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Research Paper

## Losing the edge: trends in core versus peripheral populations in a declining migratory songbird

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**ABSTRACT.** Knowledge of rangewide variation in abundance, and the processes driving such variation, may be the key to predict species tolerance to large-scale changes in climate and land use. Processes influencing population trends have been shown to vary between the edge and the core of a species' range. Here, we examined shifts in occurrence and abundance of a declining species, the Wood Thrush (*Hylocichla mustelina*), toward the northern edge of its breeding range over two to three decades. We examined those shifts at both coarse (breeding-bird atlases) and fine (individual forest fragments) spatial scales in Ontario and Québec, Canada. We hypothesized that populations would be less stable at the periphery of the range than in the core, as a result of combined effects of lower habitat quality and lower immigration rates in the periphery. At the fine spatial scale in the core of the Canadian distribution, we predicted that populations would show turnovers between years, but occurrence would remain stable at the landscape scale. As expected, Wood Thrush occurrence remained relatively stable in fragmented forests in the core of the breeding range (at both coarse and fine spatial scales), in contrast to peripheral regions. The influence of mature forest cover varied between ecoregions and spatial scales. The instability of coarse-scale occurrence patterns in peripheral versus core populations is consistent with the prediction that large-scale declines are more likely to be detected at the periphery of a species' range. However, populations declined within the core as well, albeit at a lower rate. The greater stability of core populations probably results from higher habitat quality and higher immigration rates. Yet, local recruitment within the core is expected to be low, owing to the negative effects of habitat fragmentation on productivity documented elsewhere.

### Perte en périphérie : les tendances dans les populations du centre des territoires par rapport aux populations périphériques d'une espèce d'oiseau chanteur migrateur en déclin

**RÉSUMÉ.** La connaissance des variantes en termes d'abondance sur un territoire et des conditions qui déterminent ces variantes, peut être la clé pour prédire la tolérance des espèces aux changements à grande échelle du climat et de l'exploitation des terres. On a constaté que les conditions qui influencent les tendances de la population varient entre la périphérie et le centre du territoire d'une espèce. Nous avons examiné ici les évolutions de l'occurrence et de l'abondance d'une espèce en déclin, la grive des bois (*Hylocichla mustelina*), en direction de la bordure nord de son territoire de reproduction sur deux à trois décennies. Nous avons examiné ces évolutions sur des échelles spatiales brutes (atlas des oiseaux reproducteurs) et fines (fragments de forêts individuels) dans les provinces canadiennes de l'Ontario et du Québec. Nous avons supposé que les populations seraient moins stables à la périphérie qu'au centre de leur territoire, en conséquence des effets combinés de la baisse de la qualité de l'habitat et des taux d'immigration moindres à la périphérie. Sur l'échelle spatiale fine au centre de la répartition canadienne, nous avons prédit que les populations se remplaceraient d'une année sur l'autre, mais que l'occurrence resterait stable à l'échelle du paysage. Comme prévu, l'occurrence de la grive des bois est restée relativement stable dans les forêts fragmentées au cœur du territoire de reproduction (à la fois sur les échelles spatiales brute et fine), contrairement aux régions périphériques. L'influence de la couverture forestière mature variait entre les écorégions et les échelles spatiales. L'instabilité des modèles d'occurrence sur l'échelle brute dans les populations périphériques par rapport aux populations centrales est cohérente avec la prédiction que les déclinés à grande échelle sont plus susceptibles d'être détectés à la périphérie du territoire d'un oiseau. Toutefois, les populations centrales ont décliné également, mais dans une moindre mesure. La stabilité supérieure des populations centrales résulte probablement d'une qualité meilleure de l'habitat et de taux d'immigration plus élevés. Pourtant, le recrutement local au centre du territoire devrait être faible, en raison des effets négatifs de la fragmentation de l'habitat sur la productivité, documentés par ailleurs.

**Key Words:** *habitat fragmentation; Hylocichla mustelina; landscape ecology; neotropical migrant birds; population trends; spatiotemporal dynamics; species range dynamics*

## INTRODUCTION

Predicting species response to climate change and land use intensification requires an understanding of rangewide spatiotemporal dynamics in distribution and abundance, as well as the processes driving such variation (Guo et al. 2005, Lloyd et al. 2005, Hargreaves et al. 2015). Across a species' range, abundance is not evenly distributed and varies from center to margin, often as a function of environmental covariates (Manthey et al. 2015, Devenish et al. 2017). Although some patterns are commonly observed at the periphery of species ranges, generalizations across species remain elusive.

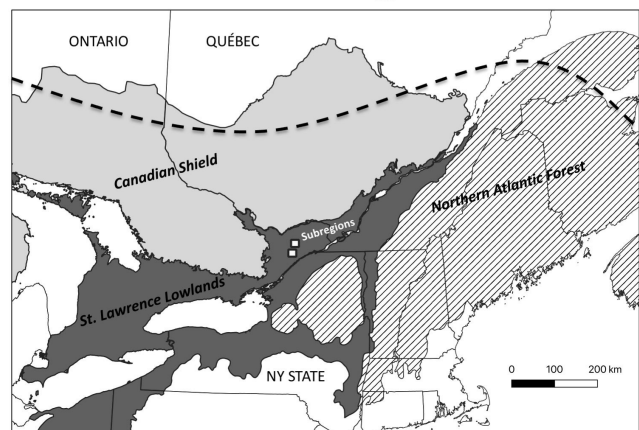
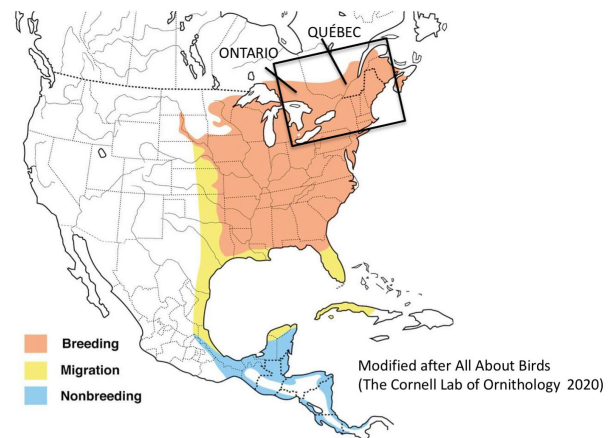
From the center to the periphery of a species' range, habitat quality tends to decrease as environmental conditions become gradually limiting (Brown 1984, Root 1988), habitat becomes more patchy (Vallecillo et al. 2010), and the intensity of biotic interactions tends to increase (Case and Taper 2000, Gaston 2009). The resulting decline in productivity toward the periphery of a breeding range may be compensated by immigration from populations located closer to the core of the range, although rescue effects are unlikely in declining species (e.g., Ward 2005, Schaub et al. 2013, but see Melles et al. 2011). Ultimately, peripheral populations may be more vulnerable to environmental changes, leading to their decline and, in some cases, range contraction (Opdam and Wascher 2004, but see Channell and Lomolino 2000). Yet, under climate change, peripheral populations may sometimes contribute to maintaining or expanding a species' range (Melles et al. 2011). In the UK, for example, Taheri et al. (2020) found that range shifts across the southern edge of northerly distributed bird species were best explained by climate change, whereas shifts at the northern edge of southerly distributed species were best explained by changes in land cover.

Here, we examined shifts in occurrence and abundance of a declining species of Neotropical migrant, the Wood Thrush (*Hylocichla mustelina*), toward the northern edge of its breeding range. According to the North American Breeding Bird Survey (BBS), Wood Thrush has experienced a global population decline of approximately 1.3% per year since 1966, corresponding to a decline of 50% between 1966 and 2019 (Sauer et al. 2019). However, there are considerable variations in trends across the breeding range (Rushing et al. 2016a, Sauer et al. 2019). Wood Thrush is considered threatened in Canada (COSEWIC 2012) and breeding bird atlases (BBAs) suggest a contraction of its Canadian range over the past 25 to 30 years (Cadman et al. 2007, Stewart et al. 2015, Robert et al. 2019). This contraction is especially apparent in the Canadian Shield and Northern Atlantic Forest (Appalachian) ecoregions, at the periphery of the breeding range (Fig. 1). In contrast, the species is relatively abundant in the St. Lawrence Lowlands ecoregion (Sauer et al. 2019; see the map of seasonally averaged estimated relative abundance in Evans et al. 2020, and the density map in Boreal Avian Modelling Project 2020). Wood Thrush occurrence patterns have also remained remarkably stable in that ecoregion over the 20-year period separating the two Ontario and Québec BBA periods (Cadman et al. 2007, Robert et al. 2019).

Because Wood Thrush population dynamics vary geographically, we aimed to compare trends in occurrence and abundance

between populations of the Canadian Shield (hereafter "Periphery") and core populations located in the St. Lawrence Lowlands (hereafter "Core"; Fig. 1) to investigate the factors underlying those trends. This distinction is based on the apparent stability of the distribution and higher relative abundance of the species in the St. Lawrence Lowlands.

**Fig. 1.** Range map of the Wood Thrush (*Hylocichla mustelina*), and location of the study area and focal ecoregions in the northern portion of the breeding range. In the study area map, the northern edge of Wood Thrush breeding range is represented by a dashed line. The two subregions in the St. Lawrence Lowlands of eastern Ontario sampled for the fine-scale surveys are represented by squares (Metcalf, square in the north, and Heckston, square in the south). Populations of focus for coarse-scale analyses (breeding bird atlas squares, in Ontario and Québec) and abundance trend analyses (sites of the Forest Bird Monitoring Program, in Ontario only) are located in the St. Lawrence Lowlands ecoregion (core populations/Core) and in the Canadian Shield ecoregion (peripheral populations/Periphery). The Northern Atlantic Forest corresponds to an intermediate ecoregion in terms of habitat quality (i.e., more acidic soils than in the St. Lawrence Lowlands, but different surficial geology than the Canadian Shield, except the Adirondacks in New York State, which is the western part of the ecoregion).



**Table 1.** Summary of the main predictions tested and data sets used in this study. Core populations (Core) correspond to the St. Lawrence Lowlands ecoregion, whereas peripheral populations (Periphery) correspond to the Canadian Shield ecoregion.

Predictions tested	Data set used in the study
(P1) Occurrence patterns in the Core are relatively stable at the coarse scale.	Breeding bird atlases
(P2) The probability of continuous detection is lower at the Periphery than in the Core at the coarse scale.	
(P3) The probability of continuous detection increases with percent mature cover in both ecoregions at the coarse scale.	
(P4) The probability of continuous detection increases more with percent mature cover at the Periphery than in the Core at the coarse scale.	
(P5) Occurrence patterns in the Core are relatively stable at the fine scale.	Transect surveys in forest fragments
(P6) The probability of continuous detection increases with percent mature cover in the Core at the fine scale.	
(P7) Abundance is consistently lower at the Periphery than in the Core.	Forest Bird Monitoring Program in Ontario
(P8) Abundance in both the Core and Periphery ecoregions decreases over time.	
(P9) Abundance decreases at a faster rate at the Periphery than in the Core.	

According to the model developed by Taylor and Stutchbury (2016), winter habitat deforestation, especially in eastern Central America, should have a more severe impact on Wood Thrush population trends than habitat loss on the breeding grounds. Both of our focal populations (Periphery and Core) are thought to winter in eastern Central America (Nicaragua and Costa Rica; see Stanley et al. 2015) and, as such, should be subjected to similar environmental conditions during the nonbreeding period. According to Rushing et al. (2016b), BBS trends in Wood Thrush abundance for the two focal breeding populations cannot be attributed to habitat loss or climate change, either on breeding or nonbreeding grounds. However, their analyses focused on a relatively recent period (2001–2013) and they did not investigate finer scale patterns.

In the Core, farming and, more recently, exurban development have caused a severe loss and fragmentation of mature forest cover (Watelet 2009). Wood Thrush response to landscape change appears to vary as a function of the spatial scale considered (Desrochers et al. 2010, Richmond et al. 2012). On the one hand, its probability of occurrence increases with the area of individual forest fragments (Villard et al. 1995, Burke and Nol 2000; R. Torrenta, *personal observation*) and with the proportion of forest cover within 500 m of a sampling point (Torrenta et al. 2018). However, Wood Thrush has been shown to be relatively tolerant to habitat amount (or loss) and fragmentation at the landscape scale in various portions of its breeding range (Villard et al. 1999, Austen et al. 2001, Donovan and Flather 2002, Lloyd et al. 2005) and its occurrence is apparently unrelated to the configuration of mature forest in agricultural landscapes (Villard et al. 1999). Nonetheless, proximity to forest edges had a negative effect on nest survival rates and productivity in the northeastern United States (Weinberg and Roth 1998, Driscoll and Donovan 2004) and in southern Ontario (Friesen et al. 1999). This effect has been attributed to edge-related increases in nest predation and brood parasitism in agricultural or semirural landscapes (Trine 1998, Burke and Nol 2000, Etterson et al. 2014, Ladin et al. 2016, but see Friesen et al. 1999).

Considering the negative effects of habitat fragmentation by agriculture on nest survival and also the high relative importance of tropical deforestation, we hypothesized that populations in forest fragments of the Core would act as demographic sinks,

sustained by immigration from elsewhere. Hence, we predicted that abundance would decline, but that occurrence patterns in the Core would be relatively stable over the study period, as indicated by Ontario and Québec BBAs (Cadman et al. 2007, Robert et al. 2019). Thus, occurrence patterns would actually mask population declines.

At the Periphery of the breeding range, we hypothesized that populations would be less stable than in the Core as a result of the combined effects of lower immigration and more marginal habitat quality. Although forest cover is relatively unbroken at the Periphery compared to the Core, soils are more acidic and, thus, less productive (Ministry of Northern Development, Mines, Natural Resources, and Forestry 2012). Soil acidity has a negative effect on the biomass of litter invertebrates with high calcium content (Hames et al. 2002). Because the Wood Thrush mainly feeds on invertebrates of the leaf litter (Evans et al. 2020), the resulting lower quality habitat would, in turn, result in more extensive declines at the Periphery. Immigration in this species has also been shown to be more strongly driven by conspecific density and patch quality than by habitat amount (Rushing et al. 2021). Thus, at the Periphery, immigration would not allow persistence of declining populations. We further predicted that both abundance and the probability of continuous detection would be consistently lower at the Periphery than in the Core. We also predicted that the probability of continuous detection in atlas squares or forest fragments would increase with percent-mature forest cover. This would particularly be observed at the Periphery, where habitat quality is expected to be lower. Finally, we predicted that Wood Thrush abundance would decline at a faster rate at the Periphery than in the Core.

To test these predictions (Table 1), we used different bird data sets covering the two to three decades from the 1980s until the 2010s. First, we used BBA data from Ontario and Québec (coarse scale), covering both the Periphery and Core. Then, we analyzed transect data from forest fragments of the Core in eastern Ontario (fine scale). At these two spatial scales, we quantified shifts in occurrence and determined whether they were related to mature forest cover and changes therein. Finally, we compared Wood Thrush population trends between the Periphery and Core using point count data from large forest blocks that have remained essentially undisturbed over the time period considered.

## MATERIAL AND METHODS

### Coarse-scale atlas data and forest cover

We compiled BBA data from Ontario (1981–1985 versus 2001–2005) and Québec (1984–1989 versus 2010–2014). Atlas squares were 10 x 10 km, with a few exceptions (because of the configuration of the Universal Transverse Mercator grid). We only included squares > 80 km<sup>2</sup> in the analyses. We characterized land use changes by using land cover maps of Canada from 1985 and 2005, in an attempt to approximate the years of the first and second BBAs (Latifovic and Pouliot 2005). Data were acquired by the National Oceanic and Atmospheric Administration (NOAA) advanced high-resolution radiometer (AVHRR) sensors, with a 1-km spatial resolution. The overall map accuracy was 61% at a thematic resolution of 12 land cover classes (Latifovic and Pouliot 2005). We computed areas for each land cover class in each atlas square and we pooled mature deciduous and mixed forest classes to approximate Wood Thrush habitat.

For the spatial analyses, we only included squares (1) whose location was within Wood Thrush distribution range (Fig. 1); (2) with presence of Wood Thrush over one or both atlas periods; (3) comprising at least one pixel of deciduous or mixed forest, in 1985 or in 2005; and (4) characterized by a minimum sampling effort > 20 h in each of the two atlas periods (Cadman et al. 2007, Robert et al. 2019). For each province and each square, we computed the proportion of mature forest cover in 1985 ( $PF_{\text{atlas}}$ ), and mature forest cover change between 1985 and 2005. We did not use the latter variable, because only 1.6% of the 1189 atlas squares exhibited a loss of mature forest cover exceeding 5% of their terrestrial area (range: 5–43.1%; mean:  $11.4\% \pm 8.8\%$ ), within the 20-year period and at the 1-km resolution considered. Hence, changes in mature forest cover were unlikely to account for the variability observed in atlas square occurrence patterns of Wood Thrush. Finally, we accounted for ecoregion as a proxy for habitat quality. Areas within an ecoregion were similar in their biotic (e.g., plant and wildlife) and abiotic (e.g., bedrock, soils, drainage patterns, temperature, and annual precipitation) characteristics. The two ecoregions sampled were the Canadian Shield (Periphery, Ontario and Québec; Fig. 1), and the St. Lawrence Lowlands (Core, Ontario and Québec; Fig. 1). These ecoregions coincide with Bird Conservation Region boundaries (see NABCI Bird Conservation Regions Map: <https://www.usgs.gov/media/images/terrestrial-bird-conservation-regions-north-america>).

### Fine-scale fragment surveys and forest cover

Targeted Wood Thrush surveys were conducted in 1989 and 2014 (26 May to 10 July) to investigate fine-scale variations in occurrence over a 25-year period, in forest fragments of eastern Ontario, south of Ottawa (in two subregions; Fig. 1; see also Torrenta and Villard 2017 and Torrenta et al. 2018 for further details). We used a transect method (Villard et al. 1995) to determine the presence or absence of Wood Thrush. Transects consisted of recording any visual or auditory detection while walking slowly along transects following the long axis of a forest fragment. Three visits per fragment were performed for each period. Wood Thrush absences were validated using playbacks of conspecific vocalizations. A fragment was considered to be occupied if at least one detection was recorded during any of the three visits. A fragment was defined as a contiguous area of

mature woodland separated from surrounding fragments by gaps of at least 30 m, or connected to other fragments by wooded strips < 30 m wide.

Over the 25-year period, four of 101 forest fragments were further fragmented, and forest cover converted into cropfields. Therefore, we surveyed a total of 97 fragments (> 3 ha) that could be compared between 1989 and 2014. We analyzed the influence of fragment area and time spent per visit as covariables in models estimating the probability of detection of Wood Thrush, using PRESENCE Version 2.12.10 (<https://www.mbr-pwrc.usgs.gov/software/presence.html>). For transect surveys conducted in 2014, sampling effort was significantly and positively related to fragment area ( $r^2 = 0.430, p < 0.001$ ). However, neither fragment area nor time spent per visit had an effect on detectability (Appendix 1).

Following Villard et al. (1995), we calculated Wood Thrush local extinction (ER) and recolonization rates (RR) as follows:

$$ER = 100 \times PA / (PA + PP), \text{ and}$$

$$RR = 100 \times AP / (AP + AA),$$

where PA is the number of fragments that were occupied the first year (P) and unoccupied the second year (A); AP is the opposite; PP are fragments that were occupied in both time periods; and AA are fragments that were unoccupied during both periods.

We assessed forest cover loss in the two subregions using cloudless Landsat images downloaded from the USGS Global Visualization Viewer website (<http://glovis.usgs.gov/>): a Landsat 5 TM (Thematic Mapper) image for 1989 and a Landsat 8 OLI (Operational Land Imager) image for 2014 (acquisition date in June, 30-m spatial resolution). We selected and combined relevant composite bands for vegetation analysis (spectral bands 3–4–5 for Landsat 5; spectral bands 4–5–7 for Landsat 8). We calibrated the two images through geometric and radiometric corrections, to avoid atmospheric effects and to reduce differences due to sensor detection (Congedo 2016). Pixels were then classified as either “forest” or “matrix” (i.e., non-forest), using a supervised classification and the maximum likelihood method (Congedo 2016). “Forest” was defined as mature deciduous or mixed stands, and the classification was validated by comparing the results with field observations. Finally, we superimposed the two images to detect changes in forest cover. We used buffers centered on each fragment (1-km radius) to compute the percentage of mature forest cover in 2014 ( $PF_{\text{frag}}$ ) and the percentage of mature forest loss between 1989 and 2014 ( $FL_{\text{frag}}$ ) within the local landscape. Image preprocessing and spatial analyses were performed using ArcGIS 10.1.

### Long-term abundance trends in relatively undisturbed forest tracts

We analyzed point-count data from the broad scale, long-term Forest Bird Monitoring Program (FBMP). Data were collected between 1987 and 2014 in large, relatively unbroken tracts of mature forest in Ontario, including some protected areas (Schalk et al. 2002). The area surveyed comprised both the Core and the southern portion of the Periphery. The FBMP was designed to sample forest birds away from roads (i.e., in large forest fragments, at least 100 m from a forest edge), in contrast to the BBS. Though forest cover around FBMP stations did not vary substantially

between years, habitat was still exposed to natural or anthropogenic disturbances such as ice-storms, acid precipitation, or habitat degradation by deer (*Odocoileus virginianus*; Cadman et al. 1998). However, compared to BBS routes, they represented a rare source of data from relatively undisturbed sites. Among the 377 sites surveyed by the FBMP, we selected those (1) including 5 point-count stations (i.e., located in large forest tracts); (2) whose stations were visited twice during the breeding season; and (3) where Wood Thrush was detected at least one year. For the 196 sites meeting these criteria, we used the highest counts per visit recorded each year from 1987 to 2014 (Schalk et al. 2002). Then, as a response variable, we computed the total count per site over five stations (one observation per site per year). As for BBA data, we accounted for the ecoregion in Ontario to identify geographical patterns in Wood Thrush abundance trends, although the Periphery suffers from gaps in geographic coverage compared to the Core (Francis et al. 2009).

## Statistical analyses

At the fine/coarse spatial scales (fragment/atlas data), we analyzed the probability of continuous detection in fragments/atlas squares by Wood Thrush as a function of landscape variables:  $FL_{frag}$ ,  $PF_{frag}/PF_{atlas}$ . The probability of continuous detection was defined as the probability that Wood Thrush was detected in a fragment/atlas square in both the first and second sampling periods (i.e., 1 - probability of local extinction). Data were analyzed with mixed-effects logistic regression models, where the ecoregion was used as a fixed-effect covariable (for atlas data), and the subregion was included as a random variable (for fragment data). We fitted two different models for Québec and Ontario (atlas data) because the sampling periods differed between the two provinces. We used a bootstrapping approach with the “pbm” package (Banghart 2015) to better assess significance in the mixed models for fragment data (i.e., more accurate p-values). At the fine scale, we also investigated differences in  $FL_{frag}$  among the four categories of changes in fragment occurrence (AA, AP, PA, PP), as a fixed variable, with a Kruskal-Wallis test.

Using FBMP data, population trends for Wood Thrush between 1987 and 2014 were estimated by fitting generalized linear mixed effects models (GLMMs) for the two ecoregions. In these models, the response variable represents count data (i.e., the highest site counts over two surveys, summed across five stations), and site was included as a random effect, to account for the fact that the same site was surveyed each year. The trend is the slope of the Poisson regression on year. As these slopes represent instantaneous rates, they were also transformed into their discrete time equivalents to show the percent change per year. All the analyses were performed using the R statistical language Version R 3.4.3 (R Foundation 2017), and the packages “DHARMA,” “lme4,” and “pscl.”

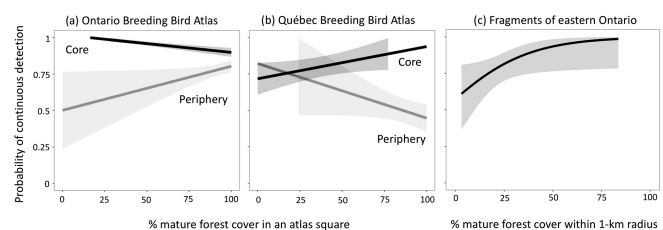
## RESULTS

### Changes in occurrence at the coarse scale (atlas squares)

As expected from predictions P1 and P2 (Table 1), local extinction rates were nearly five times higher in atlas squares at the Periphery (28.8%,  $n = 577$ ) than in those of the Core (6.0%,  $n = 612$ ). The difference between the two ecoregions was even greater (more

than eight times) in Ontario (21.7%,  $n = 437$  versus 2.5%,  $n = 486$ ) than in Québec (50.7%,  $n = 140$  versus 19.8%,  $n = 126$ ). For both provinces, the influence of the net amount of mature forest in an atlas square on the probability of continuous detection of Wood Thrush varied significantly between ecoregions (Table 2a). For example, in Ontario, the probability of continuous detection of Wood Thrush at the Periphery increased with forest cover in 1985, while this trend was much weaker in the Core (Fig. 2a). In Québec, we found the opposite trend between the two ecoregions (Fig. 2b). Thus, predictions P3 and P4 were only partly supported.

**Fig. 2.** Influence of the amount of mature forest on the probability of continuous detection of Wood Thrush (*Hylocichla mustelina*) at coarse (atlas squares) and fine (forest fragments) scales. The probability of continuous detection is the probability that Wood Thrush was detected in a fragment/atlas square in both the first and second sampling periods (1981–1985 versus 2001–2005 for the Ontario Breeding Bird Atlas,  $n = 923$ ; 1984–1989 versus 2010–2014 for the Québec Breeding Bird Atlas,  $n = 266$ ; 1989 versus 2014 for the fragments of eastern Ontario,  $n = 97$ ). At the coarse scale, the interaction effect between percentage mature forest cover and the ecoregion (Core/St. Lawrence Lowlands versus Periphery/Canadian Shield) is represented. At the fine scale, forest fragments are located in the Core/St. Lawrence Lowlands ecoregion. Confidence intervals around the fitting curves of the logistic regression models are displayed.



### Changes in occurrence at the fine scale (forest fragments)

As expected from P5, the frequency of occurrence of Wood Thrush in forest fragments of eastern Ontario was high and similar between 1989 (72.3%,  $n = 101$  fragments) and 2014 (75.5%,  $n = 106$ ). Over the 25-year period, we observed a moderate local extinction rate (19.4%,  $n = 72$ ) and a high recolonization rate (56.0%,  $n = 25$ ). However, the number of newly occupied fragments was the same as the number of local extinctions. Population turnover rates (i.e., local extinction and recolonization rates) were higher in the Metcalfe subregion, whose mature forest cover was lower and more fragmented, than in the Heckston subregion (see Fig. 3).

Over the 25-year period, the probability of continuous detection in a given fragment increased with forest cover within 1 km (Table 2b; Fig. 2c), as expected from P6. However, changes in Wood Thrush occurrence in forest fragments (AA, AP, PA, PP) were not significantly related to loss of forest cover within a 1-km radius (chi-square = 1.285,  $p = 0.733$ ), nor did the latter influence the probability of continuous detection (Table 2b).

**Table 2.** Mixed effects logistic regression models predicting the probability of continuous detection by Wood Thrush, *Hylocichla mustelina* (a) in atlas squares over two atlas survey periods (coarse scale) and (b) in eastern Ontario forest fragments between 1989 and 2014 (finer scale). With respect to breeding bird atlases, the effect of the ecoregion (Core/St. Lawrence Lowlands versus Periphery/Canadian Shield) and interaction effects are indicated. At the scale of forest fragments (in the Core/St. Lawrence Lowlands), the subregion was used as a random variable. For mixed effects models (forest fragments), a bootstrapping approach was used for more accurate p-values related to the fixed effect. Significant results are indicated in bold ( $p < 0.05$ ).

Estimates are on the logit scale.

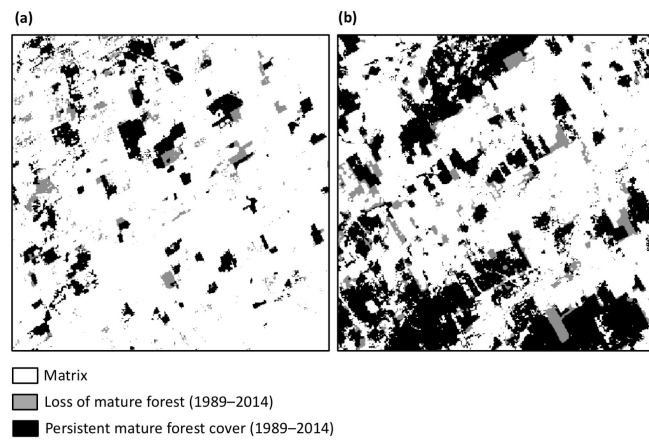
PF<sub>atlas</sub>: % of 1985 mature forest cover in an atlas square.

FL<sub>frag</sub>: % of mature forest loss between 1989 and 2014 within the local landscape (1-km radius) of a fragment.

PF<sub>frag</sub>: % of mature forest cover within the local landscape (1-km radius) of a fragment.

	n	Estimate	CI (lower)	CI (upper)	SE	p-value
<b>(a) Atlas</b>						
Ontario	923					
Intercept		-0.129	-1.489	1.278	0.696	0.853
PF <sub>atlas</sub>		0.015	0.000	0.030	0.007	<b>0.041</b>
Effect-Core		7.144	4.753	10.257	1.360	<b>&lt; 0.001</b>
PF x Effect-Core		-0.069	-0.104	-0.041	0.016	<b>&lt; 0.001</b>
Québec	266					
Intercept		1.368	-0.124	3.067	0.800	0.087
PF <sub>atlas</sub>		-0.016	-0.034	0.001	0.009	0.072
Effect-Core		-0.499	-2.305	1.133	0.865	0.564
PF x Effect-Core		0.031	0.009	0.056	0.012	<b>0.009</b>
<b>(b) Fragments</b>						
Intercept	97	0.738	-0.423	1.936	0.595	0.215
FL <sub>frag</sub>		0.066	-0.031	0.180	0.053	0.203
Intercept		0.307	-0.812	1.425	0.564	0.586
PF <sub>frag</sub>		0.047	0.006	0.098	0.023	<b>0.023</b>

**Fig. 3.** Change in mature forest (deciduous or mixed) cover between 1989 and 2014 in two subregions of eastern Ontario (Core/St. Lawrence Lowlands ecoregion): (a) Metcalfe, and (b) Heckston (10 x 10 km each; see Fig. 1 for location). The matrix is dominated by cropland, pastures, with scattered open water, roads, and buildings. Forest gain was so limited that it is not shown.



### Population trends in undisturbed forest tracts of Ontario

Wood Thrush was almost two times more abundant in the Core than at the Periphery (Fig. 4), as expected from P7. Consistent with P8 and P9, abundance in both the Core and Periphery

ecoregions decreased, although at a faster rate at the Periphery (Table 3, Fig. 4). Over the 1987–2014 period, Wood Thrush showed a nearly significant decline of -1.75% per year (corresponding to a global decline of -38% over the period) in the Core ( $n = 158$  sites,  $CI_{lower} = -3.90\%$ ,  $CI_{upper} = 0.44\%$ ) and a significant decline of -3.95% per year (corresponding to a global decline of -62% over the period) at the Periphery ( $n = 38$  sites,  $CI_{lower} = -6.83\%$ ,  $CI_{upper} = -0.99\%$ ).

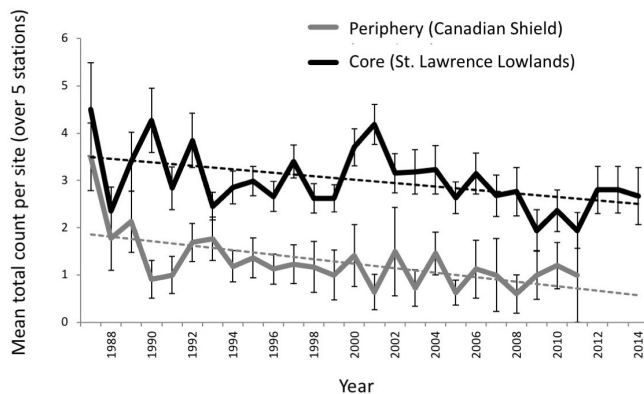
### DISCUSSION

At the northeastern edge of its Canadian breeding range, Wood Thrush distribution and abundance have changed dramatically over the study period (1980s–2010s). As expected, we found substantial differences in occurrence and abundance patterns between the Canadian Shield (peripheral populations) and the St. Lawrence Lowlands (core populations). BBA data suggest a contraction of the breeding range at the Periphery (Cadman et al. 2007, Stewart et al. 2015, Robert et al. 2019), whereas occurrence patterns have remained remarkably stable in the Core. In general, we found that changes in mature forest cover on the breeding grounds were low to moderate over the study period, and in turn only had moderate effects on Wood Thrush occurrence, either at coarse or fine spatial scales. However, more recent, high-resolution global forest cover change analyses have shown extensive loss of forest cover in the Periphery and Northern Atlantic Forest ecoregions (Hansen et al. 2013). These changes took place since the beginning of the 21st century (Hansen et al. 2013), i.e., during the second breeding bird atlassing periods considered here and over the following 10–15 years thereafter. Hence, they may only have had a recent influence on Wood Thrush distribution in these ecoregions. In contrast, the St. Lawrence

**Table 3.** Generalized linear mixed effects models (GLMMs) predicting Wood Thrush (*Hylocichla mustelina*) abundance from point count data of the Forest Bird Monitoring Program in Ontario between 1987 and 2014. Site was included as a random effect in the model. Significant results are indicated in bold.

	n	Estimate	CI (lower)	CI (upper)	SE
Periphery (Canadian Shield)	38				
Intercept		<b>81.802</b>	21.371	142.620	30.870
Year		<b>-0.040</b>	-0.071	-0.010	0.015
Core (St. Lawrence Lowlands)	158				
Intercept		38.446	-5.670	82.601	22.515
Year		-0.018	-0.040	0.004	0.011

**Fig. 4.** Comparison of Wood Thrush (*Hylocichla mustelina*) abundance trends between the Periphery/Canadian Shield (n = 38 sites) and the Core/St. Lawrence Lowlands (n = 158 sites) ecoregions of Ontario, according to the Forest Bird Monitoring Program. Standard errors and trend lines are indicated for each ecoregion. For the Canadian Shield, 2012 and 2013 were omitted because standard errors exceeded 1 and, therefore, were not reliable enough for estimating trends. The year 2014 was omitted because of lack of data.



Lowlands (Core) have been fragmented since the 19th century. Using the same high-resolution (30-m) forest cover data set, Rushing et al. (2016b) reported no effect of breeding habitat loss on Wood Thrush abundance (BBS trends) in the two ecoregions considered in our study, and over the 2001–2013 period.

As predicted, the net amount of breeding habitat (i.e., deciduous and mixed mature forest cover) was a significant predictor of Wood Thrush continuous detection, both in Ontario atlas squares and within forest fragments. Interestingly, the strength of this effect varied between ecoregions and spatial scales (Fig. 2). At the Periphery, acidic soils are expected to host a lower biomass of litter invertebrates with high calcium content (Hames et al. 2002). Higher cover of mature forest might thus compensate for lower quality habitat (see Haché et al. 2013 for local scale effects). However, this pattern was found in Ontario, but not in Québec. In fragmented forests of the Core, where soils are richer in nutrients, abundance was consistently higher than at the Periphery over the same time period (Fig. 4), and we observed minor changes in Wood Thrush occurrence at both fine and coarse spatial scales.

The latter changes may be attributed to reforestation in parts of the region (Friesen 2007).

Long-term population trends may also be influenced by natural disturbances and vegetation succession. In a long-term monitoring study conducted in an undisturbed forest of New Hampshire, Wood Thrush reached its highest abundance in early- to mid-successional stands (Holmes and Sherry 2001). During our study period, a severe ice storm occurred in January 1998, damaging forest canopies across the Core and spurring the growth of a dense sapling layer within ~two years (Brommit et al. 2004). This weather event would be expected to favor species associated with understory and a dense sapling layer such as the Wood Thrush (Faccio 2003; L. Friesen, Canadian Wildlife Service, *personal communication*). Data from Ontario across our different data sets point in that direction. We found high recolonization rates in forest fragments of the Core by Wood Thrush between 1989 and 2014 (fine scale), compared to inter-annual variability observed either in 1989–1990 (Villard et al. 1995) or more recently (2014–2015; R. Torrenta, *unpublished data*). Also, Wood Thrush population trends in Ontario forest stands that have remained relatively undisturbed by humans over the same 25-year period (i.e., FBMP data) showed a peak in mean Wood Thrush abundance shortly after the ice storm, but only in the Core, where the ice storm took place (Fig. 4). Hence, changes in habitat quality at a fine scale may have had positive effects for core populations.

The apparent stability of Wood Thrush occurrence patterns in the Core contrasts with (1) global declining trends revealed by the North American BBS in the same region between 1966 and 2015 (-1.4% per year) and between 1993 and 2015 (-1.7% per year; Sauer et al. 2019); and with (2) the relatively continuous decline in abundance (although nearly significant) we found in Wood Thrush populations in relatively undisturbed forest tracts of Ontario over the study period. This suggests that detection/non-detection data (versus counts per BBS route or in FBMP sites) can mask population declines or make population trends appear more stable than they actually are. This is especially the case in large (100 km<sup>2</sup>) atlas squares, and when population density and/or detectability are high (Joseph et al. 2006).

To explain spatiotemporal patterns in the regional abundance of migratory birds, one must account for factors operating during the nonbreeding period. The difficulty of tracking individuals or populations between seasons and over long distances makes it challenging to separate factors operating during the breeding and nonbreeding periods, and to link the abundance of breeding

populations to events occurring in specific wintering areas or along migration routes (Rushing et al. 2016b). No sources of information were available to document nonbreeding population trends in our focal Wood Thrush populations. We reasoned that abundance trends observed in areas where breeding habitat is nearly undisturbed by human activities would mainly reflect effects of factors operating during the nonbreeding period, and so FBMP data may actually represent a good proxy to assess those effects. Also, the fact that declines in abundance were observed in both Periphery and Core (Fig. 4) is consistent with an overwhelming influence of events taking place during the nonbreeding period. Taylor and Stutchbury (2016) and Taylor (2017) also report evidence suggesting that Wood Thrush populations are primarily driven by factors operating during the nonbreeding season, namely tropical deforestation.

According to Rushing et al. (2016b), climate change was not a driver of variation in Wood Thrush abundance in our focal populations over the recent decades. Yet, there is a potential for climate-induced distributional shifts over the long term (Melles et al. 2011, Virkkala and Lehikoinen 2014, Bateman et al. 2016), including in the Wood Thrush, as shown in predictive distribution models (National Audubon Society 2019). According to these models, the risk of Wood Thrush extinction near the edge of its breeding range could be mitigated by a northward expansion in response to climate change in the context of leading-edge population dynamics. However, this potential subsidization may be constrained by conditions experienced during the tropical winter (Rushing et al. 2020). Besides, it may not compensate for the marginal habitat quality at the Periphery. For example, sugar maple (*Acer saccharum*), an important component of Wood Thrush habitat, is not likely to expand its distribution northward fast enough to compensate for the abiotic and biotic constraints imposed by soils of the boreal forest (Carteron et al. 2020). Thus, even if the climatic niche of the Wood Thrush moved northward (National Audubon Society 2019), limiting soil and leaf litter conditions resulting in lower availability of invertebrate prey may not allow a northward shift in its breeding range.

The biogeochemical profiles of Wood Thrush feathers we sampled as part of a parallel study (R. Torrenta et al., *unpublished data*) are consistent with the hypothesis that immigration by yearling Wood Thrushes plays a role in the recruitment of individuals in forest fragments of the Core. Nol et al. (2005) have shown that distance from large forest fragments was a significant predictor of Wood Thrush occurrence in small forest fragments of southern Ontario, suggesting the importance of source-sink dynamics for the persistence of fragmented populations (see also Tittler et al. 2006). Regions with scattered human population in the northeastern United States might act as demographic sources for populations of eastern Ontario fragments (Lloyd et al. 2005). However, in the United States in general, and in many states bordering Canada, Wood Thrush populations have shown significant declines during our study period (Sauer et al. 2019), reducing the potential for rescue effects. Considering that juvenile Wood Thrushes may disperse between 60 and 80 km from their natal site (Tittler et al. 2006), rescue of Canadian populations from more central States in the U.S. might be possible over several generations. For example, Ohio has shown increasing or stable populations and relatively high abundances over the study period (Sauer et al. 2019). In the Canadian breeding range, immigration

would also be expected to be higher in the Core than at the Periphery, through the combined effects of shorter distance, higher density of conspecifics, and higher-quality habitat (Rushing et al. 2021).

## CONCLUSION

The apparent tolerance for mature forest loss and fragmentation shown by Wood Thrush in the St. Lawrence Lowlands (core populations) might be explained by both higher habitat quality and subsidization through immigration from populations located elsewhere. In contrast, Wood Thrush populations of the boreal transition forests of the Canadian Shield (peripheral populations) appeared to be more prone to local extinctions over the short term. A combination of different processes might be involved. First, climatic, vegetation, and soil conditions are expected to be less suitable at the periphery of the range (Cumming et al. 2014). Second, factors known to alter habitat quality such as acid precipitation (Hames et al. 2002, 2006), deer overbrowsing (Côté et al. 2004), or increased interspecific competition (Dellinger et al. 2007) may have a higher impact. And third, rescue effects in the Canadian Shield through immigration from declining populations might not compensate for declines due to events occurring during the breeding or nonbreeding periods, especially if core populations of eastern and southern Ontario actually act as demographic sinks.

Future technological advances and the use of intrinsic markers (e.g., stable isotopes, trace elements, genetic markers) should allow tracking the movements of natal dispersers over long distances to assess the potential for immigration across the range of species of conservation interest. In the meantime, our results and the fast declines reported for Wood Thrush lead us to strongly recommend (1) maintaining connectivity between source and sink populations; and (2) protecting blocks of high-quality breeding habitat and high forest cover in the core of the breeding range. Indeed, Peach et al. (2019) found that the efficiency of protected areas to promote the persistence of bird populations was context-specific, and especially high when they were established in landscapes with low forest cover.

*Responses to this article can be read online at:*  
<https://www.ace-eco.org/issues/responses.php/2146>

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### Author Contributions:

*R. T. and M.-A. V. conceived the study; R. T. and M.-A. V. collected the field data; R. T. performed satellite image analyses, and spatial and statistical analyses. All authors contributed to the writing of the manuscript, with R. T. and M.-A. V. leading the writing.*

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Appendix 1: Presence-absence site-occupancy models estimating the probability of occupancy and detection of Wood Thrush in fragments of eastern Ontario (Core/St. Lawrence Lowlands ecoregion), using the program PRESENCE. Fragment area (in 1989, and 2014) and time spent per visit (only in 2014) were included as covariables for detection during transect surveys (see Methods). Detectability also varied among the three visits (results not presented).

Covariable	Estimate	SE	CI (lower)	CI (upper)
<i>Models with one covariable</i>				
Fragment area (1989)	0.001	0.002	-0.004	0.006
Fragment area (2014)	0.004	0.003	-0.002	0.009
Duration (2014)	-0.017	0.014	-0.043	0.010
<i>Model with two covariables</i>				
Fragment area (2014)	0.006	0.003	-0.001	0.013
Duration (2014)	-0.031	0.016	-0.062	0.000