Density of neotropical bird migrants is highest at stopover
sites with an intermediate amount of forest in the
surrounding landscape and a low proportion of forest in
conifer

by

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Abstract

Some nearctic-neotropical migrant forest-breeding songbirds have suffered large population declines in recent decades. Declining availability of high-quality habitat where birds refuel during the long migration may be contributing to these declines. Our objective was to identify landscape attributes that make sites likely to be used as stopover sites during fall migration. We sampled birds at 37 sites in southeastern Ontario, Canada. Bird density was highest at sites with an intermediate amount of surrounding forest within 2 km, and where deciduous trees were in higher proportions in surrounding forests within 8 km. These results suggest that birds are attracted to landscapes with an intermediate amount of forest cover. Their densities may decrease at higher forest amounts due to dilution, conifer avoidance, or reduced edges for foraging. Our study highlights the importance of retaining sites with around 50% forest cover, particularly deciduous forest, as stopover habitat for migrating songbirds.

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1. Introduction

Over the past 50 years, populations of birds in North America declined by about 30%, representing a net loss of almost three billion birds (Rosenberg et al. 2019).

Shorebirds, grassland birds and aerial insectivores showed the steepest declines, while waterfowl and birds of prey had positive trends (NABCI 2020). Some of the largest declines were for nearctic-neotropical migrant forest-breeding birds (NABCI 2020), birds that migrate to Central and South America for the non-breeding season.

Survival of migratory birds depends upon several factors throughout their life cycle: on breeding grounds, during migration, and in winter (Runge et al. 2015). Birds are limited by different factors at different times, and these factors remain understudied for the full annual cycle (Faaborg et al. 2010), especially for non-breeding seasons (Marra et al. 2015; Imlay & Leonard 2019). Habitat loss and climate change have been considered important drivers of population decline for migratory bird species (Bairlein 2016; Kentie et al. 2018). For example, both factors were linked to declines in Wood Thrush (*Hylocichla mustelina*) populations during the breeding season (Rushing et al. 2016b), and deforestation was linked to declines in several neotropical songbirds migrants in non-breeding grounds (La Sorte et al. 2017; Ruiz-Sanchez et al. 2017). Lower habitat quality on non-breeding grounds can also result in "carry-over effects" of lower bird reproductive fitness on breeding grounds, as found for American Redstarts (*Setophaga ruticilla*; Rushing et al. 2016a). Similarly, Rockwell et al. (2012) reported lower reproductive success for Kirtland's Warblers (*Setophaga kirtlandii*) in years with drier weather on non-breeding grounds the preceding winter.

Some studies have suggested that much of the annual mortality for some migratory bird species occurs during migration (Silleet & Holmes 2002; Klaassen et al. 2014). Migratory birds may be killed by storms (Wiedenfeld & Wiedenfeld 1995), or by predators (Woodworth et al. 2014), or may die from exhaustion on long flights if their energy reserves are reduced (Alerstam 2011). Indirectly, predator risk (Pomeroy et al. 2006), competition (Moore & Yong 1991), or poor-quality stopover habitats (Rushing et al. 2016a) may impact their foraging ability and affect survival. Many migratory birds depart at night after dusk and land before dawn, possibly because weather conditions are better at night, and because they then have more foraging time (Alerstam 2009). Typically, many species are thought to fly at an average altitude of 1-2 km (Gauthreaux 1991). However, they may adjust flight height to make use of favourable wind conditions (e.g., tail winds) or avoid strong head winds (Schmaljohann et al. 2009), sometimes flying at double their usual height (Sjöberg et al. 2018). Nevertheless, birds may be susceptible to mortality from collisions with human-made structures (Gehring et al. 2009), especially at take-off or landing when they are at lower altitudes, or if attracted to artificial lights (McLaren et al. 2018). Landing pre-dawn may also make it more challenging to find good foraging habitat in areas where habitat has been heavily altered by humans.

Habitat availability could also be a limiting factor on migration (Faaborg et al. 2010). Migratory landbirds spend up to 95% of their migration period at stopover sites (Buler & Dawson 2014), where they refuel and build fat stores for the high energy expenditure of long migratory flights (Alerstam 2011). Stopover habitats during fall

migration may be especially important because fall migration includes a new cohort of juveniles (Dokter et al. 2018). If sufficient high-quality habitats are not available, with less experience or lower social status than adults, juveniles may be forced to use less optimal habitats like agricultural fields which may reduce their survival (Yong et al. 1998).

For migrating landbirds, the importance of a stopover site likely depends not only on local habitat, but also on surrounding habitat within a relevant distance of the site. Buler et al. (2007) measured the influence of forest cover at multiple spatial extents on migratory landbird density, and found the strongest relationship, i.e. the “scale of effect” (Jackson & Fahrig 2015), to be within 5 km. Forest cover can serve as a cue both before and after landing, suggested by landbird species moving different distances after they land. Birds that move short distances after landing, such as ovenbirds (*Seiurus aurocapilla*; Buler 2006), likely use forest cover as a cue for choosing where to land. In contrast, species such as summer tanagers (*Piranga rubra*), which can move 1 km per day after landing (Aborn & Moore 1997), may search out high-forest sites before and after landing.

Several studies found different conclusions on the importance of surrounding forest cover for bird density. Buler et al. (2007) found higher nearctic-neotropical migrant landbird density in stopover sites surrounded by more deciduous forests. Contrastingly, Buler & Dawson (2014) found higher landbird density in stopover sites surrounded by developed lands or by water bodies. McCabe & Olsen (2015) found a similar result using a different landscape metric; migrating birds were more often captured at stopover sites with relatively little vegetated habitat in the surrounding landscape.

The type of forest around a site might influence its use as a stopover site, possibly due to food resource availability. During the breeding season, many North American songbird migrants are more strongly associated with deciduous forests than coniferous forests (Krikun et al. 2018), and this association might extend to the migration period. This is supported by McLaren et al. (2016) who used weather surveillance radar to estimate density of nocturnal songbird migrants in 1-km² sites; they found that migrant density increased with the amount of deciduous forest, and was unaffected by the amount of coniferous forest, in the surrounding landscape within 5 km of sites. While the link between forest type and food resource availability during migration has been relatively little studied, deciduous amount in the landscape surrounding stopover sites correlates with fuel deposition rates of Red-eyed Vireos (*Vireo olivaceus*) during spring migration (Cohen et al. 2014). Furthermore, some studies have found that deciduous forests hosted more caterpillars than coniferous forests during the breeding season (Blondel et al. 1991; Wilkin et al. 2009), which are important prey for migrating songbirds.

This study aims to evaluate the influence of the surrounding landscape on the use of forest sites by migrating songbirds in southeastern Ontario, Canada. Specifically, we asked whether the density of nocturnal, migrating songbirds at forested sites during fall was related to the proportion of the surrounding landscape in forest. For this we had two competing hypotheses. One possibility was that migrating songbirds may avoid landscapes with relatively little remaining forest, resulting in lower densities in the remaining forest sites in landscapes with a low amount of forest. Alternatively, they may be concentrated in the remaining forest in these landscapes, resulting in higher local densities there. In addition to the amount of forest, we asked whether the density of

migrating songbirds at stopover sites decreased with the proportion of surrounding forest that was coniferous.

2. Methods

We assessed the influence of two landscape variables, the percent of the surrounding landscape in forest and the percent of that forest in coniferous trees, on the average number of calling birds per minute during the day (as an index of bird density) at 37 bird sampling sites. We selected our sample sites to maximize variation in the two landscape variables of interest (percent landscape in forest and percent forest in conifers), while minimizing spatial autocorrelation among sites. We first modelled the number of calling birds at a site on each landscape variable, measured within multiple spatial extents around the site, to find the scales of effect of the two landscape variables. We then created a model for each landscape variable at its maximum effect, including sample site, date, and time as covariates.

2.1 Selection of sampling sites

In brief, we selected sites to maximize variation in the two landscape variables of interest (percent landscape in forest and percent forest in conifers). To do this, we used a CanVec land cover map of southeastern Ontario to create a spatial dataset with the following information for each 30 x 30-m pixel: (i) whether the area within 100 m of the pixel was entirely forested, i.e., a “forested site,” (ii) the percent of the surrounding landscape in forest within 1 km and 5 km of the pixel, hereafter “percent forest” and (iii) the percent of the forest within 1 km and 5 km of the pixel that was in coniferous trees, hereafter “percent conifer.” We then selected forested sites while maximizing variation in percentages of forest and conifer. We then further sub-selected sites at least 5 km apart to

minimize spatial autocorrelation between sites. We minimized the correlation between water within 1 km and 5 km of sites and the two landscape variables of interest within 1 km and 5 km of sites. We controlled for water amount as it might influence the location of migrating birds (Alerstam & Pettersson 1977; Buler et al. 2007), potentially confounding our ability to detect effects of percent forest and percent conifer, our two landscape variables of interest.

Our spatial data were based on the vector-based CanVec series land features from Natural Resources Canada (geographic coordinate system: NAD 1983 CSRS; scale 1:50 000), created between 1999 and 2002 with ortho-images from Landsat, and using an EODS land cover classification (Wulder & Nelson 2003). We selected sites from the area within 50 km of Franktown, Ontario (45.0455° N, 76.0617° W), which is the location of the nearest weather radar to Ottawa (chosen so that we can make future comparisons of our results with data on bird movements from weather radar). We extracted polygons from the land-feature file "Wooded Area," based on the "wood coverage descriptor" attribute which listed land cover types based on multiple sources (see section "Wooded Area" in CanVec metadata catalogue: NVCP 2018). We created two new layers: (i) one "all forests," which included polygons representing deciduous/broadleaf forests, coniferous forests, and mixed forests, and excluded polygons representing shrubs and wetlands, and (ii) one based on just the coniferous forest attribute (no mixed forests). Deciduous/coniferous classifications by satellite imagery have uncertainties ([Lisein et al. 2015](#)); we acknowledge this but argue that a conifer-only layer has less uncertainty than a mixed-forest layer. We then converted these two vector layers to raster layers using 30 x 30-m pixels.

We then used the raster layers to determine, for each pixel, the percent of surrounding landscape in forest and the percent of surrounding forest that was coniferous. We did this at three spatial scales, 100-m, 1-km and 5-km radii from each pixel, using a Moving Window Analysis. This is a technique that moves pixel by pixel and calculates a value of interest based on a defined "window" or spatial extent around the pixel. In this case, the desired values are the percent of the window in forest and the percent of forest (within the window) in conifer. As such, we obtained six raster layers, one layer for each of the two variables at each of the three spatial scales.

Using these raster layers, we then selected 41 bird sampling sites in southeastern Ontario, Canada, with varying percent forest and percent conifer in the surrounding landscape. Potential sites were limited to pixels that were entirely forested within a 100-m radius. To maximize the ranges of the landscape variables across sites at a given scale, and to minimize the correlation between them, we selected one site per 10-20% increment (a "stratum") of each landscape variable from its lowest to highest possible value, within each stratum of the other variable. We selected sites by visually examining the map and choosing an arbitrary pixel that met the desired criteria. For example, we selected a site at the lowest percent forest and percent conifer possible, and then a second site at a similar percent forest and 20% higher for conifer, etc. To minimize any potential effect of regional gradients in our landscape variables, we attempted to maximize their ranges in each of four geographic quadrants centered on Franktown. To do this, we first selected a site in the first quadrant and the first strata combination, and then a site in the second quadrant with that same strata combination, changing combination after the four quadrants have been considered at least once. The manual selection, including multiple

sites in the same strata but different quadrants, resulted in 83 sites; we ignored some combinations because they did not occur in the study area (e.g., very low forest percent and high conifer percent within 5 km of a site). To limit spatial autocorrelation between sites, we removed sites that were not at least 5 km from all other sites. To minimize the influence of water availability on our results, we removed sites with very high (over 20%) water within 1 and 5 km of sites, and we ensured there was no correlation between percent water and our landscape variables of interest, percent forest and percent conifer (Appendix 1). We obtained permissions from landowners to sample birds at 41 of the selected sites.

2.2 Recording birds

We set up an SM4 autonomous recording unit at the centre of each of the 41 bird sampling sites to estimate the relative density of migrating songbirds from August 16 to October 25, 2018. Previous studies have shown that bird activity at stopover sites estimated using recorders was correlated with that estimated using human surveys (Roark & Gaul 2020; Tran Nguyen et al., see Appendix 20 for the unpublished analysis). All recorders were set up between August 9 and August 22, and retrieved between October 27 and October 30. Each SM4 was scheduled to record for five minutes every half hour between sunrise and sunset. We recorded during daytime only as we wished to measure on-the-ground site use by nocturnal migrants, which includes the majority of migrating nearctic-neotropical forest songbirds (Alerstam 2009). Nighttime recordings would likely include mainly calls of birds migrating overhead. We obtained data from 37 of the original 41 recorders (Figure 1; Appendix 2), due to human error and recorder failures.

Using the software Raven Pro (Center for Conservation Bioacoustics 2014), we listened to the recordings to count individual calling birds. We used call characteristics to avoid double-counting individuals within each minute sampled. These included call pitch, intensity, frequency and overlap. We had initially planned to listen to one minute every hour from sunrise to sunset, every day for every site. However, acoustic processing turned out to take much longer than expected; we had to reduce our effort, resulting in a variable number of minutes processed across sites (Appendix 2). Every group of four recorders we processed included one from each quadrant to avoid relationships between effort and percent forest or percent conifer. At each site, we listened to recordings from between 5 and 29 days, evenly distributed across the sampling period, with a mean of 15 days per site (Appendix 3). For each day sampled at a given site, we listened to at least one minute from each of the first eight hours recorded, for a mean of 130.68 min per site. The sampled minute for each hour was the first minute with unobstructed sound, i.e., calm wind and little rain. Our predictor variables of interest were not correlated with the number of minutes processed per site (Appendix 4), the sampled dates (Appendix 3), nor the sampled hours (Appendix 5). We included the following families in our study, as most of their species are nocturnal songbird migrants: Mimidae (mimids), Parulidae (warblers), Passerellidae (New World sparrows), Regulidae (kinglets), Thraupidae (tanagers), Troglodytidae (wrens), Turdidae (thrushes), Tyrannidae (flycatchers), and Vireonidae (vireos) (Appendix 6).

2.3 Statistical Analyses

To estimate the scale of effect for each of the landscape predictors, we modelled the mean number of calling birds per minute at a site in relation to each landscape

variable separately, at each of 11 scales, i.e., 0.1, 0.5, 1, 2, 3, 4, 5, 6, 8, 10 and 15-km radius from the sample site, using a default, Gaussian generalized additive model (GAM) (Appendix 7; Appendix 8). We defined the scale of effect as the scale where the r -squared value was largest (Appendix 9).

To test our predictions about the effects of percent forest and percent conifer on bird density at stopover sites, we fitted a negative binomial GAM (R Core Team 2017; mgcv R-package: Wood 2018) for each landscape variable separately, at its scale of effect. We were able to evaluate the effects of the variables in separate models because there was no correlation between them (Figure 2). We included site, date (Appendix 10) and time of day (i.e., hour from sunrise; Appendix 11) as covariates. Since the default GAM plots suggested a possible dome-shaped relationship between percent forest and number of calling birds, this relationship was modelled as a smoothed three-knot, thin-plate spline ($k = 3$), allowing up to one peak in the model. The default GAM plots suggested a linear relationship between percent conifer and number of calling birds; therefore, conifer was modelled as a linear term. We also fitted site and date as random intercepts, and hour from sunrise, all with smoothed thin-plate splines and generalized cross-validation (GCV).

3. Results

We detected a mean of 0.86 calling nocturnal songbird migrants per minute across sites (± 0.42 SD; Figure 3), with the mean at each site ranging from 0.34 to 2.11 calling birds per minute. The detected songbird migrants belonged to nine passerine families (Appendix 6).

3.1. Prediction 1: forest percent

The scale of effect for % landscape in forest was 2 km ($R^2 = 0.296$, $p = 0.015$; Appendix 7, Appendix 9). The relationship between the number of calling birds per minute and % landscape in forest at this scale was peaked, with the maximum number of calling birds per minute at 55% landscape in forest (Figure 3). This maximum number of calling birds was 1.6 times the number of calling birds at the minimum forest cover (23%) and 2.2 times the number of calling birds at the maximum forest cover (94%).

3.2. Prediction 2: conifer percent

The scale of effect for percent forest in conifer was 6 km ($R^2 = 0.202$, $p = 0.003$; Appendix 8, Appendix 9). As predicted, the mean number of calling birds declined with increasing % forest in conifer. There was a decrease of 50% in the number of calling birds with a 50% increase in the percent forest in conifer (Figure 4).

4. Discussion

Our study suggests that density of songbird migrants during fall migration is highest at stopover sites surrounded by an intermediate amount of forest, i.e. 55% of the landscape within 2 km of the site covered in forest. We had hypothesized either (i) a positive effect of forest cover on bird density if birds avoided landscapes with less remaining forests in the surrounding landscape, or (ii) a negative effect of forest cover on bird density if birds congregated in these remaining forests. It is possible that the combination of these would produce a peaked relationship if in the lower half of the curve, i.e. at low forest cover, migrating birds avoided landing in forested sites with low surrounding forest amount. This would lead to an increase in bird density with increasing forest in the surrounding sites. This effect would not continue into the upper half of the

curve if all sites with more than 50-55% of surrounding forest were equally attractive to migrating birds. In the upper half of the curve, i.e. at high forest cover, this would lead to a decrease in bird density with increasing forest because a given number of landing birds would be spread through more forest, reducing the density at a given sample site in the landscape.

Few previous studies have looked at the influence of landscape attributes on migrants. Buler et al. (2007) found a positive relationship between landbird migrant density on forested survey transects and proportion of hardwood forests in the surrounding landscape over a similar range of forest proportions to our study. McLaren et al. (2016) also found a positive relationship between numbers of migrating birds departing from a site at dusk, as estimated by weather surveillance radars, and forest cover at the site. However, the latter study was not directly comparable to ours; the authors' local "stopover sites" were grids of 1 km² that were not entirely forested (our local sites of 100-m radii were entirely forested), and they measured total density across all habitat in the grid. The percent of forest in these grids was likely correlated with forest cover in the surrounding landscape, thus confounding local and landscape effects. Both studies differed from ours in the main landscape metric; while the authors measured the proportion of the landscape that was hardwood forests, we measured total forests of all types. After further analyses, we found that migrant density increased with non-coniferous forest in the surrounding landscape, without a peak (Appendix 14). Although we tried to minimize correlations between total forest and proportion of forest in conifer, this finding suggests that migrant density might have decreased after an intermediate amount of total forest because birds were disproportionately, negatively affected by

conifers. As such, our result corroborates that of Buler et al. (2007) if we consider our variable "non-coniferous forest" as similar to their "hardwood forest."

Other factors could also lead to the pattern we observed of greater density of birds in forest patches within landscapes with an intermediate amount of forest. For example, the amount of forest edge tends to be highest in landscapes with intermediate percent forest (Fahrig 2003). If birds seek out forest edges to forage (Terraube et al. 2016), where insect prey tends to be more abundant (González et al. 2017), this might lead to greater densities in landscapes with more edge. We cannot directly test this hypothesis, as our observations were all made at least 100 m from an edge.

We suggest that future studies evaluate the effects of forest cover along other bird migration routes. Most stopover habitat studies in North America have focussed on eastern migration routes (e.g., Mississippi coast: Buler et al. 2007; Buler & Moore 2011, and Northeast America: Buler & Dawson 2014; McLaren et al. 2016), where land cover is more forested than central migration routes (Smith et al. 2012). Along the central routes, stopover sites with more agriculture and less forest in the surrounding landscape are more common (Smith et al. 2012). We speculate that whenever the range of surrounding forest percentages is below 50%, an occurrence likely more common in Central North America, if birds avoid stopover sites with little forest amount, the influence of surrounding forest on bird density would be positive instead of peaking. Weather surveillance radars, such as those used by McLaren et al. (2016), could be used to study larger geographic areas encompassing multiple migration routes. Analyses of the Franktown radar could allow for a direct comparison with our field study.

We found a lower density of nocturnal songbird migrants during fall migration at stopover sites where the proportion of conifer in the surrounding forest was higher. This supports our hypothesis that deciduous forests contain more prey insects than coniferous forests (Blondel et al. 1991; Wilkin et al. 2009; Cohen et al. 2014). In apparent contrast to our result, McLaren et al. (2016) found no effect of the amount of conifer in the surrounding landscape on landbird migrant density, using land cover data from the Agriculture and Agri-Food Canada (AAFC) Annual Crop Inventory. However, McLaren et al. (2016) measured the total area of coniferous forest in the landscape surrounding sampling sites, while we measured the proportion of the surrounding forest in coniferous forest. We speculate that the area of conifer in McLaren et al. (2016) may have been correlated with the total amount of forest in their landscapes, counteracting any negative response of bird density to conifer itself.

We found a scale of effect of 2 km for the proportion of forest in the surrounding landscape and of 6 km for the proportion of conifer in the surrounding forest. The scales of effect were far from the lowest and highest scales examined of 0.1 km and 15 km; therefore, it is likely that we correctly identified the scales of effect (Jackson & Fahrig 2015). Buler et al. (2007) found a scale of effect of 5 km for the proportion of deciduous forest cover in the landscape surrounding transect surveys of migrant birds. McCabe & Olsen (2015) measured the effect of the ratio between landscape-scale and local-scale proportion of vegetation on capture rate of migrating birds. They found that the strongest influence of this ratio occurred when the landscape-scale vegetation proportion was measured within 4 km of the bird-capture sites. Overall, these scales of effect indicate

that effects of landscape structure on migrating birds occur within several kilometers of a potential stopover site.

We speculate that these scales of effect are related to the behaviour of migrating birds as they evaluate or explore stopover sites based on landscape structure before or after landing, or both. Migrant species vary in after-landing dispersal distances, some exploring up to 10 km away from the initial landing site (e.g., Aborn & Moore 1997; Buler 2006; Chernetsov 2011). Many may evaluate the landscape from above, land, and readjust if forest cover does not meet expectations. We encourage further evaluations of both in-air and on-ground stopover movements to understand when and why different scales of effect are relevant to the influence of landscape structure on bird density.

We acknowledge that percent forest and percent conifer are not the only cues used by birds when deciding where to stop during migration. Neotropical bird migrants show seasonal plasticity and can be associated with developed land cover types (Zuckerberg et al. 2016). Migratory landbirds near urban areas, distracted by artificial lights, are less influenced by surrounding forest cover (McLaren et al. 2018). Similarly, migratory landbirds near coastal stopovers are less influenced by surrounding forest cover and more by a need to land from depleted energy or adverse weather conditions (Buler & Moore 2011).

Our results suggest that to conserve nearctic-neotropical songbird migrants, we should ensure the availability of sufficient stopover sites that are surrounded by about 50% forest that is predominantly deciduous, within about 5 km of the site. Meeting the target of 50% forest will become more challenging over time, because many forests continue to be replaced by agriculture or urban expansion. If we stop focussing on conifer

plantations, and promote balanced and species-rich forests (Parker et al. 2001), we can more easily meet the target of more deciduous than coniferous trees (Smith 1993; Price et al. 2013).

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Figures

Figure 1. 37 sampling sites where songbirds on fall migration were recorded in southeastern Ontario, Canada. The inner/outer circles show 1-km/5-km radii from the centers of the sites. H/L refers to High % of landscape in forest/Low % of forest in conifer at the two illustrated spatial extents, i.e. values above or below the medians of the landscape variables at the respective scales. Note this is for display purposes only; landscape variables were modelled as continuous variables in all analyses.

Figure 2. The relationship between % of the surrounding landscape that is forested and % of that forest that is conifer, within 1 km and 5 km of 37 bird sampling sites in southeastern Ontario, Canada. Each data point represents data from one site. Sample sites were selected to avoid any correlation between the two variables at both spatial extents, allowing the effects of the two landscape variables to be evaluated in separate analyses.

Figure 3. Relationship between the number of calling migrant songbirds recorded per minute at stopover sites during fall migration and the % of landscape in forest within 2 km of 37 bird sampling sites in southeastern Ontario, Canada. The grey area is the 95% confidence band for the predicted curve of the negative binomial GAM. Removing the one outlier does not qualitatively change the results (Appendix 12).

Figure 4. The relationship between the number of calling migrant songbirds recorded per minute at stopover sites during fall migration and the % of forest in conifer within 6 km of 37 bird sampling sites in southeastern Ontario, Canada. The grey area is the 95% confidence band for the predicted curve of the negative binomial GAM. Removing the one outlier does not qualitatively change the results (Appendix 12).

Appendices

Appendix 1. The relationship between % of the landscape in water and % forest or % conifer, within 1 km and 5 km of 37 bird sampling sites in southeastern Ontario, Canada. Each data point represents data from one site. First row: Pearson's $r = 0.032$, $p = 0.85$; $r = 0.26$, $p = 0.13$. Second row: $r = -0.27$, $p = 0.10$; $r = -0.23$, $p = 0.18$.

Appendix 2. Description of 37 bird sampling sites in southeastern Ontario, including geographic coordinates in decimal degrees, total number of days and minutes for which recordings were interpreted (sampled), and % forest, conifer, and water within 0.1, 1 and 5 km of each site.

Site	Longitude	Latitude	Sample		% forest			% conifer			% water	
			Days	Min	0.1	1	5	0.1	1	5	1	5
1	-75.8103	45.0757	29	300	100	98	80	100	55	70	1	1
2	-75.8612	45.0359	25	259	100	53	69	100	71	69	1	1
3	-76.0333	45.0845	26	300	100	68	65	1	31	49	1	1
4	-75.5079	45.3583	23	258	100	73	50	1	1	4	2	1
5	-75.5457	45.1146	23	266	100	74	28	100	55	11	1	1
6	-76.0530	45.2625	5	40	100	44	62	1	3	5	1	1
7	-75.6497	45.1170	14	97	100	61	31	1	16	8	1	5
8	-76.4707	45.1005	10	80	100	90	88	97	70	43	2	4
9	-76.4355	45.1636	15	111	100	71	89	80	57	46	1	3
10	-76.1753	45.2692	15	94	100	92	30	100	70	34	1	1
11	-76.6248	45.2189	11	91	100	94	92	1	37	33	6	6
12	-76.2302	45.3233	15	105	100	81	20	1	27	17	1	1
13	-76.4294	45.0575	13	105	100	60	75	100	60	45	1	4
14	-76.4512	45.3200	20	226	100	32	68	1	8	3	11	10
15	-76.3699	45.1849	18	163	100	80	78	25	28	39	15	11
16	-75.7274	44.8888	20	133	100	29	47	1	65	38	1	1
17	-76.2914	45.2242	14	94	100	77	63	25	26	32	2	3
18	-76.4238	44.9872	17	128	100	99	81	49	48	42	2	4
19	-76.5075	44.9987	11	88	100	96	82	56	29	40	1	7
20	-76.5994	44.8720	13	100	100	70	82	69	39	33	1	4
21	-76.0894	44.7443	20	194	97	35	43	90	36	15	1	6
22	-75.9769	44.9783	17	113	100	82	42	100	59	58	1	2
23	-75.5806	44.8525	12	101	100	80	59	1	24	33	1	1
24	-75.9008	44.9870	15	94	100	30	52	1	17	60	2	1
25	-75.5291	44.9103	13	103	100	30	56	1	2	13	2	1
26	-75.9905	44.9244	14	57	100	32	23	35	66	36	2	3
27	-75.8937	44.7228	13	95	100	32	34	18	53	20	1	2
28	-75.7552	44.9295	12	91	100	61	47	7	35	50	1	1
29	-75.8323	44.8889	11	88	100	61	40	100	69	45	1	6
30	-75.7657	45.0437	11	89	100	76	71	100	74	59	1	3
31	-76.5115	45.1535	16	189	100	84	89	1	14	32	4	4
32	-76.0965	45.2073	14	96	100	47	30	1	20	19	1	2
33	-75.8739	44.9449	14	104	100	58	47	73	48	50	1	4
34	-76.2165	44.8702	13	105	100	57	42	1	25	16	6	12
35	-76.3637	44.8336	12	96	100	34	52	97	47	25	2	4
36	-75.9325	45.1308	11	85	100	27	44	11	23	41	1	1
37	-76.4130	45.2767	12	97	100	66	81	1	2	9	2	5

Appendix 3. The relationship between the median date of the minutes sampled at each site for calling birds from automated recording units (ARUs) and % forest or % conifer, within 1 km and 5 km of 37 bird sampling sites in southeastern Ontario, Canada. Each data point represents data from one site. There was no relationship between the median date sampled and the landscape variables. First row: Pearson's $r = -0.14$, $p = 0.40$; $r = -0.09$, $p = 0.59$. Second row: $r = -0.08$, $p = 0.62$; $r = -0.22$, $p = 0.18$.

Appendix 4. The relationship between the total number of minutes sampled at each site for calling birds from automated recording units (ARUs) and % forest or % conifer, within 1 km and 5 km of 37 bird sampling sites in southeastern Ontario, Canada. Each data point represents data from one site. There was no relationship between the number of minutes sampled and the landscape variables. First row: Pearson's $r = 0.15$, $p = 0.38$; $r = 0.13$, $p = 0.45$. Second row: $r = -0.02$, $p = 0.91$; $r = 0.08$, $p = 0.63$.

Appendix 5. The relationship between the median hour from sunrise of the minutes sampled at each site for calling birds from automated recording units (ARUs) and % forest or % conifer, within 1 km and 5 km of 37 bird sampling sites in southeastern Ontario, Canada. Each data point represents data from one site. There was no relationship between the median time of day sampled and the landscape variables. First row: Pearson's $r = 0.19$, $p = 0.25$; $r = 0.31$, $p = 0.06$. Second row: $r = -0.21$, $p = 0.21$; $r = -0.09$, $p = 0.59$.

Appendix 6. Total number of birds in each taxonomic group recorded using autonomous recording units (ARUs) across 37 bird sampling sites in southeastern Ontario, Canada. Birds were classified as passerine/non-passerine, and among passerines, were grouped by migration flight habits (nocturnal, diurnal, resident) and taxonomically at the family or species level. Only data for nocturnal migrants were analyzed in the thesis.

			Total number of individuals
		Group, family or species	
Passerine	Nocturnal	Mimidae (mimids)	26
		Parulidae (warblers)	508
		Passerellidae (sparrows)	1,667
		Regulidae (kinglets)	440
		Thraupidae (tanagers)	23
		Troglodytidae (wrens)	9
		Turdidae (thrushes)	817
		- <i>Turdus migratorius</i> (American Robin)	702
		Tyrannidae (flycatchers)	231
		Vireonidae (vireos)	221
		Unidentified	6
	Diurnal	Bombycillidae (waxwings)	326
		Corvidae (corvids)	5092
		Fringillidae (finches)	83
		Icteridae (blackbirds)	133
	Resident	<i>Cardinalis cardinalis</i> (Northern Cardinal)	31
		<i>Certhia americana</i> (Brown Creeper)	164
		Paridae (chickadees)	13401
		Sittidae (nuthatches)	530
		<i>Spinus tristis</i> (American Goldfinch)	469
Non-passerine		Columbidae (doves and pigeons)	12
		Phasianidae (turkeys and grouse)	9
		Raptors	79
		Shorebirds	1
		Waterfowl	363
		Woodpeckers	485
		Unidentified	68

Appendix 7. GAM modelled relationships between mean number of calling migrant songbirds per minute sampled and the % landscape in forest, at different landscape scales between 0.5 and 15 km—i.e., the radius in km from site centres—across 37 bird sampling sites in southeastern Ontario, Canada. The figure includes GAM fits to raw means, R-squared values and p-values at each scale, each model containing only the predictor and the response. The function `Plot.gam()` from the R package `mgcv` was used.

Appendix 8. GAM modelled relationships between mean number of calling migrant songbirds per minute sampled and the % forest in conifer, at different landscape scales between 0.5 and 15 km—i.e., the radius in km from site centres—across 37 bird sampling sites in southeastern Ontario, Canada. The figure includes GAM fits to raw means, and R-squared values and p-values at each scale, each model containing only the predictor and the response. The function `Plot.gam()` from the R package `mgcv` was used.

Appendix 9. R-squared values (A and C) and p-values (B and D) of the GAM modelled relationships between mean number of calling birds per minute sampled and % forest (first row) or % conifer (second row) at increasing landscape scales—i.e., the radius in km from site centres—from 37 bird sampling sites in southeastern Ontario, Canada. The r-squared and p values were extracted from simple GAM models at each scale, each model containing one of the two landscape variables.

Appendix 10. The relationship between mean number of calling migrant songbirds per minute sampled and date at 37 bird sampling sites in southeastern Ontario, Canada. Each point is a sampled site on a given date. Different colours represent different sites. The line connects the mean numbers of birds across sites on each date. Not all sites were sampled on all dates, due to time constraints on listening to the recordings.

Appendix 11. The relationship between mean number of calling migrant songbirds per minute sampled and hour from sunrise at 37 bird sampling sites in southeastern Ontario, Canada. The boxplot shows the means, standard deviations, minima and maxima. Each point is a sampled site at a given hour from sunrise. Different colours represent different sites. Few sites were sampled beyond eight hours from sunrise, due to time constraints on listening to the recordings.

Appendix 12. Removing site outlier in final models: There was an outlier at 55% landscape in forest and 27% forest in conifer. We ran the model after removing the site point, and this did not qualitatively change the results. For both models below, we provide means for the site (ID: 13) and results without the data point.

Appendix 13. The relationship between the number of calling migrant songbirds recorded per minute at stopover sites during fall migration and the % landscape in conifer within 6 km of 37 bird sampling sites in southeastern Ontario, Canada. The grey area is the 95% confidence band for the predicted curve of the negative binomial GAM. We tested our results using the variable % landscape in conifer instead of % forest in conifer following a similar study by McLaren et al. (2016).

Appendix 14. The relationship between the number of calling migrant songbirds recorded per minute at stopover sites during fall migration and the % landscape in non-coniferous forest within 2 km of 37 bird sampling sites in southeastern Ontario, Canada. The grey area is the 95% confidence band for the predicted curve of the negative binomial GAM. Because a peak occurred for bird density (i.e., the number of calling birds recorded per minute within 100 m of sites) vs. the % of landscape in total forest (see Figure 3), we assessed the relationship between bird density and the % of landscape in forest excluding coniferous forest (i.e., deciduous and mixed forest—see spatial data in Methods).

Appendix 15. The relationship between an index of bird abundance during fall migration over the entire landscape within 2 km of 37 bird sampling sites in southeastern Ontario, Canada, and the percentage of that landscape in forest. The grey area is the 95% confidence band for the predicted curve of the negative binomial GAM. The goal of this analysis and graph was to compare the relationship between bird density and % forest and that between bird abundance and % forest within 2 km of sites (the scale of effect); we found a peak in bird density (measured within 100 m of stopover sites) at intermediate percentages of surrounding forest, but the total number of birds (“bird abundance”) within 2 km of sites may have differed. To convert from local bird density within 100 m of sites to an index of bird abundance within 2 km of sites, we multiplied the local number of calling birds by the total forest area within 2 km and divided the results by the forest area within 0.1 km (i.e., the local site). This calculation assumes a linear increase in the number of calling birds (i.e., a constant density) with forest area.

Appendix 16. The relationship between an index of bird abundance during fall migration over the entire landscape within 2 km of 37 bird sampling sites in southeastern Ontario, Canada, and the percentage of that landscape in non-coniferous forest. The grey area is the 95% confidence band for the predicted curve of the negative binomial GAM. Because a peak occurred for both bird density (measured within 100 m of stopover sites) and “bird abundance” within 2 km of sites vs. the % of landscape in forest (see Appendix 14), we assessed the relationship between the index of bird abundance and the % of landscape in non-coniferous forest. This relationship is positive, and suggests % conifer may have negatively and disproportionately influenced bird abundance after the peak.

Appendix 17. The relationship between % forest or % conifer and distance from Ottawa (45.4215° N, 75.6972° W), within 1 km and 5 km of 37 bird sampling sites in southeastern Ontario, Canada. Each data point represents data from one site. First row: Pearson's $r = -0.0043$, $p = 0.98$; $r = 0.42$, $p = 0.010$. Second row: $r = -0.27$, $p = 0.10$; $r = -0.23$, $p = 0.18$.

Appendix 18. Distance from Ottawa vs. % landscape in forest: Noting a potential effect of distance to Ottawa on % landscape in forest at a 5-km landscape scale (Appendix 17), we fitted this variable as smoothed thin-plate splines to the final models at the scales of effect. We then removed the variable due to non-significance in the models ($p > 0.4$).

Forest nbGAM + distance from Ottawa	Conifer nbGAM + distance from Ottawa
<p>Family: Negative Binomial(0.787) Link function: log</p> <p>Formula: callm ~ s(f2, k = 3) + s(site, bs = "re") + s(date2, bs = "re") + s(diffSunnr) + s(distOtt)</p> <p>Parametric coefficients: Estimate Std. Error z value Pr(> z) (Intercept) -0.50631 0.09282 -5.455 4.9e-08 *** --- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>Approximate significance of smooth terms: edf Ref.df Chi.sq p-value s(f2) 1.894 1.908 12.672 0.00619 ** s(site) 28.719 34.000 534.265 < 2e-16 *** s(date2) 46.754 68.000 389.572 < 2e-16 *** s(diffSunnr) 3.671 4.533 304.993 < 2e-16 *** s(distOtt) 1.002 1.002 0.556 0.45706 --- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>R-sq.(adj) = 0.156 Deviance explained = 21.3% -REML = 5579.2 Scale est. = 1 n = 4835</p>	<p>Family: Negative Binomial(0.787) Link function: log</p> <p>Formula: callm ~ c8 + s(site, bs = "re") + s(date2, bs = "re") + s(diffSunnr) + s(distOtt)</p> <p>Parametric coefficients: Estimate Std. Error z value Pr(> z) (Intercept) -0.069787 0.170314 -0.410 0.68199 c8 -0.013700 0.004544 -3.015 0.00257 ** --- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>Approximate significance of smooth terms: edf Ref.df Chi.sq p-value s(site) 29.608 34.000 452.143 < 2e-16 *** s(date2) 46.816 68.000 394.482 < 2e-16 *** s(diffSunnr) 3.669 4.530 305.228 < 2e-16 *** s(distOtt) 1.006 1.007 0.012 0.913 --- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>R-sq.(adj) = 0.156 Deviance explained = 21.3% -REML = 5581.7 Scale est. = 1 n = 4835</p>

Appendix 19. In-person surveys of birds within 100 m of autonomous recording units (ARUs). In-person surveys were done in two rounds (rnd) at each of 41 bird sampling sites. Shown are the date, site ID, time, number of nocturnal migrant songbirds detected (ind), total number of birds detected (indTot), number of nocturnal migrant songbird species detected (sp), total number of bird species detected (spTot), temperature before a survey began (temp), wind speed (windSpeed; Beaufort scale), wind direction (the wind origin, based on compass), sky condition (1: clear skies, 2: partly cloudy, 3: fully cloudy, 4: drizzling), and general tree types within 100 m of each recorder in decreasing order of estimated abundance (veg). See supplementary file for raw data by species.

rnd	date	site	time	ind	indTot	sp	spTot	temp	windSpeed	windDir	sky	veg
1	2018-09-13	1	9:45	6	11	5	9	17	0	0	1	cedar, elm, spruce
1	2018-09-08	3	10:30	1	6	1	3	13	2	e	3	cedar, pine, birch, aspen
1	2018-09-08	4	9:15	2	9	1	6	12	1	n	3	fir
1	2018-09-04	5	14:45	2	8	2	5	23	2	w	2	ash, birch, fern, maple
1	2018-09-01	6	11:05	7	7	2	6	25	2	se	2	maple
1	2018-09-01	7	7:20	9	17	5	8	17	0	0	2	cedar, maple
1	2018-09-16	9	12:06	2	6	1	3	28	0	0	3	cedar, spruce
1	2018-09-04	10	8:00	7	13	3	7	18	0	0	2	cedar, elm, buckthorn, spruce
1	2018-09-15	11	11:05	3	12	2	7	28	0	0	3	cedar, pine
1	2018-09-16	12	13:38	6	10	3	6	28	0	0	3	ash, cedar, fir, elm
1	2018-09-12	13	13:32	3	9	1	5	20	0	0	2	fir, birch, pine
1	2018-08-30	14	11:03	4	13	1	6	21	2	sw	3	fern
1	2018-09-15	16	8:00	4	11	3	6	26	0	0	2-4	maple, hemlock, cedar
1	2018-09-04	17	12:42	0	2	12	2	24	0	0	2	cedar, birch
1	2018-09-12	18	11:30	11	19	3	8	22	0	0	3	aspen, birch, cattails
1	2018-09-12	19	10:08	4	14	3	7	16	0	0	3	hemlock, aspen
1	2018-09-13	20	11:55	5	11	4	7	17	0	0	1	aspen, birch, cattails
1	2018-09-24	21	13:49	2	4	2	4	17	2	n	1	ash, aspen, maple

1	2018-08-30	23	12:30	4	13	3	6	21	1	e	1	maple, cedar, ash
1	2018-09-19	24	11:30	5	14	2	6	14	1	n	2	cedar, spruce
1	2018-09-03	25	9:41	1	9	1	5	23	1	s	1	maple, ash, buckthorn, oak
1	2018-09-24	26	9:08	1	9	1	5	7	2	ne	2	elm, maple, cedar
1	2018-09-19	27	14:05	2	14	1	5	16	0	0	2	cedar, maple
1	2018-09-15	29	13:35	3	11	2	6	28	0	0	3	cedar, fir, fern
1	2018-09-08	30	11:30	5	14	3	5	15	2	w	3	oak, maple, ash
1	2018-09-13	33	12:33	2	10	2	7	20	0	0	1	buckthorn, fern
1	2018-09-08	34	13:50	1	7	1	4	17	2	ne	1	maple, elm
1	2018-09-13	36	8:17	5	17	3	9	15	0	0	3	maple, elm
1	2018-09-01	37	13:50	4	9	1	4	27	2	s	3	cedar, elm
1	2018-09-24	38	11:45	1	10	1	6	15	2	s	3	maple
1	2018-09-01	39	9:01	4	8	1	3	20	2-3	s	2	maple, cedar, elm
1	2018-09-03	40	13:24	0	5	0	4	28	1	s	3	pine, shrubs, cedar, buckthorn
1	2018-09-04	41	9:30	6	16	4	9	25	0	0	2	cedar
1	2018-09-19	42	10:15	7	19	5	11	13	0	0	2	maple, birch
1	2018-09-15	101	9:17	4	14	3	7	27	0	0	3	maple, elm, cedar
1	2018-09-12	102	8:42	6	12	4	7	15	0	0	2	oak, ash, cedar, pin, maple, beech
1	2018-09-24	103	10:25	2	12	2	6	9	2	n	2	maple, elm, cedar
1	2018-09-16	104	8:25	6	17	5	11	19	0	0	3	cedar, maple
1	2018-09-19	105	8:03	7	11	4	7	12	0	0	2	cedar, maple
1	2018-09-03	106	11:50	3	13	2	8	27	1	s	1.5	ash, maple, cedar
1	2018-08-30	107	9:11	2	8	1	4	17	2	s	2	spruce, maple, goldenrod, ash

2	2018-10-18	1	8:57	0	3	0	2	-2	1	nw	1	cedar, elm, spruce
2	2018-10-03	3	13:08	4	10	3	7	11	0	0	2	cedar, pine, birch, aspen
2	2018-10-21	4	14:40	0	9	0	4	3	3	ne	2	fir
2	2018-10-15	5	9:10	1	6	1	4	5	1	n	2-4	ash, birch, fern, maple
2	2018-10-03	6	9:00	5	13	3	8	10	0	0	2	maple
2	2018-10-03	7	14:18	5	9	3	6	12	0	0	2	cedar, maple
2	2018-10-07	9	14:30	2	5	2	4	11	1	nw	2	cedar, spruce
2	2018-10-03	10	12:05	6	15	3	9	12	0	0	2	cedar, elm, buckthorn, spruce
2	2018-09-30	11	15:04	3	8	1	3	11	0	0	2	cedar, pine
2	2018-10-06	12	11:17	1	7	1	4	8	0	0	2	ash, cedar, fir, elm
2	2018-09-30	13	9:47	5	11	3	7	10	1	sw	2	fir, birch, pine
2	2018-09-30	14	13:55	4	9	3	5	11	0	0	2-4	fern
2	2018-09-29	16	12:50	3	15	2	7	13	0	0	2-4	maple, hemlock, cedar
2	2018-10-06	17	12:44	6	10	2	4	8	0	0	2	cedar, birch
2	2018-09-29	18	14:13	10	14	4	7	13	0	0	4	aspen, birch, cattails
2	2018-10-21	19	11:00	3	8	3	5	2	2	n	2	hemlock, aspen
2	2018-10-15	20	12:15	6	15	3	7	10	1	ne	2	aspen, birch, cattails
2	2018-09-26	21	9:53	8	16	5	10	8	0	0	2	ash, aspen, maple
2	2018-10-13	23	12:30	2	3	2	3	9	3-4	w	3	maple, cedar, ash
2	2018-10-07	24	10:10	0	7	0	2	9	1	n	3	cedar, spruce
2	2018-10-01	25	8:16	2	7	2	5	9	0	0	2-4	maple, ash, buckthorn, oak
2	2018-09-29	26	9:05	9	18	4	8	10	0	0	3	elm, maple, cedar
2	2018-10-21	27	12:42	1	6	1	5	3	3-4	w	2	cedar, maple

2	2018-09-29	29	10:54	4	10	2	4	10	1	s	2	cedar, fir, fern
2	2018-10-07	30	12:57	0	7	0	2	11	1	nw	2	oak, maple, ash
2	2018-10-08	33	10:41	1	10	1	5	9	1	w	2	buckthorn, fern
2	2018-10-06	34	9:14	5	9	4	6	6	1	nw	2	maple, elm
2	2018-10-15	36	10:30	1	4	1	4	9	0	0	4-5	maple, elm
2	2018-10-07	37	9:00	1	4	1	3	9	3	n	2	cedar, elm
2	2018-10-13	38	14:25	1	4	1	3	8	3	w	3	maple
2	2018-10-13	39	10:20	1	5	1	3	3	2-4	w	2	maple, cedar, elm
2	2018-10-21	40	10:45	3	8	2	5	2	3-4	e	1-3	pine, shrubs, cedar, buckthorn
2	2018-10-08	41	12:23	1	6	1	3	10	1	n	2	cedar
2	2018-10-06	42	14:20	0	1	0	1	8	0	0	2	maple, birch
2	2018-09-26	101	11:48	4	18	3	11	13	0	0	3	maple, elm, cedar
2	2018-10-21	102	9:00	1	3	1	2	-3	2-3	ne	3	oak, ash, cedar, pin, maple, beech
2	2018-10-22	103	12:30	1	10	1	4	2	2	w	3	maple, elm, cedar
2	2018-09-30	104	11:57	5	9	4	7	11	0	0	2	cedar, maple
2	2018-10-22	105	8:35	4	11	1	4	-2	0	0	2	cedar, maple
2	2018-10-03	106	10:30	8	25	5	11	11	0	0	2	ash, maple, cedar
2	2018-09-30	107	7:56	4	15	3	9	6	0	0	2	spruce, maple, goldenrod, ash

Appendix 20. Relationship between the number of individuals observed during 10-min surveys and the number of calling birds recorded per minute on the same date, of nocturnal songbird migrants at stopover sites during fall migration. The grey area is the 95% confidence band for the predicted curve of the negative binomial GLM. Two in-person surveys were carried out at each site. 69 in-person surveys had matching recording data: 33 for the first survey and 36 for the second. In-person surveys had missing recording data due to obstructed sound (e.g., strong wind).