QUANTIFYING THE SPATIAL RELATIONSHIP BETWEEN LANDCOVER HETEROGENEITY AND SPECIES’ DISTRIBUTIONS

by

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Quantifying the spatial relationship between landcover heterogeneity and species’ distributions

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Although considerable research has been invested in disentangling the factors limiting species’ ranges at local and continental spatial scales, less attention has been granted to the relationship between species’ spatial distributions and landscape attributes at intermediate spatial scales. This research investigates the spatial relationship between avian species’ distributions (Ontario Breeding Bird Atlas [2001-2005] data) and landcover heterogeneity (Ontario Land Cover [1991-1998] data) in terms of their respective boundary locations (i.e., high rates of change in landcover composition and avian species turnover) in a vulnerable transitional zone in southern Ontario. Significant spatial overlap was found between landcover and avian boundaries. Given that land management decisions are most often made at the regional or landscape scales, this positive spatial relationship has important implications for conservation efforts. Future research should focus on assessing the spatial relationship between landcover heterogeneity and avian species’ distributions for different functional and taxonomic groups.
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GENERAL THESIS INTRODUCTION

“What limits species’ spatial distributions?” This is perhaps the most fundamental, yet baffling question contemplated by ecologists and evolutionary biologists, both past and present. Gaston (2003) suggested that species’ geographic ranges cannot be understood without addressing three levels of limits: i) abiotic and biotic factors; ii) population dynamics; and iii) genetic mechanisms. All three levels are related to each other, and the relative impact of any one level can be appreciated fully only if it is considered within the context of the other two. For instance, a decline in population size at a given geographic location is the result of unfavourable abiotic and biotic conditions only because individuals have not been able to adapt to those conditions, and in turn change population rates of birth, death, immigration, and emigration. However, the rate of adaptation may itself depend on these local population dynamics. These processes inevitably work at different temporal and spatial scales; for example, population dynamics may vary annually, whereas genetic mechanisms operate at historical time scales. Consequently, the process of pinpointing what determines species’ geographic ranges is extremely complex.

The structure and dynamics of species’ geographic ranges have been addressed on a broad spectrum, from the smallest to the largest ecological scales. The role of population dynamics in defining species’ borders has been delineated at the population scale (Keitt et al. 2001), whereas research at the community scale has investigated the extent to which competitive interactions determine range limits, and consequently shape biotic communities (Case et al. 2005). At larger spatial and organizational scales, a macroecological perspective on species’ ranges has frequently been adopted to identify the evolutionary and environmental factors driving observed gradients in species richness and turnover (McInnis et al. 2009).

A considerable amount of research has focused on identifying the abiotic and biotic factors limiting geographic ranges, producing some compelling evidence that many species’ spatial distributions are strongly influenced by spatial variation in these variables (e.g., Root 1988; Boone and Krohn 2000; Bullock et al. 2000; Holt and Keitt 2000; Gaston 2003; Bowman et al. 2005; Case et al. 2005; Illera et al. 2006; Hulbert and White 2007; McInnes et al. 2009).
Little consensus has been reached, however, as to what factors are most important; instead, the vast body of literature on the subject suggests that the relative influence of each factor depends on the species, spatial and temporal scales, and the geographic location of interest.

Understanding why a species might persist in one area, but perish in another is vital to planning effective protected area networks, making land-management decisions that promote long-term species persistence, predicting future patterns of global biodiversity due to climate change, and preventing or abating species invasions. The current rate of global change necessitates that our knowledge of species’ geographic ranges be efficiently transferred into practical conservation decisions. Applying a multi-species conservation approach that preserves species interactions is integral to ensure long-term persistence; therefore, identifying the features that maintain species diversity, the aggregated signal of many species’ distributions, may be of higher conservation priority than building a comprehensive understanding of range structure for any one species. Furthermore, the relationship between environment and diversity needs to be investigated at a scale that is complementary to reserve planning and land management – the regional or landscape scale (Opdam and Wascher 2004).

This research contributes to our understanding of how environmental factors shape species’ spatial distributions at the regional scale. Specifically, I investigate the spatial relationship between landcover heterogeneity and avian spatial distributions in a transitional zone in southern Ontario. Ontario Land Cover data (OMNR 1998) and bird occurrence data from the Ontario Breeding Bird Atlas (Bird Studies Canada et al. 2006) were used to assess the spatial heterogeneity of landcover and breeding bird diversity. The spatial relationship between landcover boundaries and avian boundaries was quantified at the regional scale. The results are discussed with respect to the group of avian species analyzed. Finally, I suggest some future research directions, and comment on the use of landcover heterogeneity as a surrogate for biodiversity.
Quantifying the spatial relationship between landcover heterogeneity and species’ distributions

1 INTRODUCTION

Climate change and other anthropogenic forces such as land-use change, habitat fragmentation, pollution, over-exploitation, and unplanned biological invasions are expected to drive future changes in species’ geographic ranges, such as range contraction, expansion and shifts (Gaston 2003; Opdam and Wascher 2004). These changes will be more detectable at range limits, where the abiotic and biotic factors that previously prevented further spread become more or less favourable to it (Gaston 2003; Gaston 2009). Internal margins may also be created as abundance structure across the range adjusts to shifting environmental conditions (Davis and Shaw 2001; Opdam and Washer 2004; Fortin et al. 2005). As ranges undergo spatial changes, new sets of species distributions will overlap and generate novel patterns of species richness and turnover, resulting in non-analogous species assemblages (Williams and Jackson 2007). Identifying the spatial pattern of range changes and consequent species turnover will help us quantify the effect of global change on species interactions, and ultimately on the long-term persistence of species. Given the current rate of global change due to anthropogenic forces, research into the factors affecting species distributions, and consequently turnover, has never been more urgent.

Considerable research effort has been invested in disentangling the factors limiting species’ spatial distributions, especially at range margins (Boone and Krohn 2000; Holt and Keitt 2000; Gaston 2003; Case et al. 2005; Hulbert and White 2007; McInnes et al. 2009; and many others). Although population dynamics and genetics are recognized to play significant roles, much of this research has focused on the abiotic and biotic factors constraining species geographically (Brown et al. 1995). At local spatial scales, these factors are often studied using a single- or two-species approach (but see Williams et al. 2002), and include competition (Bullock et al. 2000; Case et al. 2005) and habitat structure (Illera et al. 2006). At continental scales, the factors shaping individual species range boundaries are also likely
to be involved in driving coarse-scale diversity patterns (Currie et al. 2004; Algar et al. 2009; McInnes et al. 2009). Consequently, broad-scale studies have tended to adopt a macroecological perspective on species limits. Climate-related variables (e.g. water-energy balance, ambient energy availability; Hawkins et al. 2003a; Currie et al. 2004) have consistently been proposed as the most important drivers of global biodiversity, although habitat heterogeneity (Kerr and Packer 1997; Rahbek and Graves 2001; Melo et al. 2009), and historical contingency (Hawkins et al. 2003b) are also thought to influence geographic patterns of species richness and turnover.

Less attention has been granted to exploring the relationship between environmental factors and biodiversity at the regional or landscape scale. Research to date suggests that while climate remains an important factor at these scales, incorporating habitat heterogeneity (i.e. elevation gradients, landcover diversity) provides a more comprehensive understanding of species’ range limits (Bohning-Gaese 1997; Veech and Crist 2007; McInnes et al. 2009). The response of species richness to landscape attributes has been shown to be both taxon- and scale-dependent, but there is a consistently positive relationship between high heterogeneity, avian richness, and avian species turnover at the landscape scale (Atauri and de Lucio 2001; Tews et al. 2004; van Rensburg et al. 2004; McInnes et al. 2009). Given that land-management decisions are most often made at the regional scale, understanding what features of the landscape maintain biodiversity is critical to the effective implementation of conservation strategies (Barbault 1995; Waldhardt 2003; Opdam and Wascher 2004).

One obvious regional location of high species turnover is the transitional zone between vegetation communities, which is commonly characterized by high concentrations of range-restricted species, and high species richness (Odum 1953; Williams et al. 1999; Boone and Krohn 2000; van Rensburg et al. 2004; Kark et al. 2007; McInnis et al. 2009). This relationship exists, at least in part due to the diversity of habitat available within transitional zones. The composite of both habitats from the adjacent regions, and habitats unique to the transitional zone, provide a greater diversity of niches that support a higher-than-usual number of species (Holland et al. 1991; Risser 1995; Kark and van Rensburg 2006). By virtue of being transitions in major vegetative zones, these areas also frequently coincide
with the edges of many species’ ranges (Gaston 2003; McInnis et al. 2009). Species approaching their distributional limits may maintain only peripheral populations in fragmented suitable patches within the transitional zone, and consequently fail to establish long-term persistence and spread. Furthermore, transitional zones are considered valuable centers of diversification and speciation (Schilthulzen 2000), and are of significant conservation interest as they may not only generate biodiversity, but may also help to maintain it (Smith et al. 2001). They provide an ideal location and context to explore the relationship between landscape features and species’ distributions.

This research investigates the spatial relationship between avian geographic ranges and landcover heterogeneity at the regional scale. Identifying the key landscape features that enhance biodiversity at the regional scale, and quantifying how that relationship varies through space will further our understanding of the consequences of global change on species’ geographic ranges (Fortin et al. 2005). Such knowledge can then be used in the selection and design of protected areas within the context of current global changes. For this research, the area of interest is an ecological transitional zone in southern Ontario where many avian species converge at the southern or northern limits of their geographical range (Cadman et al. 2007). Although it has been recognized for its distinct geomorphologic, hydrologic, and biotic features (Couturier 2009), the zone has not been formally delineated. It is, however, of major conservation concern due to increasing rates of exurban development in the area (Conway and Shrestha 2009).

The central question of my thesis asks whether ecological boundaries emerging from the convergence of high rates of change in avian species’ distributions spatially overlap boundaries created by changes in landcover composition, which characterize the area of interest. I use Ontario Land Cover (1991-1998) data (OMNR 1998) and Ontario Breeding Bird Atlas (2001-2005) data (Bird Studies Canada et al. 2006) to assess the spatial heterogeneity of landcover composition and avian diversity, which allows me to quantify the spatial relationship between landcover and breeding bird spatial boundaries at the regional scale.
This research addresses the following questions:

- Is there a positive spatial relationship between boundaries resulting from high rates of change in landcover composition and boundaries resulting from high avian species turnover at the regional scale?
- If so, how strong is the relationship between the two sets of boundaries (landcover and birds)? Do boundaries spatially overlap?
- How does the relationship between boundaries vary over the study area? Is the relationship limited to the transitional zone? Does it occur across the entire transitional zone, or are there hotspots of association?
2 MATERIALS AND METHODS

2.1 Study Area

The area of interest, referred to as the Land Between (LB), is a distinct geomorphologic transitional zone in southern Ontario (Canada) where the south-eastern Lake Simcoe-Rideau (LSR) ecoregion meets the north-western Southern Shield (SS) ecoregion (Figure 1). Granite barrens and limestone plains, thin soils, an abundance of small lakes and wetlands, and high biotic diversity characterize the area. To capture the full extent of the variation in landcover and bird diversity that exists along the north-south axis, the area analyzed covers 92,000 km² and extends approximately 30-120 km south, and 40-120 km north of the LB (Figure 1a).

The unique physiographic attributes of the LB landscape become evident moving south-to-north from the LSR ecoregion to the SS ecoregion. Elevation gently increases, and the relief becomes more rugged. The terrain changes from gently undulating, with well-developed glacial till deeply covering Ordovician limestone bedrock, to broken terrain of exposed Precambrian bedrock (the Canadian Shield) covered in mineral till of variable depth (Chapman and Putnam 1966; Crins et al. 2007). The area of interest also features exposed limestone plains that support globally rare alvar ecosystems (Crins et al. 2007).

The hydrologic features of the LB stand out from those of adjacent ecoregions in the study area. Long, narrow, “finger-like” lakes formed through erosion by sub-glacial melt-waters are particularly prominent along the southern boundary of the LB (Shaw and Gilbert 1990). Soil buffering capacity is high throughout the LSR, and generally low in the southern portion of the SS (Crins et al. 2007). Consequently, both acidic and alkaline waters are mixed in the rivers that flow through the transitional zone. Parts of the area have the highest shoreline density in Ontario, and the numerous lake and river systems support a variety of wetland habitat and their associated fauna.

Moving from the LSR to the SS, mean annual precipitation slightly increases, mean annual temperature range decreases from 4.9-7.8°C to 2.8-6.2°C, and the mean length of the
growing season decreases from 205-230 days to 183-219 days (Mackey et al. 1996; Crins et al. 2007). Together with the geological, physiographic, and hydrologic gradients, the change in climate drives a shift in vegetation. Hardwood species like sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) are common across the study area, as are conifers like eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus stobus*), and red pine (*P. resinosa*) (Rowe 1972; Crins 2007). White ash (*Fraxinus americana*), black cherry (*Prunus serotina*), and oaks (*Quercus spp.*) also occur throughout, but are less common and more scattered in the SS (Rowe 1972). However, there is an increased presence of boreal species like black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*) in localized sites within and north of the transitional zone (Rowe 1972; Crins et al. 2007).

Due to the transitional nature of the study area and the abundance of shorelines and wetlands, the LB provides a great variety of habitats for bird species, and has been identified as a region of significant biodiversity in southern Ontario (Cadman et al. 2007; Couturier 2009). The area supports both boreal species like the Boreal Chickadee (*Poecile hudsonica*) and the Black-backed Woodpecker (*Picoides arcticus*), which favour spruce, balsam fir, and jack pine dominated forests, and species specializing in mature coniferous and mixed forest, like the Blackburnian Warbler (*Dendroica fusca*). Also present are grassland-nesting species that prefer agricultural pastures and open meadows, such as the Savannah Sparrow (*Passerculus sandwichensis*) and the Bobolink (*Dolichonix oryzivorus*). Additionally, abandoned farmland in the LB has provided ideal habitat for species associated with early successional forest, scrub and edge habitat, like the Magnolia Warbler (*Dendroica magnolia*) and Field Sparrow (*Spizella pusilla*). Many species that occur in the LB and surrounding area are at the northern or southern edge of their distribution, and demonstrate either abrupt changes or gradual transitions in abundance between the SS and LSR ecoregions (Cadman et al. 2007; Couturier 2009). A handful of species have distributions that are largely limited to the area. The Golden-winged Warbler (*Vermivora chrysoptera*), which requires successional shrub habitat for breeding and forest for foraging, has close to 80% of its Ontario population restricted to the LB (Cadman et al. 2007; Couturier 2009).
In addition to the environmental transitions occurring across the LB, there is a gradient of anthropogenic development that further shapes landcover heterogeneity in the area. Road density sharply decreases at the southern edge of the Canadian Shield as population density decreases from 10-50 persons/km² to fewer than 10 persons/km² (NRC 2006). Although there are a few moderately sized communities within the transitional zone, urban development is sparse compared to the densely settled urban growth centers of southern Ontario. Instead, there is an increased presence of provincial parks, enhanced management areas, and conservation reserves (Crins et al. 2007). On account of the geomorphological character of the study area, agriculture is prevalent in the LSR, rare in the SS, and limited in the transitional zone to small, localized pockets (Crins et al. 2007). Recently there has been a surge of interest in exurban development in the area, especially shoreline development of family homes and cottages. The threat of development has increased pressure to protect the ecological and cultural heritage of the LB.

2.2 Ontario Land Cover

I used Ontario Land Cover (OLC) data derived from digital, multispectral Landsat Thematic Mapper data (OMNR 1998) to assess landcover heterogeneity across the study area (Figure 1b). Ontario Land Cover data were collected between 1986 and 1997, with the majority of data recorded in the early 1990s, and information on forest cutovers and burns updated in 1996. While OLC data are too generalized for detailed site-specific studies, it is appropriate for the analysis of landcover change at the regional scale. The original data set has a spatial resolution of 25 m, and is projected in the Universal Transverse Mercator (UTM) coordinate system (Zones 15 to 18) based on the NAD83 datum (North American Datum of 1983). The LB covers two UTM zones (17 and 18), so I have re-projected the data to a Lambert Conformal Conic coordinate system (NAD83 datum) in order to create a seamless and flat GRID of the study area that minimizes distortion. False easting and false northing values were set to 930,000 m and 6,430,000 m, respectively.

Ontario Land Cover data identifies 28 classes of both vegetated and non-vegetated surfaces, and reflects the nature of the land surface rather than land use. To identify regional-scale changes in the landscape, I reclassified the data into six broad landcover classes: (i) mixed
forest (both mainly coniferous mixed forest and mainly deciduous mixed forest); (ii) coniferous forest (sparse and dense coniferous forest and plantations); (iii) deciduous forest (sparse and dense deciduous forest); (iv) water (water bodies, marshes, swamps, fens and bogs); (v) agricultural (pasture, abandoned fields and cropland); and (vi) urban (settlement and developed land, mine tailings, quarries, and bedrock outcrops). Preliminary analysis had indicated that alvars in the study area were too localized and sparse to contribute to the LB boundary; therefore, this landcover type was not included in the final analysis.

2.3 Elevation

Elevation and measures of topographic complexity (i.e. slope and aspect) are frequently identified as important factors driving spatial variation in species diversity patterns (Kerr and Packer 1997; Atauri and de Lucio 2001). Consequently, I used elevation data derived from the Canada3D digital elevation model (DEM; NRC 2001) to better capture the factors that may influence species distribution in the study area. The DEM is a Canada-wide survey of ground elevations measured and recorded at regular spaced intervals. Elevations are expressed in meters with respect to sea level at a resolution of 30 arc-seconds (approximately 837.7 meters) in accordance with the NAD83 datum. I projected elevation data to a Lambert Conformal Conic coordinate system (NAD83 datum) to match existing landcover data.


The Ontario Breeding Bird Atlas, 2001-2005 (OBBA) is a large-scale survey carried out to delineate breeding bird distributions in Ontario (Cadman et al. 2007). While it was primarily intended to describe species’ ranges, this recent atlas also includes point counts in an attempt to map the relative abundance of bird species across the province. Field collection was carried out using roadside surveys during peak breeding season (late May to early July for most species) between the years 2001 and 2005. Atlas volunteers were assigned a 10 km square area, and asked to survey at least 25 randomly prescribed locations along roads, although off-road counts were assigned for habitats that were underrepresented. To maintain statistical independence between samples, road-side locations were separated by at least 500 m, and off-road sites were located at least 100 m from the road, and separated by at least 300 m. Point counts involved standing at each location for 5 minutes, and recording all birds
seen or heard during that interval within two distance classes, of less than 100 m, and of
more than 100 m (Cadman et al. 2007).

I used OBBA point counts to evaluate the spatial heterogeneity of bird distributions in the
study area (Bird Studies Canada et al. 2006). Only counts recorded within the first distance
class (<100 m) were used to ensure statistical independence. As species ranges are dynamic,
and large annual variation in distributional limits is not uncommon (i.e. Bowman et al. 2005),
I used all point counts collected between 2001-2005 to capture a more comprehensive
approximation of species distributions (35,955 individual point counts). By using data from
all five years, I reconstructed bird distributions more reliably in the north of the study area,
where OBBA survey effort and coverage were lower (Cadman et al. 2007).

Despite the amalgamation of data encompassing 5 years, there remained a large gap in point
count coverage across the study area (Figure 2). The LSR area received full coverage (≥25
points counts between 2001 and 2005) in 50% of 10 km squares, but only 25% of squares in
the SS area were fully covered, and some 10 km squares were not sampled at all (Cadman et
al. 2007). Preliminary analyses showed that this discrepancy created high rates of change in
species composition and richness in the north, resulting in false boundaries being detected.
To smooth out the sampling bias, I used indicator kriging (IK; Goovaerts 1997) to interpolate
across the survey gaps for each species. Indicator kriging is a geostatistical technique that
estimates the probability that a point at a given location exceeds a pre-defined threshold
based on the behaviour and correlation of data points within the neighbourhood (Journel
1983; Goovaerts 1997). This technique was selected because it is a non-parametric
technique that can be applied to zero-inflated data (Goovaerts 2001), and which has been
previously shown to be appropriate for mapping distributions of avian species from census
data (Walker et al. 2008). Moreover, IK handles binary data, and given that I am only
interested in species occurrence, treating the data as presence/absence reduces the uncertainty
associated with abundance data collection (i.e., observer bias). I implemented IK using the
Geostatistical Analyst toolbox in ArcMap version 9.3 (ESRI 2009), setting the threshold to 0
so that all abundances greater or equal to 1 were treated as presences. The interpolation was
restricted to 10 km to prevent distorting species ranges beyond the scale of our analysis, and
a smoothing factor of 1 was applied to create more realistic distribution contours. Using the IK analysis, I derived probability of occurrence maps for selected species in the study area.

The accuracy of probability surfaces acquired by IK depends on both the reliability of point data (i.e. accurate representation of the pattern of interest), and the spatial structure of that data. The OBBA used ordinary kriging, a related approach, to create relative abundance maps for a subset of bird species, which were then screened based on their amenity to the technique (Cadman et al. 2007). Many species with low population numbers, low detectability, and restricted geographical range (i.e. waterfowl, nocturnal birds, rare and colonial species) did not meet the criteria, and were considered inappropriate for abundance mapping. I selected species for my analysis based on the group of species approved by the OBBA (Cadman et al. 2007). Of the 130 species for which abundance maps were created, 113 had distributions within the study area. I additionally excluded species that had fewer than 150 presences recorded in the study area, and those that had been identified in the OBBA as being possibly under- or over-detected in point counts.

Maps of probability of occurrence were created for the resulting subset of 68 species by applying IK to point counts of each species, and a cross-validation (CV) approach was used to assess the performance of the interpolations. The CV approach used in this analysis reiteratively removes a value from the dataset, applies IK to the new dataset, and computes an estimate at the site of the removed value (Jerosch et al. 2006). Prediction-error statistics that reflect the difference between measured and estimated values can be used to evaluate the reliability of the estimation models (Jerosch et al. 2006). I used the root-mean-square of standardized error (RMSSE), a commonly used CV statistic that reflects the relationship between measured and estimated variances. Ideally, RMSSE values should be 1, with higher values suggesting that kriging variances are underestimated and lower values indicating that kriging variances are overestimated. Species with RMSEE between 0.925 and 1.075 (i.e. ± 0.075) were selected for inclusion in the species boundary analysis (Table 1).
2.5  **Data Preparation and Resampling**

A 10×10 km sampling grid of 920 individual and adjacent sampling units (i.e. grid cells) overlapping the study area was constructed in ArcMap version 9.3 (ESRI 2009) to sample both landcover heterogeneity, and species probability of occurrence. Some 10×10 km sampling units located along the edges of the study area extended past the available landcover data (i.e. sampling units overlapping both landcover types and no data type). To reduce edge effects, only cells with more than 50% landcover were included in the sampling grid. This threshold is equivalent to the one used in a resampling majority rule algorithm. Sampling units with more than 75% of their surface area occupied by open water, such as those overlapping lakes Nipissing and Simcoe, were also removed from the analysis to prevent large fluctuations in landcover composition between adjacent cells.

2.5.1  **Landcover**

To assess landcover heterogeneity I measured the change in landcover composition across the study area. Heterogeneity due to mixed, deciduous and coniferous forest, and agricultural and urban landcover types was measured by calculating the proportion of each 10×10 km sampling unit that was occupied by each type. The sampling grid and landcover layer were spatially overlapped in ArcMap version 9.3 (ESRI 2009), and the number of 25×25 m pixels of each landcover type was counted using Zonal Statistics in the Spatial Analyst toolbox. Proportions were calculated based on the number of 25×25 m pixels in each sampling unit, which was usually 1,600 (40×40 pixels), but lower if the sampling unit was on the edge of the study area, or if it had unclassified pixels in it. Elevation data were summarized using Zonal Statistics by calculating the mean elevation in each 10×10 km sampling unit.

The number of small lakes and wetlands is one of the distinguishing features of the LB. At the spatial grain used in this analysis (10×10 km), the impact of those small bodies of water on landcover heterogeneity is lost when they are sampled based on area. Therefore, I sampled lakes and wetlands twice using two different measures: perimeter and count. To estimate the amount of shoreline habitat across the study area, water bodies, marshes, swamps, fens and bogs were converted to polygons in ArcMap version 9.3 (ESRI 2009), and
the perimeter of polygons was summed for each 10×10 km sampling unit. Occurrence was obtained by counting the number of water polygons for each sampling unit using the Polygon in Polygon Analysis in the Hawth’s Tools extension.

Eight layers representing different landcover attributes and elevation were derived from the OLC (OMNR 1998) and DEM (NRC 2001) data: i) deciduous forest; ii) coniferous forest; iii) mixed forest; iv) urban; v) agricultural; vi) water perimeter; vii) water count; and viii) elevation. Landcover classes were expressed in terms of proportion (deciduous forest, coniferous forest, mixed forest, urban, agricultural), sum (water perimeter), or count (water occurrence), and elevation was expressed as a mean, for each of 920 sampling units.

2.5.2 Birds
To reconstruct regional bird distributions, the probability of occurrence of each species was sampled with ArcMap version 9.3 (ESRI 2009) using the same 10×10 km sampling grid. For each species, the mean probability of occurrence was calculated in each sampling unit using Zonal Statistics in the Spatial Analyst toolbox, resulting in 60 distribution maps of 920 sampling units.

2.6 Boundary Detection
In an ecological context, boundaries can be defined as spatially adjacent locations where there is a high degree of change in abiotic or biotic features (Fortin 1994; Fortin and Dale 2001). Based on this interpretation, I quantified boundaries in species distributions and landcover using a lattice-wombling edge detection algorithm (Fortin 1994) implemented in Boundary Seer software (TerraSeer, Inc. 2001). This algorithm computes rates of change (i.e. first partial derivative) between adjacent units for each 2×2 unit window in the study area, and assigns the average rate of change at the centroid of the window (Fortin 1994; Fortin and Drapeau 1995). The result is a map of rates of changes, or boundary likelihood values, which has the dimensions of the original map minus one row and one column. To spatially delineate boundaries, boundary likelihood values are ranked, and an arbitrary threshold is applied such that values exceeding the threshold become boundary elements (BEs). For example, selecting a threshold of 20% identifies rates of change above the 20th
percentile rank as boundaries. Given transitional zones are likely to be characterized both by sharp (abrupt) and soft (gradual) transitions (Kark and van Rensburg 2006), I defined boundaries at three thresholds for comparison: 10%; 15%; and 20%. A conservative threshold like 10% indicates ‘hotspots’ of heterogeneity, whereas more liberal thresholds (15% and 20%) reveal softer transitions that connect hotspots to form large boundaries of variable strength. Given the spatial grain and extent used in this analysis, thresholds lower than 10% would result in too few BEs being delineated to form cohesive boundaries (Fortin 1999). Too liberal thresholds (i.e. higher than 20%) should also be avoided as they can result in the detection of noise in the form of many scattered, single BEs (St-Louis et al. 2004).

I was interested in the combined effect of landcover heterogeneity on regional bird diversity patterns, rather than the influence of individual landcover features on single species; therefore I used a multivariate approach to look at boundaries in landcover (eight layers) and bird distributions (60 species). Three sets of composite landcover boundaries were delineated and overlapped with bird boundaries. To capture the abundance of small water bodies that is characteristic of the LB, one set of boundaries (LC1) was delineated using elevation, water as a count, and five other landcover types (deciduous forest, coniferous forest, mixed forest, urban, and agricultural). A second set (LC2) was delineated to capture changes in shoreline density and, therefore, included water as perimeter instead of a count. Also, because the occurrence of water, and the amount of available shoreline habitat may explain different attributes of bird distributions, a third boundary set (LC3) was delineated including both water as a count and as perimeter such that eight different layers were used in the multivariate boundary analysis.

To determine turnover among several variables, I used a multivariate approach such that boundary likelihood values were evaluated for each attribute (i.e., landcover type or bird species), and then averaged at centroids for the set of attributes. Attribute maps were imported as GRID ASCII files and standardized using a 0-1 scaling technique to allow cross-comparisons. All attributes within a set were equally weighted because I had no reason to believe that any one attribute contributes more strongly to the processes generating the boundary. Boundaries signaling landscape heterogeneity were expected to occur between
sampling units where there was a high turnover in landcover composition. Bird boundaries were anticipated in areas where many species’ distributions encounter changes in probability of occurrence, and overlap spatially.

Due to the diversity and amount of landcover types available in the LB, some bird species have populations that are more concentrated in the LB than elsewhere in their Ontario range (Couturier 2009). This might be generating any observed bird boundaries occurring in the area. To test whether bird boundaries in the LB are driven by species that preferentially associate with the area, I split species into two groups (Table 1) - species that have at least 15% of their Ontario population in the LB (26 species), and species that have less than 15% of their Ontario distribution in the LB (34 species) - and delineated boundaries for each group separately. Species population estimates were obtained from Couturier (2009). These estimates were based on the previously delineated LB boundaries shown in Figure 1a and calculated for species that were at least three times more abundant in the Land Between than would be expected based on catchment area alone (Couturier 2009).

2.7 **Boundary and Overlap Statistics**

The presence of high rates of change in attributes is not sufficient to imply the presence of boundaries, which are also characterized by the spatial arrangement of BEs. Cohesive boundaries should be long in length, and fewer in numbers (Fortin and Drapeau 1995; Fortin and Dale 2005). A too liberal boundary threshold (i.e. more than 20%) will inevitably result in spatially adjacent BEs; however, these boundaries may not exhibit the desirable properties of cohesive boundaries. Furthermore, if a range of thresholds fails to delineate cohesive boundaries, either there is no cohesive boundary to be detected, the attributes selected are not representative of the boundary, or the analysis is being carried out at the wrong extent and/or grain (Fortin and Dale 2005). To reduce some of the subjectivity introduced by boundary threshold selection, and to verify the occurrence of ecologically relevant boundaries, boundary statistics (Fortin 1994) were used to analyze contiguity of landcover and bird boundaries at the 10%, 15%, and 20% thresholds.
Boundary statistics may suggest one of three possible cases: contiguous boundaries; fragmented boundaries; or no significant boundaries. Contiguous boundaries are expected where an underlying boundary-generating process creates high rates of change in the attribute of interest through space, such that BEs tend to be adjacent to each other. In such a scenario, I anticipate fewer singletons ($N_1$ - single, unconnected BEs), fewer sub-boundaries ($N_S$ - two or more connected BEs), higher sub-boundary length ($L_{\text{MAX}}$ and $L_{\text{MEAN}}$ - number of BEs in a sub-boundary) and diameter ($D_{\text{MAX}}$ and $D_{\text{MEAN}}$ - number of BEs separating the opposite ends of a sub-boundary), and lower branchiness ($D/L$ - mean diameter-to-length ratio) than might be expected if boundaries were to occur by chance. Boundary statistics are compared to a randomized reference distribution created by repeatedly permuting observed boundary likelihood values across sample locations using a randomization procedure, and recalculating statistics each time. For multivariable data sets, each attribute is randomized independently. Data with underlying spatial structure (i.e. spatial autocorrelation) can be analyzed using a restricted randomization procedure that preserves some of this configuration; however, I used a randomized permutation that assumes complete spatial randomness as it requires fewer statistical decisions, and results in conservative significance testing (Oden et al. 1993; Fortin et al. 1996). Both landcover and bird boundaries were tested using this randomization procedure ($n = 9999$ permutations), and the significance of boundary statistics was assessed using a one-tailed test ($p < 0.01$). I used a one-tailed test because I am only interested in detecting cohesive boundaries (Fortin 1994).

I used overlap statistics to determine whether bird distributions spatially coincide with landcover heterogeneity on the regional scale (Jacquez 1995; Fortin et al. 1996; St-Louis et al. 2004). Three properties were measured that test whether landcover boundaries and bird boundaries are occurring closer together than expected by chance: i) the direct spatial overlap of boundary elements in the two sets of boundaries ($O_3$); ii) the simultaneous association of landcover and bird boundaries ($O_{LB}$); and iii) the directional association of bird boundaries to landcover boundaries ($O_{B}$). The direct spatial overlap of boundary elements ($O_3$) represents the number of boundary elements that the two sets of boundaries have in common, and was expected to be high if both sets of boundaries characterize the transitional zone. The simultaneous association of landcover and bird boundaries ($O_{LB}$) and the directional
association of bird boundaries to landcover boundaries ($O_B$) represent the mean distance between the two sets of boundaries; they were consequently expected to be low, because I propose that turnover in bird distributions is dependent on changes in landcover composition. Again, I tested the significance of overlap statistics using a randomization reference distribution ($n = 9999$ permutations) and a one-tailed test ($p < 0.01$), given that I was only interested in the positive spatial association and overlap of landcover and bird boundaries and I was aware of no *a priori* reason to expect negative associations.
3 RESULTS

3.1 Boundary Delineation and Boundary Statistics
Boundaries were delineated using a lattice-wombling algorithm resulting in 821 rates of change from 920 sampling units of 10×10 km. The top 10%, 15% and 20% rates of change (from more conservative to more liberal) were considered boundary constituents generating 82, 123, and 164 boundary elements (BEs), respectively. Both landcover and bird boundaries, defined here as areas of spatially adjacent BEs, appeared to be concentrated in the LB at all three boundary thresholds.

3.1.1 Landcover: Composite landcover (LC1, LC2, and LC3)
At a conservative threshold of 10%, BEs delineated for LC1, LC2, and LC3 showed a few clear, but isolated and relatively small boundaries (LC1: diameter 8 and 9 BEs; LC2: diameter 8, 6, and 7 BEs; LC3: diameter 8 and 10 BEs) occurring within the LB (N: 12,036,100 m; W: 1,347,090 m; S: 11,996,100 m; E: 1,627,090 m; Figures 3-5). For all three composite landcover boundaries, BEs delineated at the two more liberal thresholds (15% and 20%) connected these shorter boundaries, and formed a zone of high rates of change that delineated the LB and split the study area along a north-south transect (N: 12,056,100 m; W: 1,347,090 m; S: 11,996,100 m; E: 1,627,090 m). Other sectors within the study area also showed small clusters of BEs, specifically in the northwest of the study area (N: 12,186,100 m; W: 1,257,090 m; S: 12,126,100 m; E: 1,297,090 m), and in the northeast (N: 12,136,100 m; W: 1,527,090 m; S: 12,096,100 m; E: 1,677,090 m). Not surprisingly, boundaries delineated for LC3 were a blend of those delineated for LC1 and LC2. At the 20% threshold, 24 BEs delineated for LC3 were shared with either LC1 or LC2 boundaries, and 133 BEs occurred in both.

According to the boundary statistics taken jointly (\(N_S\), \(N_I\), \(L_{MAX}\), \(L_{MEAN}\), \(D_{MAX}\), \(D_{MEAN}\), \(D/L\); Table 2), composite landcover boundaries (LC1, LC2 and LC3) were significantly contiguous at all three thresholds based on a randomization procedure with 9999 permutations (\(p < 0.01\); except \(D/L[10\%]\) LC2 which was not significant). Therefore, BEs tended to be situated adjacent to each other, and resulted in fewer isolated, single BE
boundaries \((N_i)\), as well as fewer, but longer and more open boundaries \((N_s, L_{MAX}, L_{MEAN}, D_{MAX}, D_{MEAN})\) than expected by chance. The number of sub-boundaries increased at higher thresholds for all three composite boundaries. Taking LC1 as an example, 14 sub-boundaries were delineated at both the 10% and 15% threshold, and 5 additional sub-boundaries were identified at the 20% threshold. At more liberal thresholds (15% and 20%), observed values of boundary length \((L_{MAX}, L_{MEAN})\) and diameter \((D_{MAX}, D_{MEAN})\) for LC1, LC2, and LC3 were much higher than expected, falling between 10 and 20 standard deviations beyond the values expected if BEs were randomly distributed on the landscape (N.B. z-scores are included as a reference to indicate the strength and direction of the difference between observed values and expected values). The largest composite landcover boundary (i.e., longest length and largest diameter) was delineated for LC1 at the 20% threshold, and measured 67 BEs in length and 32 BEs in diameter.

Boundary statistics indicated that the three composite landcover boundaries generally exhibited very similar properties (Table 2). The values of most of the statistics calculated for LC1, LC2, and LC3 were comparable, especially at the 10% and 15% thresholds. The largest LC1 boundary (delineated at the 20% threshold) was 22 BEs longer, and at least 8 BEs wider than the largest boundary identified for either of the two other composite boundary sets. However, this is only because fewer BEs were delineated in the mid-western portion of the LB for either LC2 or LC3 (N: 12,036,100 m; W: 1,417,090 m; S: 12,016,100 m; E: 1,437,090 m; Figures 4 and 5), resulting in two adjacent boundaries occurring in the area. In contrast, a single boundary spanned the entire length of the transitional zone for LC1. Despite this difference, boundaries delineated based on LC1, LC2, and LC3 were remarkably congruent, both in terms of spatial location and boundary properties.

3.1.2  Landcover: Cover types separately

The boundaries emerging from high landcover heterogeneity (Figures 3-5) resulted from the contribution of boundaries in individual landcover types (Figures 6-9), which varied in their spatial location and properties. Boundaries arising from individual landcover types tended to occur over a greater extent of the study area than the more localized composite landcover boundaries. However, all landcover types had one property in common: they demonstrated
high rates of change in the LB. For example, boundaries delineated from water landcover based on count information (Figure 6) occurred everywhere, although long boundaries were exclusive to the LB (N: 12,076,100 m; W: 1,437,090 m; S: 11,996,100 m; E: 1,627,090 m). Water boundaries based on perimeter information (Figure 7) were differently distributed across the study area, but BEs were also scattered, and heterogeneity hotspots were in the same general location (N: 12,066,100 m; W: 1,477,090 m; S: 11,996,100 m; E: 1,627,090 m). Mixed-forest boundaries (Figure 8) were confined to the northern portion of the study area, but the southern-most boundaries occurred in the transitional zone (S: 11,016,100 m). High rates of change in urban landcover (Figure 9) created large hotspots of heterogeneity rather than boundaries, but three large hotspots occurred within the LB (N: 12,076,100 m; W: 1,367,090 m; S: 12,016,100 m; E: 1,577,090 m). Therefore, although the LB cannot be delineated using individual landcover boundaries, the high heterogeneity that results from the contribution of all landcover types effectively identifies the transitional zone.

Boundary statistics (Table 2) indicated that at a 20% threshold, water count and mixed-forest landcover boundaries were significantly contiguous to some degree ($p < 0.01$ for water count: $N_S$, $L_{\text{MAX}}$, $L_{\text{MEAN}}$, $D_{\text{MAX}}$, $D_{\text{MEAN}}$ and mixed forest: $N_S$, $N_1$, $L_{\text{MEAN}}$, $L_{\text{MAX}}$, $D_{\text{MEAN}}$, $D_{\text{MAX}}$). Water boundaries based on perimeter were also contiguous according to statistics ($p < 0.01$: $N_S$, $N_1$, $L_{\text{MEAN}}$, $L_{\text{MAX}}$, $D_{\text{MEAN}}$, $D/L$). However, statistics also indicated that these boundaries were less contiguous than the composite landcover boundary, in that they were characterized by a greater number of sub-boundaries ($N_S$) and singletons ($N_1$) at the 20% threshold. At this threshold, 25 and 28 sub-boundaries were delineated for water and mixed-forest landcover, respectively, compared to 18-20 sub-boundaries delineated for the composite landcover boundary sets. Consequently, individual landcover boundaries also tended to be shorter ($L_{\text{MAX}}$, $L_{\text{MEAN}}$, $D_{\text{MAX}}$, $D_{\text{MEAN}}$). The longest water and mixed-forest boundaries delineated at the 20% threshold measured 35 BEs and 26 BEs in length, respectively. Other boundaries lacked contiguity altogether; boundaries delineated from urban landcover were neither significantly long, nor significantly few in number.
3.1.3  Birds: All species combined together

Like landcover boundaries, bird distribution boundaries occurred predominantly in the LB at all three boundary thresholds, and delineated the transitional zone at the 20% threshold (N: 12,066,100 m; W: 1,347,090 m; S: 11,996,100 m; E: 1,647,090 m; Figure 10). Whereas landcover boundaries were rather narrow and linear, bird boundaries were wide and sinuous, with apparent peninsulas (i.e., N: 12,046,100 m; W: 1,557,090 m; S: 12,026,100 m; E: 1,587,090 m) characterizing both sides of the boundary (Fortin and Dale 2005). At its widest point along a north-south transect, the bird boundary was seven BEs thick (N: 12,046,100 m; W: 1,547,090 m; S: 11,976,100 m; E: 1,557,090 m), whereas two landcover boundaries (LC1 and LC2) were four BEs thick (N: 12,036,100 m; W: 1,487,090 m; S: 11,996,100 m; E: 1,497,090 m; Figures 3 and 4). Another obvious characteristic of the bird BEs was that the highest rates of change (10% threshold) were highly aggregated. These hotspots of high species turnover were located in the LB (i.e., N: 12,026,100 m; W: 1,427,090 m; S: 11,966,100 m; E: 1,507,090 m; Figure 10).

Bird distribution boundaries were significantly contiguous at the 10%, 15%, and 20% thresholds ($p < 0.01$; Table 3). At each threshold, they were both fewer in number ($N_b$) and longer ($L_{MAX}, L_{MEAN}$) than those of landcover (Tables 2 and 3). For example, only nine bird boundaries were delineated at the 20% threshold, and the longest bird boundary measured 118 BEs, 51 BEs more than the longest landcover boundary ($L_{MAX}[20\%]^{LC1}$). Also, there were fewer isolated bird boundaries ($N_l$) than landcover boundaries at higher thresholds (15% and 20%). Diameter ($D_{MAX}, D_{MEAN}$) was lower for landcover boundaries than bird boundaries, especially for LC2 and LC3 boundaries. This pattern in boundary statistics reflects the observed tendency of bird BEs to be more localized and connected than those of landcover.

3.1.4  Birds: Two species groups separately

At the 20% threshold, both species with distributions that are positively associated with the LB (species with 15% or more of their Ontario population within the LB), and species that show less preference for the area (species with less than 15% of their population in the LB) showed high rates of change in the transitional zone (N: 12,066,100 m; W: 1,347,090 m; S: 11,996,100 m; E: 1,647,090 m; Figure 10).
11,946,100 m; E: 1,637,090 m; Figure 11). However, BEs of the <15% species group appeared to be more scattered across the study area (i.e., N: 12,196,100 m; W: 1,277,090 m; S: 12,076,100 m; E: 1,557,090 m) than those of the ≥15% species group, which were generally concentrated within the LB. Boundary statistics (Table 3) confirmed that the former species group had nine more isolated BEs than the latter group, and that boundaries for this group tended to be both shorter in length \( (L_{\text{MAX}}, L_{\text{MEAN}}) \), and smaller in diameter \( (D_{\text{MAX}}, D_{\text{MEAN}}) \). Regardless, boundaries for both species groups were significantly contiguous at \( p < 0.01 \).

A comparison of boundary properties at the three thresholds illustrates that the sharpness of landcover and bird boundaries varied asymmetrically through space. At the 10% threshold there were significant, but isolated “hot spots” of rapid change in both sets of boundaries (Figures 3-5 and 10). Once the threshold was relaxed, and BEs with lower rates of change were included in the delineation, these boundaries connected. This process was reflected in a general increase in \( L_{\text{MAX}}, L_{\text{MEAN}}, D_{\text{MAX}}, \) and \( D_{\text{MEAN}} \) (Tables 2 and 3), such that the BEs delineated at higher thresholds tended to join boundaries delineated at the lower thresholds. However, an interesting difference between landcover and bird boundaries was the pattern of change in \( N_S \). In bird boundaries, these were relatively similar at all three thresholds (Table 3). Landcover boundaries behaved differently, and had more sub-boundaries at the 20% threshold than at 10% or 15% (Table 2). Again, this supports the observation that bird BEs were more spatially aggregated than landcover BEs at high boundary thresholds.

3.2 Spatial Boundary Overlap

The direct spatial overlap of bird and composite landcover BEs at the 20% threshold (Figures 12-14) was largely restricted to the LB (N: 12,066,100 m; W: 1,347,090 m; S: 11,996,100 m; E: 1,627,090 m), with approximately 80% or more of overlapping BEs occurring within this region. Furthermore, overlapping BEs in the LB demonstrated a high degree of adjacency. Although there was some overlap in the north-east of the study area (N: 12,136,100 m; W: 1,537,090 m; S: 12,086,100 m; E: 1,707,090 m), it was limited to no more than 10 scattered BEs that occurred either singly, or in pairs.
The spatial relationship between landcover heterogeneity and bird distributions was quantified using boundary spatial overlap statistics (Table 4). Boundary overlap, the directional association of bird boundaries to landcover boundaries, and the simultaneous association of the two boundary sets were analyzed for bird and composite landcover BEs (LC1, LC2, and LC3), delineated at the three boundary thresholds. According to OS and OB measures taken jointly, there was significant overlap between bird and landcover BEs at all three thresholds, as well as significant association of bird BEs to landcover BEs \((p < 0.01)\). Therefore, bird and landcover boundaries overlapped more often, and bird boundaries were, on average, closer to landcover boundaries than expected by chance based on 9999 permutations. The simultaneous association of bird and LC2 BEs, and bird and LC3 BEs \((O_{LB})\), was non-significant at all three thresholds. This result likely reflects the fact that landcover BEs were more spread out over the study area than bird BEs, which were localized within the LB. This increased the mean distance between any two landcover and bird BEs.

Overlap statistics suggest that boundary overlap was greater between bird and landcover BEs when landcover boundaries were delineated using water sampled as a perimeter (LC2 and LC3). Generally, the greatest overlap and association occurred between bird and LC3 BEs. At the 20% threshold, 67 BEs were included in both sets of boundaries \((OS)\), and the mean distance from bird BEs to the nearest landcover BE \((OB)\) was 11395.5 m (Table 4). This result is not surprising considering that LC3 boundaries were delineated using both water count and water perimeter information; consequently, LC3 boundaries have more information with which to explain variation in bird spatial distributions. However, overlap and association was similarly strong between bird and LC2 boundaries, and weakest between bird and LC1 boundaries at all three boundary thresholds. Although these differences are not large enough to draw any unequivocal conclusion, the overlap statistics suggest that shoreline density may be a better explanatory variable of bird species’ distributions than the regional occurrence of water bodies on the landscape.
4 DISCUSSION

This research contributes to establishing a more comprehensive understanding of how landscape features shape spatial patterns in avian species turnover at the regional scale, a scale that has thus far been given relatively little consideration. Specifically, I was interested in whether landcover boundaries and avian boundaries are spatially coinciding or associating, in the strength of the spatial relationship between them, and the ways in which that relationship changes across the study area. I also asked whether avian boundaries are driven by species that preferentially associate with the Land Between transitional zone.

I found strong support for the presence of a positive spatial relationship between landcover heterogeneity and avian species distributions at the regional scale (Figures 12-14). Most landcover and avian boundaries occurred within the Land Between, where there was significant spatial association and overlap between them (Table 4). My observations echo the predictions of the “ecotone hypothesis” (Odum 1953), which proposes that areas of ecological transition are spatially congruent with areas of high biodiversity, and affirm the conclusions of other studies that have found a similar relationship in transitional zones (i.e., Williams 1996; Araújo and Williams 2001; van Rensburg et al. 2004). Moreover, the results are consistent with those of Atauri and de Lucio (2001), which demonstrated that regional avian species richness was higher in landscapes with a high diversity of land uses. A positive spatial relationship between landscape attributes and species turnover at the continental scales has also been previously observed (Gaston et al. 2007; McInnis et al. 2009; Melo et al. 2009). From a conservation perspective, identifying the factors that shape spatial patterns of species turnover is of more interest than focusing only on species richness gradients, because information on the processes affecting species turnover can be more effectively applied to the spatial design of protected areas (Wiersma and Urban 2005).

Avian distributional boundaries delineated within the Land Between were generated both by those species that preferentially associate with the transitional zone (at least 15% of Ontario population occurs in the Land Between), and those that do not show any such selection (less than 15% of Ontario population occurs in the Land Between; Table 3 and Figure 11). The
observed high rates of change in species distributions are likely being generated by two processes: i) species occupying more patches within the Land Between than in the surrounding area in response to greater amounts of suitable habitat; and ii) species approaching their range margins and occupying fewer patches in response to environmental gradients limiting their distribution (Gaston 2003). Therefore, the Land Between may be promoting the persistence of populations both within and at the margins of species’ geographic ranges, making it an area of high biodiversity relative to the surrounding regions and consequently, an area of significant conservation interest.

Bird distributional boundaries were more localized within the Land Between than boundaries created by high landcover heterogeneity, but they were also distributed further south and beyond the hypothesized borders of the transitional zone (Figures 3-5 and 10-14). Furthermore, landcover boundaries better delineated the entire length of the transitional zone across the west-east axis. From these results I can deduce two things. Firstly, at the regional scale, birds do not always respond to landcover heterogeneity with changes to their distributions; otherwise we might expect to see pockets of high avian turnover elsewhere in the study area. Also, high rates of change in avian distributions are not exclusive to areas of high landcover heterogeneity. Secondly, the relationship between landcover and avian boundaries varies across the Land Between, so species turnover rates may not be an effective way of delineating transitional zones. These results are not surprising because landscape heterogeneity was not expected to be the sole factor generating avian species turnover; other environmental, ecological, and historical factors, many of which have already been mentioned, will affect how species distribute themselves through space to varying degrees. Likely, it is the coincidence of several of these factors (i.e., landscape heterogeneity, climatic gradients, interspecific interactions, niche conservation) that drives species diversity patterns, with some factors explaining more variation in richness patterns than others at different spatial and temporal scales (Gaston 2003; Gonzáles-Megías et al. 2007).

In a study linking spatial turnover of species and environmental conditions at a global scale, Buckley and Jetz (2008) found that the relationship between high environmental turnover and high species turnover was either weakly significant, or not significant in temperate
realms. Yet McDonald et al. (2005) observed that at a resolution of 50 × 50 km, transitions between ecoregions across North America (including those occurring in southern Ontario) did not correspond to high rates of avian species turnover, except where these transitions occurred across biomes, or other areas with abrupt changes in abiotic conditions (i.e., mountain ranges). My results show that at regional scales, transitional zones between ecoregions can be spatially coincident with avian species boundaries, and high turnover rates. I believe this emphasizes that when species turnover rates are evaluated across a large extent (i.e. continental or global), areas with regionally high biodiversity like the Land Between become “lost” because turnover rates in these areas will appear low compared to those observed across steep environmental gradients or in tropical realms. This lends support to the view that the presence of a spatial relationship between landscape heterogeneity and species distributional boundaries is highly scale-dependent, and emphasizes the importance of studying boundaries at a variety of spatial scales (Fortin et al. 2005).

Species diversity patterns resulting from the aggregated response of individual species to environmental gradients can vary depending on the evolutionary histories, and the variation of morphological (i.e., body size) and ecological (i.e., trophic position) traits within the species group in question (Gregory 1998; Bini et al. 2004; Soininen et al. 2007; Carnicer and Díaz-Delgado 2008). For example, Bini et al. (2004) found that order-level predictors, such as body size and diversification level, explained variation in avian richness patterns driven by climate and habitat heterogeneity in South America. Of the 60 species analyzed in my study (Table 1), 55 belong to the monophyletic order Passeriformes (passerines). Therefore, the spatial overlap and association between landcover heterogeneity and avian species’ distribution observed in the Land Between (Table 4; Figures 12-14) may only apply to this taxon. Other taxonomic groups like Anseriformes (waterfowl) could have demonstrated a different response to the same landscape attributes at the regional scale, if suitable data were available to be analyzed. Given that Passeriformes include more than half of all extant bird species, the results of this study are nevertheless of interest to both ecologists and conservation biologists. Any interpretation of the results of this study, however, can only be comfortably extended to species with similar life history traits.
Despite the heavy bias towards Passerines, the 60 species analyzed are more diversified at the family level. New World warblers were best represented in the analysis, with 14 of the 60 selected species (23.3%) belonging to the Parulidae family (Table 1). The American sparrows (Emberizidae) and tyrant flycatchers (Tyrannidae) were both represented by six species (10%), whereas 15 other families were represented by fewer than six species. Just over half of the species are believed to belong to a group of New World nine-primaried oscines, which are described as an assemblage of closely related families that share a common ancestor (Tordoff 1954; Klicka et al. 2000). Like order-level traits, family-level traits may help to explain the bird distribution patterns observed in this study. However, species within families can occupy significantly different ecological niches (Wiens and Graham 2005), so it may be more useful to characterize the species set based on functional groups such as feeding guild (Root 1988), or habitat association (French and Picozzi 2002).

It is reasonable to suggest that the strong overlap between high rates of change in landcover composition and in species’ distributions occurring in the Land Between results, at least in part, from birds responding to the greater diversity of habitat that is available in the transitional zone. As almost half of the species analyzed (27 of 60 species; Table 1) are associated with woods and forests, an obvious question that arises is whether the spatial turnover patterns observed are being driven by the change in forest cover and forest type across the study area. Indeed, the Land Between spatially coincides with a significant increase in large tracts of forest due to a decline in agriculture and urban settlement, and an increase in the number of protected areas (e.g., Figure 8). Increases in the amount of forest habitat available to forest generalists and specialists should create a gradient of species richness across the Land Between, and generate pronounced changes in the probability of occurrence of some species. Also, there is a shift in vegetation across the Land Between as forest composition changes between the Lake Simcoe-Rideau ecoregion and the Southern Shield ecoregion. Vegetative transition zones have been shown to spatially coincide with higher densities of range limits of forest birds in eastern North America, particularly for forest specialists (Boone and Krohn 2000), and a similar response is likely to be occurring across the Land Between.
An almost equal number of species analyzed, however, are associated with non-forested habitats: ten species prefer shrub and early successional habitat, 11 are associated with grasslands and agricultural, or open habitats, and seven of the 60 species analyzed breed in urban and suburban habitats (Table 1). The progression from intensive agriculture common to the Lake Simcoe-Rideau ecoregion, to the abandoned farmland undergoing succession in the Land Between, and then to forested landcover in the Southern Shield ecoregion contributes to the high rates of change in landcover composition observed in the transitional zone. Species associated with more open habitats will therefore experience decreases in abundance and occupancy within and beyond the Land Between due to a patchier distribution of suitable habitat. Alternatively, species sensitive to disturbance, but associated with non-forested habitat may find a refuge there, because disturbance due to active agriculture is largely absent.

In this study, landcover types such as forest type and elevation implicitly integrate climatic and geomorphological gradients, whereas agricultural and urban landcover capture the influence of anthropogenic features on avian species turnover. Previous studies on the relationship between species diversity distribution and environmental factors have tried to avoid, or control for the influence of anthropogenic land transformation (van Rensburg et al. 2009). Understanding the relationship between landscape heterogeneity and regional biodiversity within the context of human-related land-use change is relevant to conservation efforts in southern Ontario; therefore, human-transformed landcover types were explicitly included in the analysis.

Due to the detectability issues identified for point-count surveys, wetland-inhabiting species were the least-represented functional group included in our analysis, with only five of 60 species associating with this habitat (Table 1). One of the unique landscape features delineating the Land Between, which contributes to the landcover heterogeneity found within it, is the high density of shorelines and water habitat (Figures 6 and 7). Consequently, excluding wetland-associated species from the analysis means excluding species that are of particular conservation concern to the region, and which significantly enrich regional biodiversity. If these species were better represented in the analysis, greater spatial overlap
might have been observed between landcover and avian boundaries. Future work in the area should thus focus on capturing a greater diversity of species, especially those associated with wetland and water habitats, in order to gain a more complete understanding of how avian species turnover varies regionally. Similar work outside of the area, however, should take into consideration that the hydrological features of the Land Between are characteristic of that region, and the same association may not necessarily exist in other transitional zones. Nevertheless, it would be both interesting and beneficial to conservation efforts to build our understanding of how the spatial relationship between avian species turnover and landscape heterogeneity varies at the regional scale among higher-level taxa (Carnicer and Diaz-Delgado 2008). One question that could be posed in the future is whether passerines and non-passerines respond to landscape features at the same spatial scale.

It is important to note that the bird distributions estimated for our analysis are representative of species’ summer ranges only; consequently, the spatial relationships observed are limited to the breeding season. During the winter season avian species richness in southern Ontario drops as migrating species occupy their winter ranges. At this time, other environmental factors may drive regional species turnover patterns. This type of seasonal variation was observed in the distributions of Scottish birds, which were controlled by land-use variables during summer months and by climatic factors during the winter (French and Picozzi 2002). It would therefore be of interest to determine how the spatial relationship between bird distributions and landcover features changes across fine and coarse temporal scales. Such work should be conducted at the regional scale, as it could have implications for land-use management and conservation strategies in the Land Between and surrounding ecoregions.

Finally, one weakness of using occurrence data to look at species turnover is that it does not differentiate between two locations with similar species composition, but with different dominant species (McDonald et al. 2005). Future analysis examining spatial variation in species-landscape associations would therefore benefit from incorporating relative abundance data, especially where species geographic ranges are concerned (French and Picozzi 2002; McDonald et al. 2005). Unfortunately, acquiring such data for large spatial scales is often costly and impractical. Although not an ideal solution, using indicator kriging
to produce probability of occurrence surfaces rather than binary occupancy surfaces may help to capture some of the information regarding species’ abundance structure, and better estimate avian species turnover in the Land Between. Nevertheless, if more reliable abundance data become available, it would be interesting to investigate whether incorporating the abundance structure of species’ geographic ranges strengthens the spatial overlap between species distributions and high landscape heterogeneity.
5 CONCLUSIONS

This research indicates that, at the regional scale, there is a significant and positive spatial relationship between landscape heterogeneity and avian species turnover in the Land Between. A variety of species, and not only those that preferentially associate with the area, drive this turnover. However, the association of avian boundaries to landcover boundaries is restricted to some parts of the transitional zone, and both high landcover heterogeneity and high avian turnover can occur independently of each other. This is to be anticipated since the suite of factors shaping species distributions extends far beyond those captured by landcover heterogeneity; but it does limit how far the results can be extrapolated. Furthermore, since the vast majority of species analyzed are passerines, the relationship observed in this study may apply only to species with similar physiology. Future research directions should consider how the relationship between avian species’ distributions and landscape heterogeneity varies among different functional and taxonomic groups, as well as incorporate relative abundance structure into the analysis.
Identifying the environmental and historical factors that generate and maintain biodiversity at multiple spatial scales is an important precursor to understanding how future species geographic ranges will respond to anthropogenic forces. This research lends support for a positive spatial relationship between landscape heterogeneity and species turnover at the regional scale, and has important implications for conservation efforts. A continuing challenge facing research at intermediate spatial scales, however, is the availability of data on several species distributions. At these scales, the acquisition of distribution data on a study-by-study basis is impractical due to the large study area extent. Furthermore, existing data (e.g. range maps) may not be available at the desired resolution. Without reliable distribution data for several taxonomic groups, planning for the persistence of multiple species is difficult. Therefore, it is important to explore other opportunities that exist for estimating regional patterns of species diversity.

One emerging question concerns the spatial congruence of species turnover patterns among taxonomic groups (McKnight et al. 2007; Buckley and Jetz 2008; Qian 2009). Such a pattern has been observed in the Neotropical realms, although the strength of the relationship was shown to vary from strong to weak, depending on the taxonomic groups considered (McKnight et al. 2007; Buckley and Jetz 2008). Like the relationship between species diversity patterns and environmental variation, this relationship is likely to be highly dependent on the species groups, spatial scale, and geographic location of interest (McKnight et al. 2007). The presence of such congruence, however, suggests that some common fundamental processes might be shaping species’ ranges. Identifying these processes and the conditions under which they generate congruence in biodiversity patterns would greatly improve the predictive power of species distribution models (Thuiller et al. 2004). Furthermore, understanding the spatial variation of these patterns would inform regional conservation priorities and lead to more effective spatial planning of protected areas, as carefully selected reserves would support several taxonomic groups concurrently.
There is reason to believe that the Land Between maintains high rates of turnover in amphibian species distributions since high shoreline density, a mix of acidic and alkaline waters, and relatively low anthropogenic impact offer a diversity of high quality wetland and water habitat. Given the positive relationship between avian species turnover and landcover heterogeneity in the Land Between, future research in the area should explore whether this relationship holds for other taxonomic groups as well. Such work could lead to evaluating the extent to which high rates in species turnover spatially coincide for different taxonomic groups at the regional scale in temperate zones (as opposed to tropical zones), and would have profound implications for conservation efforts and land-use decisions in the area. While there has been some debate regarding targeting transitional zones for conservation (Brooks et al. 2001; Smith et al. 2001), there is no doubt that these areas frequently accommodate high species diversity, and need to be integrated consistently into both conservation policy, and future research efforts (Araújo 2002; van Rensburg et al. 2009).

The current rate of global change necessitates that the process of selecting protected areas to conserve biodiversity be efficient, economical, and well-informed (Pressey et al. 2007; Paterson et al. 2008). Recently, Buckley and Jetz (2008) suggested that turnover in amphibian species could be an effective surrogate for avian species turnover in conservation planning due to the high sensitivity of amphibians to changes in environmental conditions. Indeed, the use of distributional data for selected species as surrogates is a popular conservation practice (Ferrier 2002; Rodrigues and Brooks 2007). While surveys of species diversity are valuable, they are also time-consuming, expensive, and often difficult to carry out. Acquiring reliable remote-sensing data, however, has become increasingly easy and cost-effective. Identifying which environmental variables could serve as effective surrogates for biodiversity has consequently become a promising research direction in conservation biology (Ferrier 2002).

The use of environmental surrogates assumes that there is a positive spatial relationship between species’ distributions and the underlying abiotic and/or biotic conditions at a given geographic location (Lapin and Barnes 1995). Unfortunately, support for them has been inconsistent. For instance, Cushman et al. (2008) found that even when vegetation cover was
mapped at the fine scale, habitat variables generally explained very little of the total variance in avian species abundance at both local and landscape scales. When habitat did have some predictive power, the effectiveness of the surrogate depended highly on the species guild and spatial scale. Similarly, environmental diversity (i.e., spatial variation in climate parameters) was identified as a poor surrogate for species diversity at the continental scale, possibly because it fails to explain distributions of range-restricted species (Araújo et al. 2001). On the other hand, vegetation heterogeneity measured as NDVI texture was successful at predicting avian species richness (St-Louis et al. 2009). These results stress that environmental variables should be used as biodiversity surrogates only when there is an informed understanding of how the species of interest respond to their environment.

This research shows that there is a positive spatial relationship between landcover heterogeneity and avian species’ distributions at the regional scale. Hence, I propose that landcover heterogeneity be explored as a potential surrogate for avian diversity, and a coarse-scale filter of identifying areas of priority in regional conservation planning. Maintaining landscape heterogeneity may not only maximize the representation of biodiversity, but also protect the processes that generate and maintain it (Moritz 2002). However, further research is needed to determine the generality of the relationship observed in my results. For one, high landcover heterogeneity does not necessarily guarantee high species turnover, and high species turnover can occur in the absence of it. In that case, an important question that still needs to be addressed concerns the conditions under which this relationship occurs. Does it apply to all transitional zones characterized by gradients in both vegetative features and anthropogenic disturbance? Since my analysis was limited to a relatively small group of closely related species, I cannot infer that it would be an effective surrogate for avian diversity in general. To gain a more comprehensive understanding of the factors affecting species’ geographic ranges, future research must focus on assessing the spatial relationship between landcover heterogeneity and avian species’ distributions at the regional scale for different taxonomic levels (i.e. passerines and non-passerines) and functional groups (i.e. habitat specialists and habitat generalists).
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Table 1. Bird species selected to assess the spatial heterogeneity of bird distributions in the study area. Information on habitat association was obtained from Cadman et al. (2007). Column 5 (*) indicates the percentage of each species’ Ontario population that occurs in the Land Between (Couturier 2009).

<table>
<thead>
<tr>
<th>English Name</th>
<th>Latin Name</th>
<th>Family (Common Name)</th>
<th>Habitat Association</th>
<th>% LB*</th>
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Table 1 continued on following page.
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<th><strong>English Name</strong></th>
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<th><strong>Family - Common Name</strong></th>
<th><strong>Habitat Association</strong></th>
<th>% LB*</th>
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<th><strong>English Name</strong></th>
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<th><strong>Habitat Association</strong></th>
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<td>Vermivora ruficapilla</td>
<td>warblers</td>
<td>woods and forests</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Northern Waterthrush</td>
<td>Seiurus noveboracensis</td>
<td>warblers</td>
<td>wetlands</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>Seiurus aurocapilla</td>
<td>warblers</td>
<td>woods and forests</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>Dendroica petechia</td>
<td>warblers</td>
<td>shrub and early succession</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Hairy Woodpecker</td>
<td>Picoides villosus</td>
<td>woodpeckers</td>
<td>woods and forests</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Northern Flicker</td>
<td>Colaptes auratus</td>
<td>woodpeckers</td>
<td>woods and forests</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Winter Wren</td>
<td>Troglodytes troglodytes</td>
<td>wrens</td>
<td>woods and forests</td>
<td>&lt;15</td>
</tr>
</tbody>
</table>
Table 2. Boundary statistics for boundaries delineated from composite land cover (LC1, LC2, LC3) as well as boundaries delineated from water, mixed forest, and urban land cover separately. Boundary elements (BEs) delineated at the 10% \((n = 82\) BEs), 15% \((n = 123\) BEs), and 20% \((n = 164\) BEs) boundary thresholds were used in the analysis. \(N_S\) is the number of sub-boundaries (boundaries with >1 BE); \(N_I\), the number of singletons (1 BE); \(L_{MAX}\), the maximum boundary length; \(L_{MEAN}\), the mean boundary length; \(D_{MAX}\), the maximum boundary diameter; \(D_{MEAN}\), the mean boundary diameter; \(D/L\), the mean diameter to length ratio (branchiness). Statistical significance is based on 9999 permutations.

<table>
<thead>
<tr>
<th>Data</th>
<th>Threshold %</th>
<th>(N_S) (&gt;1 BE)</th>
<th>(N_I) (=1 BE)</th>
<th>(L_{MAX})</th>
<th>(L_{MEAN})</th>
<th>(D_{MAX})</th>
<th>(D_{MEAN})</th>
<th>(D/L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LC1 - 7 Land Cover Types (water count)</td>
<td>10</td>
<td>14* (-5.88)†</td>
<td>13* (-4.08)</td>
<td>13* (4.10)</td>
<td>3.04* (10.95)</td>
<td>10* (4.08)</td>
<td>2.70* (10.18)</td>
<td>0.97* (-3.56)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>14* (-7.86)</td>
<td>13* (-4.82)</td>
<td>37* (12.37)</td>
<td>4.56* (19.33)</td>
<td>22* (10.08)</td>
<td>3.41* (14.36)</td>
<td>0.93* (-8.11)</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>19* (-7.54)</td>
<td>15* (-4.76)</td>
<td>67* (17.57)</td>
<td>4.79* (17.23)</td>
<td>32* (12.38)</td>
<td>3.32* (11.26)</td>
<td>0.95* (-3.92)</td>
</tr>
<tr>
<td>LC2 - 7 Land Cover Types (water perimeter)</td>
<td>10</td>
<td>13* (-5.70)</td>
<td>15* (-3.75)</td>
<td>12* (3.56)</td>
<td>2.93* (10.29)</td>
<td>10* (4.17)</td>
<td>2.68* (10.05)</td>
<td>0.97* (-2.72)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>14* (-7.62)</td>
<td>14* (-4.60)</td>
<td>38* (12.68)</td>
<td>4.39* (18.22)</td>
<td>22* (10.15)</td>
<td>3.21* (12.65)</td>
<td>0.93* (-8.57)</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>20* (-8.13)</td>
<td>11* (-5.39)</td>
<td>45* (10.91)</td>
<td>5.26* (20.51)</td>
<td>23* (7.94)</td>
<td>3.71* (12.47)</td>
<td>0.93* (-7.23)</td>
</tr>
<tr>
<td>LC3 - 8 Land Cover Types</td>
<td>10</td>
<td>15* (-5.90)</td>
<td>12* (-4.23)</td>
<td>15* (5.30)</td>
<td>3.04* (11.03)</td>
<td>11* (4.95)</td>
<td>2.67* (9.83)</td>
<td>0.96* (-5.71)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>15* (-7.35)</td>
<td>14* (-4.59)</td>
<td>39* (13.16)</td>
<td>4.24* (16.83)</td>
<td>22* (10.20)</td>
<td>3.17* (12.14)</td>
<td>0.93* (-8.12)</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>18* (-7.70)</td>
<td>13* (-4.89)</td>
<td>45* (10.42)</td>
<td>5.26* (19.09)</td>
<td>24* (8.09)</td>
<td>3.68* (13.32)</td>
<td>0.92* (-8.34)</td>
</tr>
<tr>
<td>Water count perimeter</td>
<td>20</td>
<td>25* (-3.16)</td>
<td>24 (-1.74)</td>
<td>35* (6.13)</td>
<td>3.33* (4.10)</td>
<td>20* (5.40)</td>
<td>2.67* (3.11)</td>
<td>0.96 (-0.41)</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>25* (-4.45)</td>
<td>20* (-2.92)</td>
<td>31* (5.50)</td>
<td>3.62* (6.81)</td>
<td>15 (3.21)</td>
<td>2.76* (4.50)</td>
<td>0.93* (-4.76)</td>
</tr>
<tr>
<td>Mixed Forest</td>
<td>20</td>
<td>28* (-5.17)</td>
<td>19* (-3.84)</td>
<td>26* (4.90)</td>
<td>3.47* (8.39)</td>
<td>16* (4.32)</td>
<td>2.91* (7.45)</td>
<td>0.97* (-1.69)</td>
</tr>
<tr>
<td>Urban</td>
<td>20</td>
<td>26 (-0.82)</td>
<td>7 (0.64)</td>
<td>22 (0.97)</td>
<td>4.97 (0.82)</td>
<td>13 (1.12)</td>
<td>3.61 (0.44)</td>
<td>0.86 (0.90)</td>
</tr>
</tbody>
</table>

† Values in parentheses are standardized \(z\)-scores indicating the strength and direction of the difference between observed values and expected values. To be significant, \(N_S\), \(N_I\), and \(D/L\) should be in the lower 1% tail and \(L_{MAX}\), \(L_{MEAN}\), \(D_{MAX}\), and \(D_{MEAN}\) should be in the upper 1% tail of the randomized reference distribution. Statistical significance of values is indicated at \(p < 0.01\) (*) and \(p < 0.001\) (**).
Table 3. Boundary statistics for boundaries delineated from 60 breeding bird distributions combined (all bird species), 26 distributions of species with at least 15% of their Ontario distribution occurring in the LB (birds ≥ 15%), and 34 distributions of species with less than 15% of their Ontario distribution occurring in the LB (birds < 15%). Boundary elements (BEs) delineated at the 10% ($n = 82$ BEs), 15% ($n = 123$ BEs), and 20% ($n = 164$ BEs) boundary thresholds were used in the analysis. $N_S$ is the number of sub-boundaries (boundaries with >1 BE); $N_1$, the number of singletons (1 BE); $L_{MAX}$, the maximum boundary length; $L_{MEAN}$, the mean boundary length; $D_{MAX}$, the maximum boundary diameter; $D_{MEAN}$, the mean boundary diameter; $D/L$, the mean diameter to length ratio (branchiness). Statistical significance is based on 9999 permutations.

<table>
<thead>
<tr>
<th>Data</th>
<th>Threshold %</th>
<th>$N_S$ (&gt;1 BE)</th>
<th>$N_1$ (=1 BE)</th>
<th>$L_{MAX}$</th>
<th>$L_{MEAN}$</th>
<th>$D_{MAX}$</th>
<th>$D_{MEAN}$</th>
<th>$D/L$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Bird Species</td>
<td>10</td>
<td>10* (-8.84)†</td>
<td>8* (-5.44)</td>
<td>28* (14.32)</td>
<td>4.56* (26.07)</td>
<td>15* (8.87)</td>
<td>3.11* (15.67)</td>
<td>0.95* (-9.40)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>7* (-10.58)</td>
<td>9* (-5.79)</td>
<td>47* (18.46)</td>
<td>7.69* (46.60)</td>
<td>28* (15.36)</td>
<td>4.75* (26.55)</td>
<td>0.93* (-10.20)</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>9* (-10.70)</td>
<td>9* (-5.91)</td>
<td>118* (36.94)</td>
<td>9.06* (48.72)</td>
<td>37* (15.98)</td>
<td>4.50* (22.38)</td>
<td>0.96* (-3.94)</td>
</tr>
<tr>
<td>Birds ≥ 15%</td>
<td>20</td>
<td>11* (-8.88)</td>
<td>10* (-4.86)</td>
<td>110* (29.76)</td>
<td>7.76* (31.09)</td>
<td>41* (16.75)</td>
<td>4.24* (15.95)</td>
<td>0.94* (-4.69)</td>
</tr>
<tr>
<td>Birds &lt; 15%</td>
<td>20</td>
<td>12* (-8.41)</td>
<td>19* (-4.37)</td>
<td>95* (28.69)</td>
<td>5.26* (22.08)</td>
<td>32* (13.37)</td>
<td>3.00* (9.57)</td>
<td>0.96* (-4.06)</td>
</tr>
</tbody>
</table>

† Values in parentheses are standardized $z$-scores indicating the strength and direction of the difference between observed values and expected values. To be significant, $N_S$, $N_1$, and $D/L$ should be in the lower 1% tail and $L_{MAX}$, $L_{MEAN}$, $D_{MAX}$, and $D_{MEAN}$ should be in the upper 1% tail of the randomized reference distribution. Statistical significance of values is indicated at $p < 0.001$ (*).
Table 4. Spatial boundary overlap statistics for composite landcover (LC1, LC2, LC3) and breeding bird distribution boundaries. Boundary elements (BEs) delineated at 10% ($n = 82$ BEs), 15% ($n = 123$ BEs), and 20% ($n = 164$) boundary thresholds were used in the analysis. $O_B$ is the directional association of bird boundaries to land cover boundaries. $O_{LB}$ is the simultaneous association of bird and land cover boundaries. $O_S$ is the direct spatial overlap of boundary elements in the two sets of boundaries. Statistical significance is based on 9999 permutations.

<table>
<thead>
<tr>
<th>Data</th>
<th>Threshold %</th>
<th>Spatial Boundary Overlap Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$O_B$</td>
</tr>
<tr>
<td><strong>LC1 - 7 Land Cover Types (water count) and 60 Bird Distributions</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>13152.8* (-5.43)†</td>
<td>28720.6 (3.66)</td>
</tr>
<tr>
<td>15</td>
<td>11703.0* (-5.82)</td>
<td>22493.9 (4.02)</td>
</tr>
<tr>
<td>20</td>
<td>12255.3* (-4.26)</td>
<td>20909 (6.55)</td>
</tr>
<tr>
<td><strong>LC2 - 7 Land Cover Types (water perimeter) and 60 Bird Distributions</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>11503.8* (-6.08)</td>
<td>25538.8 (1.77)</td>
</tr>
<tr>
<td>15</td>
<td>11091.8* (-6.25)</td>
<td>20463.7 (1.92)</td>
</tr>
<tr>
<td>20</td>
<td>11925.8* (-5.16)</td>
<td>19488.1 (3.63)</td>
</tr>
<tr>
<td><strong>LC3 - 8 Land Cover Types and 60 Bird Distributions</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>11188.0* (-6.39)</td>
<td>23741.7 (0.54)</td>
</tr>
<tr>
<td>15</td>
<td>11450.7* (-5.93)</td>
<td>20572.1 (2.15)</td>
</tr>
<tr>
<td>20</td>
<td>11395.5* (-5.35)</td>
<td>19222.4 (4.06)</td>
</tr>
</tbody>
</table>

† Values in parentheses are standardized $z$-scores indicating the strength and direction of the difference between observed values and expected values. To be significant, $O_B$ and $O_{LB}$ should be in the lower 1% tail and $O_S$ should be in the upper 1% tail of the randomized reference distribution. Statistical significance of values is indicated at $p < 0.001$ (*).
Figure 1. Geographic location of the study area and the area of interest, which includes the Land Between (LB; grey). The LB is a transitional zone in southern Ontario (Canada) where the south-eastern Lake Simcoe-Rideau (brown) ecoregion meets the north-western Southern Shield (green) ecoregion (a). The study area used in analysis, shown as a 10x10 km grid consisting of 920 individual and adjacent sampling units (i.e. grid cells), covers 92,000 km² and extends approximately 30-120 km south and 40-120 km north of the LB (a). There is a discernable shift in landcover composition across the study area (b).
Figure 2. Number of point counts collected by the Ontario Breeding Bird Atlas (2001-2005) in each 10×10 km sampling unit in the study area. A minimum of 25 points counts was required by the OBBA for a square to be considered adequately covered but any square with 10 or more point counts was considered suitable for point count analyses (Cadman et al. 2007).
Figure 3. LC1 boundaries (based on five landcover types plus elevation and water sampled as count) delineated at the 10% (black; \( n = 82 \) BEs), 15% (black and green; \( n = 123 \) BEs), and 20% (black, green and brown; \( n = 164 \) BEs) boundary thresholds. Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 4. LC2 boundaries (based on five landcover types plus elevation and water sampled as perimeter) delineated at the 10% (black; \( n = 82 \) BEs), 15% (black and green; \( n = 123 \) BEs), and 20% (black, green and brown; \( n = 164 \) BEs) boundary thresholds. Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 5. LC3 boundaries (based on five landcover layers plus elevation and water sampled as count and as perimeter) delineated at the 10% (black; \( n = 82 \) BEs), 15% (black and green; \( n = 123 \) BEs), and 20% (black, green and brown; \( n = 164 \) BEs) boundary thresholds. Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 6. Boundaries delineated from water landcover (water bodies, marshes, swamps, fens and bogs) based on count information at the 20% boundary threshold (brown; n = 164 BEs). Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines reference false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 7. Boundaries delineated from water landcover (water bodies, marshes, swamps, fens and bogs) based on perimeter information at the 20% boundary threshold (brown; $n = 164$ BEs). Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 8. Boundaries delineated from mixed forest landcover (mainly deciduous mixed forest and mainly coniferous mixed forest) at the 20% boundary threshold (brown; \(n = 164\) BEs). Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 9. Boundaries delineated from urban landcover (settlement and developed land, mine tailings, quarries, and bedrock outcrops) at the 20% boundary threshold (brown; $n = 164$ BEs). Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 10. Boundaries delineated from 60 breeding bird distributions at the 10% (black; $n = 82$ BEs), 15% (black and orange; $n = 123$ BEs), and 20% (black, orange and blue; $n = 164$ BEs) boundary thresholds. Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 11. Boundaries delineated from two groups of breeding bird distributions - 26 distributions of species with at least 15% of their Ontario distribution occurring in the LB (yellow and dark blue; n = 164 BEs) and 34 distributions of species with less than 15% of their Ontario distribution occurring in the LB (yellow and light blue; n = 164 BEs) - at the 20% boundary threshold. Boundary elements that directly spatially overlap for the two groups are shown in yellow. Grey indicates that no boundary was delineated at a 20% threshold. From 920 sampling units, 821 rates of change were computed. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 12. Spatial boundary overlap between LC1 (brown; $n = 164$ BEs) and breeding bird distribution (blue; $n = 164$ BEs) boundaries at the 20% boundary threshold. Boundary elements that directly spatially overlap are shown in purple. Grey indicates that no boundary was delineated at a 20% threshold for either landcover or birds. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 13. Spatial boundary overlap between LC2 (brown; \( n = 164 \) BEs) and breeding bird distribution (blue; \( n = 164 \) BEs) boundaries at the 20% boundary threshold. Boundary elements that directly spatially overlap are shown in purple. Grey indicates that no boundary was delineated at a 20% threshold for either landcover or birds. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.
Figure 14. Spatial boundary overlap between LC3 (brown; $n = 164$ BEs) and breeding bird distribution (blue; $n = 164$ BEs) boundaries at the 20% boundary threshold. Boundary elements that directly spatially overlap are shown in purple. Grey indicates that no boundary was delineated at a 20% threshold for either landcover or birds. Dotted lines represent false easting and false northing geographic coordinates (in meters) based on a NAD83 Lambert Conformal Conic projection.