. 2001). Similarly, landscape attributes (e.g., configuration and size of patches) may influence populations of woodland bird species: winter temperatures have harsher effects on birds that occupy more isolated habitat patches (Newson et al. 2014).

In contrast, in earlier works in this study area, we found that species richness is maximal in landscapes with ~50% natural land cover (Desrochers et al. 2011, De Camargo & Currie 2015). At this proportion of natural land cover, ~20% of bird species showed reduced probability of occupancy, ~80% had higher probability of occupancy (Fig. 2). For the species

studied here, conversion of some forested cover to human-dominated covers does not necessarily have negative impacts. Probability of occupation declined significant only at the highest amounts of natural cover loss (Fig. 2).

Here, we find that the effect of forest conversion is not geographically uniform, even within habitat guilds. Northern-edge populations of southerly species increased on average by ~80% their probability of occupancy, independently of guild habitat (Fig. 3). Perhaps surprisingly, even the probability of occupancy of southerly forest-interior species was ~50–100% higher in areas with reduced natural cover (Fig. 3). Hence, this result does not support the proposition that reduced forest cover poses a barrier to species' occupancy and presumably to the movement of species tracking warmer temperatures.

Some open-habitat bird species commonly found farther south of the study area appear to benefit from land cover conversion and northward warming temperatures. Our analysis showed, for example, that the Eastern Bluebird (*Sialia sialis*), a southerly grassland species that breeds near its northern range edge in the study area, has $p_{occ} > 80\%$ higher in landscapes with 15% forest cover than in fully forested landscape. It has been suggested that its abundance has increased dramatically, potentially due to warmer temperatures, in southern Ontario since the 1970s (Cadman et al. 2009, Varrin et al. 2007).

Moderate reduction of natural covers may favour species' occurrence irrespective of whether a species is

a forest- or open-habitat specialist (Fig. 3, Figs S1.2a,b,c, Appendix S1). The current study does not address the mechanisms that generate this pattern. It is possible that interspecific competition may be reduced by some level of environmental disturbance: experimental studies have shown the importance of competition in regulating community structure along disturbance gradient (Campbell et al. 1992, Turkington et al. 1993, Violle et al. 2010). For example, habitat fragmentation could facilitate the access of nest predators or parasites into forest patches and reduce the reproductive success of the most abundant forest birds (Robinson et al. 1995). Some nectarivorous birds that are normally numerically dominant in south-eastern Australia had their flower visitation patterns disrupted by Noisy Miners (*Manorina melanocephala*, an aggressive species of honeyeater) in disturbed fragments when the nectarivorous birds were more abundant than the Noisy Miners (Bennett et al. 2014).

Different responses of southerly and northerly populations to environmental changes might reflect differences in the factors that determine those boundaries. For example, it has long been suggested that abiotic stressors are more important in limiting species' ranges at the harsh poleward edge, whereas biotic interactions should be more important at the climatically benign tropical edge (MacArthur 1972, Kaufman et al. 1995). Some literature has suggested that species' equatorward boundaries are stable despite climate change (Hampe et al. 2005). Yet, Coristine & Kerr (2015) propose the opposite. Studying temporal responses of 34 passerine bird' ranges to temperature in North America, they found that equatorward range boundaries are closer to the upper realized thermal niche limits than poleward range boundaries are to the lower thermal limit. Coristine & Kerr's (2015) results suggest that equatorward populations are more strongly affected by abiotic factors, in this case temperature.

We speculate that, for northerly species in southern Ontario, the triple stresses of physiologically extreme temperatures (Hewitt 2000, Hampe et al. 2005, Coristine et al. 2015), reduced natural forest cover, and competition from invading species from the south act together to reduce many species' probability of occurrence. Northerly species such as Cape May Warbler (*Dendroica tigrina*), Black-backed Woodpecker (*Picoides arcticus*), and Swainson's Thrush (*Catharus ustulatus*), all forest-interior species, showed extremely low p_{occ} in landscapes with reduced natural land cover (Table S1.1, Appendix S1). Some species that can be found in open forests or grass patches such as Tennessee Warbler (*Vermivora peregrine*) or Philadelphia Vireo (*Vireo philadelphicus*) also had lower p_{occ} with less human-dominated, mainly open, land cover. Although it is impossible to determine precisely whether habitat availability or climate are the proximal mechanisms lowering the species probability of occurrence of the species near the southern edge of their range, an interaction between the two stressors is plausible (Oliver et al. 2014; Mantyka-Pringle et al. 2015). In contrast, northern-edge populations may benefit from increasingly favourable temperatures.

In principle, one can study species' responses to land cover at northern and southern range limits either by using a) the same species in two different regions (at northern and southern range limits) or b) different species in the same region (as in this study). The disadvantages of design a) are that it is likely to be difficult to get similar ranges of natural land cover in the North and the South, and other environmental variables are likely to be collinear with land cover. The main disadvantage of b) is that northerly and southerly species may have very different habitat requirements. For example, northerly species include more forest-interior species, while southerly species are more often associated with open-habitat (Table 2). The patterns we reported above may reflect in part differences in the biology of avian species in the

Table 1. The ratio ($\bar{\Omega}_{15\%}$) of the probability of occupancy (\hat{p}_{occ}) at 15% forest cover, relative to \hat{p}_{occ} at 100% forest cover, as a function of each species' geographic group (mid-range species, southerly, and northerly species), and habitat guild (forest-interior, interior-edge, edge, open-habitat, urban and wetland birds) in southern Ontario, Canada. The coefficient of determination of the overall model is $R^2=0.32$.

Variables	Sum of Squares	d.f.	F	p
Geographic group	26.20	2	53.80	<0.0001
Habitat guild	5.51	5	4.52	<0.0001
Interaction	5.61	9	2.62	<0.001
Residuals	157.40	167		

Table 2. The number of species per guild observed in each geographic range group in southern Ontario, Canada. The different guilds are not equally represented in the different regions ($X^2 = 18.3$, $df = 10$, $p = 0.050$).

	Edge	Interior	Interior-edge	Open-habitats	Urban	Wetland	Total
Northerly	4	13	3	5	0	10	35
Mid-range	10	18	17	26	6	29	106
Southerly	2	2	7	14	2	10	37
Total	16	33	27	45	8	49	178

mainly coniferous northerly forests versus the mainly deciduous southerly forests. Note, however, that habitat type presumably does not limit the probability of occurrence of mid-range species within the study area because these species occur both further north and further south. The probability of occurrence of mid-range species is not strongly dependent on forest cover (Figure 3). Once again, this is inconsistent with the proposition that reduced forest cover will be a barrier to species movement in the face of climate change.

In closing, we note that our interpretation of the potential interaction between climate and land cover reduction is based entirely on correlations through space. Time series data would provide a stronger test of the effect of land cover conversion on species' probabilities of occupancy. While we would have liked to use time series data, changes in land cover in recent decades in this region have been too small to detect their effect (Desrochers et al. 2017). Instead, we used spatial gradients of land cover. Those results suggest that partial conversion of natural, mainly forested, land cover to human-dominated, mainly open land cover in Southern Ontario, does not appear to pose a serious barrier to the colonization of areas that become climatically suitable due to global climate change.

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Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Table S1. List of bird species included and excluded from the study based on the selection criteria.

Appendix S1. List of species and supporting statistical analysis.

Data accessibility statement

The Ontario Breeding Birds Atlas (ABBO) data used to obtain presences and absences of the bird species in southern Ontario are publically available at: <http://www.birdsontario.org/atlas/downloaddata.jsp?lang=en>. Satellite land cover images are also publically available at: <https://www.ontario.ca/data/provincial-land-cover>.

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