Ecological Responses of Avian Species to Land Cover Metrics at the Landscape-Level and Across Broad Spatial Extent

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ABSTRACT

Human activities have transformed natural landscapes into human-dominated areas at unprecedented rates in the last centuries. Land cover transformation is associated with loss of natural habitat, thus a threat to biodiversity. Because habitat loss will likely continue in the future due to population growth and increase demand for natural resources, an important question in ecological studies is whether land cover features (i.e. amount, variety, shape, configuration) can be used as predictors to estimate species loss from habitat modification.

This thesis investigates the predictive ability of landscape features in predicting species distributions at the landscape level and across large regions. It tests several predictions from classic hypotheses such as the species-area relationship and habitat fragmentation, utilizing a macroecological approach. Response variables (e.g. species richness, species' probability of occurrence) and independent variables (e.g. proportion of natural areas, metrics of fragmentation, temperature, etc.) are analysed in cell sizes of 25-900km^2 covering large regions (e.g. southern Ontario, New York State). Bird species were chosen as the main biological model.

Most literature assumes that species richness should vary positively as a function of remaining natural area, following the well-known species–area relationship (i.e. classic SAR). Prior studies have shown that avian species richness has a peaked, rather than a monotonic increasing, relationship with the proportion of natural land cover in landscapes of southern Ontario. The first chapter of the thesis showed improvements in the predictive power of classic SARs by proposing the "Lost-habitat SAR", which demonstrates that richness of open-habitat species can be predicted when we partition human-dominated land cover into an ''available human-dominated'' component and ''lost'' habitat (i.e. parts of the landscape that can no longer be utilized by any species).

The second chapter addresses a current contention in the literature about the effect of habitat fragmentation beyond habitat amount at the landscape level. Specifically, I tested the effect of fragmentation (e.g. number of patches) on both avian richness and the probability of occurrence (p_{occ}) of individual species, after controlling for habitat amount in 991 landscapes, each 100-km^2, in southern Ontario. The analysis showed that overall species richness responds primarily to habitat amount, and that the effect of habitat fragmentation, holding the total amount of habitat constant, is negligible. The probability of occurrence of a few bird species did relate negatively to the size, number and isolation of the patches within the landscape. We argue that the evidence is inconsistent with the hypothesis that reducing habitat fragmentation would be an effective conservation strategy for birds at the landscape level.

Chapter 3 tested the speculation in the climate change literature that habitat loss may impede the colonization or movement of species whose ranges are shifting northwards in response to climate. Using the same 100-km^2 landscapes of southern Ontario, I examined individual bird species' probability of occupancy as a function of the amount of remaining natural land cover for three groups of species: i) those whose northern range limit falls within the study area, ii) those whose southern range limit is in the study area, and iii) those whose ranges cover the entire study area. The results showed that the probability of occupancy of southern-edge species is a positive function of the amount of natural land cover (forest) in the landscape, while the probability of occupancy of northern-edge species is a negative function of natural land cover. Hence, I conclude that at southern range limits species faces the dual stresses of climatic warming and habitat conversion. Whereas, at northern (potentially expanding) range edges, partially disturbed landscapes are more readily occupied than undisturbed landscapes.

In the final chapter, I challenge widely accepted hypothesis that habitat loss causes biodiversity loss by testing whether conserving natural land cover would conserve species diversity. More specifically, I tested whether broad-extent relationships between avian species richness and natural land cover are independent of: 1) whether species distribution data come from systematic censuses (atlases) versus range maps, and 2) the grain size of the analysis in grid cells covering southern Ontario, CA, and New York State, US. My findings showed that over regional extents, range-map-based richness relates strongly to temperature, irrespective of spatial grain, and that censused species richness relates to temperature less strongly. Moreover, range-map richness is a *negative* function of the proportion of natural land cover, while realized richness is a peaked function. Therefore, I conclude that conserving natural land cover would not conserve species diversity in southern Ontario or in New York State, since greater natural cover does not imply higher richness. We argue that *habitat loss* has become a panchreston. It may be misguiding conservation biology strategies by focusing on a threat that is too general to be usefully predictive.

RÉSUMÉ

Les activités humaines ont transformé les paysages naturels en zones dominées par les humains à des taux sans précédent au cours des derniers siècles. La transformation de la couverture terrestre est associée à la perte d'habitat naturel, donc une menace pour la biodiversité. Étant donné que la perte d’habitat continuera vraisemblablement dans le futur en raison de la croissance démographique et de l'augmentation de la demande en ressources naturelles, une question importante dans les études écologiques est de savoir si les caractéristiques de la couverture terrestre (e.g., la quantité, la variété, la forme, la configuration) peuvent être utilisées comme prédicteurs pour estimer la perte d'espèces due à la modification de l'habitat.

Cette thèse étudie la capacité des caractéristiques du paysage à prédire les distributions d'espèces à l’échelle du paysage ainsi que sur de grandes régions. Elle teste plusieurs prédictions d'hypothèses classiques telles que la relation espèces-superficie et la fragmentation de l'habitat, en utilisant une approche macroécologique. Les variables dépendantes (par exemple, la richesse en espèces, la probabilité d'occurrence des espèces) et les variables indépendantes (par exemple, la proportion d'espaces naturels, les mesures de la fragmentation, la température, etc.) sont analysées dans des cellules de 25-900 km^2 couvrant de grandes régions (e.g., le sud de l'Ontario, New York State). Les espèces d'oiseaux ont été choisies comme principal modèle biologique.

La plupart de la littérature suppose que la richesse en espèces devrait varier positivement avec l'aire naturelle restante, suivant la relation espèces-superficie bien connue (SAR classique). Des études antérieures ont montré que la richesse spécifique aviaires avait une relation pointue, plutôt que monotone, avec la proportion de couverts naturels des paysages du sud de l'Ontario. « Le premier chapitre de la thèse démontre que la richesse des espèces d'habitat ouvert peut être mieux prédite par le *SAR Lost-habitat*, lequel répartit la couverture terrestre dominée par l'homme en composante «disponible» et «perdu», que par le SAR

Le deuxième chapitre traite d'une controverse actuelle dans la littérature concernant les effets distincts de la fragmentation de l'habitat de la quantité d'habitats au niveau du paysage. Plus précisément, j'ai testé l'effet de la fragmentation (par exemple, le nombre de « patches ») à la fois sur la richesse aviaire et sur la

probabilité d'occurrence (p_{occ}) d'espèces individuelles, après avoir contrôlé la quantité d'habitats dans 991 paysages (100 km^2 chaque) dans le sud de l'Ontario. L'analyse a montré que la richesse globale des espèces répond principalement à la quantité d'habitats et que l'effet de la fragmentation de l'habitat, lorsque la quantité totale d'habitats est maintenue constante, est négligeable. La taille, le nombre et l'isolement des patchs dans le paysage ont une incidence négative sur la probabilité d'occupation de quelques espèces d'oiseaux. Nous soutenons que la preuve est incompatible avec l'hypothèse selon laquelle la réduction de la fragmentation de l'habitat serait une stratégie de conservation efficace pour les oiseaux au niveau du paysage.

Le Chapitre 3 teste une spéculation provenant de la littérature sur le changement climatique selon laquelle la perte d'habitat peut entraver la colonisation ou le mouvement des espèces se déplaçant vers le nord en réponse au changement climatique. En utilisant les mêmes paysages de 100 km^2 du sud de l'Ontario, j'ai examiné la probabilité d'occupation des espèces d'oiseaux individuels en fonction de la quantité de couvert terrestre restante pour trois groupes d'espèces: i) ceux dont la limite nord de la répartition géographique se situe dans la zone d'étude, ii) ceux dont la limite sud de la répartition géographique est dans la zone d'étude, et iii) ceux dont les l’ensemble de la répartition géographique de situe dans la zone d'étude. Les résultats ont montré que la probabilité d'occupation des espèces du bord sud (groupe ii)) est une fonction positive de la quantité de couvert naturel (forêt) dans le paysage, tandis que la probabilité d'occupation des espèces du bord nord (groupe i) est une fonction négative de la quantité de couvert naturel. Par conséquent, je conclus qu’à la limite sud de leur répartition les espèces sont confrontées au double stress du réchauffement climatique et de la conversion de l'habitat. Alors qu’à la limite nord de leur répartition (potentiellement en expansion), les paysages partiellement perturbés sont plus facilement occupés que les paysages non perturbés.

Dans le chapitre final, je conteste l'hypothèse largement acceptée selon laquelle la perte d'habitat provoque une perte de biodiversité en testant si la conservation de la couverture naturelle des terres conserverait la diversité des espèces. Plus précisément, j'ai testé si les relations à grande échelle entre la richesse spécifique d'oiseaux et le couvert terrestre naturel sont indépendantes de: 1) la source des données de distribution des espèces (recensements systématiques (atlas) vs cartes de répartitions) et 2) la résolution spatiale de l'analyse de la région couvrant le sud de

l'Ontario, CA, et le New York State, aux États-Unis. Mes résultats ont montré qu’à l’échelle régionales, la richesse spécifique basée sur les cartes de répartitions se rapporte fortement à la température, indépendamment de résolution spatiale, et que la richesse spécifique basée sur les recensements systématiques se rapporte moins à la température. En outre, la richesse basée sur les cartes de répartitions est une fonction négative de la proportion de couvert naturel du sol, alors que la richesse spécifique basée sur les recensements systématiques est une fonction qui plafonne. Par conséquent, je conclus que la conservation de la couverture naturelle des terres ne conserverait pas la richesse spécifique.

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GENERAL INTRODUCTION

What is this thesis about?

Habitat loss and habitat fragmentation together pose a major threat to biodiversity. To what extent is this true? This thesis attempts to falsify this hypothesis by testing some of its predictions. Each chapter of the thesis addresses one or more predictions derived from the hypothesis.

Terrestrial natural habitats have been substantially converted into human-modified landscapes in the last century (Ramankutty & Foley, 1999; Imhoff *et al.*, 2004; Haberl *et al.*, 2007; Hansen *et al.*, 2013). It is estimated that almost 80% of the world's terrestrial surface, excluding Antarctica, has been modified to a certain degree by human activities (Ramankutty & Foley, 1999; Haberl *et al.*, 2007), with agriculture and urban development being the main drivers of land cover changes (Ramankutty & Foley, 1999; Tilman *et al.*, 2001; Ellis *et al.*, 2010). Given current rates of consumption and development imposed by humans, these modifications of natural landscapes will likely continue in the future (Tscharntke *et al.*, 2012; Tilman *et al.*, 2017).

The conversion of natural areas to human-dominated landscapes may lead to loss of natural habitats for species. Potentially, a biodiversity crisis could ensue (e.g., Wilcove *et al.*, 1998; Czech, 1997; but see reviews Pereira *et al.*, 2010; Tilman *et al.*, 2017). Hence, the general goal of this thesis is to investigate to what extent the conversion and fragmentation of natural land covers (e.g., forest) leads to loss of species.

Concepts, definitions and approach taken

Prior to the specifics of each thesis chapter, a few concepts and definitions utilised in this thesis are required. First, it is necessary to clarify the use of the concept *habitat* in the context of this thesis. “Habitat is conceived as the range of environments or communities over which a species occurs” (Whittaker *et al.*, 1973, p. 425 in Whittaker and Levin, 1975). The concept is broad, encompassing multi-dimensional characteristics of the space and time occupied by a species. Each habitat is delimited by a multidimensional *niche*, which is a summary of an organism’s tolerances and requirements (Begon *et al.*, 2006). That makes the concept species-specific and, ultimately, a large number of environmental variables may affect a single species. Peters (1993, pp. 74-104) raised several criticisms of the concepts, niche and habitat, because there are an unknown number of resources involved, and consequently the niche cannot be operationally defined to predict an organism’s ecological response to environmental conditions. When the use of these concepts is restricted to a few dimensions, it is more theoretically sound, and sufficient for a particular purpose (Peters, 1993, p. 92). Hence, throughout this thesis, I have not applied the concept of habitat *per se*. Instead, I used measurements of natural land cover (e.g., proportion of land cover types per unit of area) as a first approximation of natural habitats utilised by avian species.

Second, I have addressed most questions of this thesis by using *species richness* as a metric of species diversity. Species richness is the number of species of a given taxon in the chosen assemblage, and it is probably the simplest way of describing a community (Magurran, 2004). Even though there is debate around the definition of richness (e.g., the species concept itself and sampling methods/scale can change the number of entities that are observed at a given sampling site [Gotelli & Colwell, 2001; Magurran, 2004]), it is a measurement of species diversity that has been largely applied in ecological and conservation research (Chapin *et al.*, 2000). Species richness can be used in ecological models to predict changes in number of species through time and space when environmental conditions change. In principle, these studies should be able to guide decision makers regarding species and habitat protection.

Third, I have tested the predictions of my hypothesis using *breeding bird species* of the southern parts of Ontario, Canada, and New York State, USA. Birds have attracted the attention of biologists and amateur bird-watchers for centuries, and the fascination for these creatures has fostered the existence of a large number of datasets worldwide. For example, BirdLife International (http://www.birdlife.org/) uses thousands of volunteers to collect data on bird species' occurrences around the world. Using similar citizen science approach, other organizations around the world are managing several birding projects. In North America, The North American Breeding Bird Survey (BBS, https://www.pwrc.usgs.gov/bbs/) has set out annual surveys to monitor the status and trends of North American bird populations since 1960s. Provinces in Canada, and States in the USA, have launched their own bird surveys to build Breeding Birds' Atlases since 1980s. Specifically for this thesis, I used bird species distributions generated from the Ontario Breeding Birds Atlas (OBBA, Cadman *et al.*, 1987), the New York State Breeding Birds Atlas (NYBBA, McGowan & Corwin, 2008), and from range maps maintained by BirdLife International.

Finally, I applied macroecological approach to address my questions. Macroecology was initially defined as “the division of food and space among species on continents” (Brown & Maurer, 2013). Prof. David Currie has defined macroecology “as the study of the general, predictable patterns in the properties of natural systems” (Currie, unpublished). Macroecological approaches have been applied in ecological studies to describe and predict broad spatial and temporal patterns operating at the organism, population or ecosystem levels of organization (Smith *et al.*, 2008). It is essentially based on observations of nature and statistical correlations, which has been seen as the weakness of macroecology by some researchers (Currie, unpublished). However, correlative studies are essential in science because they suggest hypotheses and mechanisms to be tested (Currie, unpublished). Experimental studies can be used to generate hypotheses as well, but they usually happen at much smaller scales due to ethical and logistical reasons, consequently imposing limits to generalizations to much larger natural systems (Blackburn & Gaston, 2003; Kerr *et al.*, 2007).

In the last decade, ecologists and conservation biologists have applied macroecological approaches to address biotic consequences of global changes (Kerr *et al.*, 2007). The coarse scale, broad-extent focus of macroecology makes it well-suited for addressing human impact over species populations and communities (Kerr *et al.*, 2007). For example, studies have estimated species extinction risks from climate change (Parmesan *et al.*, 1999; Pearson *et al.*, 2002; Jetz *et al.*, 2007) and habitat loss (Betts *et al.*, 2017; Tilman *et al.*, 2017). Hence, theoretically, the outcome of macroecological research can be more relevant to design conservation strategies, including land management, than could be achieved through experimental studies (Kerr *et al.*, 2007).

Many macroecological studies have utilised species-area relationships (SARs) to analyse the relationship between number of species inhabiting an area and its size. Applied initially in island systems to predict the number of existing species in islands of different sizes (MacArthur & Wilson, 1967; Losos, Jonathan B.; Ricklefs, 2009), SAR models can be used to predict richness in mainland systems disrupted by human activities. The remaining portions of natural areas within a matrix of human-dominated landscape can be viewed analogously to islands (Pimm & Raven, 2000). Applying SAR modelling, Pimm et al. (1995) predicted that the Earth is facing current species extinction rates 1,000 times faster than previously observed from fossil records. SAR models have been criticized for overestimating species extinctions from habitat loss (Smith, 2010; He & Hubbell, 2011; Pereira *et al.*, 2012). Nonetheless, new SAR approaches have been proposed in the literature (Pereira & Daily, 2006; Pereira *et al.*, 2014; De Camargo & Currie, 2015), and it is a still one of the main tools in conservation biology capable of evaluating possible impacts of land use decisions (e.g., clearing, urban sprawl) on species diversity (Pimm *et al.*, 1995). I essentially applied variations of SAR models for most of the statistical analyses of this thesis.

Statements of contributions of each chapter

In Chapter 1, entitled “An empirical investigation of why species-area relationships overestimate species losses” (De Camargo & Currie, 2015), I test a new SAR model (Lost-habitat SAR) against other SAR models in order to predict how avian species richness varies in landscapes with varying amounts of natural land cover (i.e., from 0-100% natural) in 10x10km grid cells covering southern Ontario. The classic SAR model predicts that species richness should decrease with loss of habitat (Pimm *et al.*, 1995). Several studies have indicated that SARs miscalculate species loss from habitat loss (Pereira *et al.*, 2010; Smith, 2010; He & Hubbell, 2011; Fattorini & Borges, 2012), while many others have proposed modified SARs, attempting to capture better estimates (Kinzig & Harte, 2000; Tjørve, 2003; Triantis *et al.*, 2003; Pereira *et al.*, 2012; Hanski *et al.*, 2013; Proença & Pereira, 2013). Total bird species richness peaks around 50% natural land cover in landscapes of 100-km^2 in southern Ontario (Desrochers *et al.*, 2011), *not* following the monotonic richness-area predicted by the classic SAR model. Hence, Desrochers et al. (2011) hypothesised that the peaked relationship was the outcome of the sum of two SAR curves: forest bird richness increasing monotonically with forest cover, and open-habitat species richness increasing with human-modified cover within landscapes. However, the models of Desrochers et al. failed to capture the fact that richness of open-habitat bird species peaks, rather than increasing monotonically, as a function of human-dominated land cover. My Lost-habitat SAR was built upon that gap.

Therefore, this first manuscript brings an important contribution to a broader ecological question that is: what determines species richness at regional scales. Contemporary climate (e.g., temperature and precipitation) (Currie, 1991; Francis & Currie, 2003; Hawkins *et al.*, 2003) and historical/evolutionary drivers (Wiens *et al.*, 2010; Romdal *et al.*, 2013) may better explain variation in species richness at continental scales. However, at local and regional scales (e.g., national parks, provinces, states) there is no clear consensus on the environmental determinants and mechanisms giving rise to patterns in richness (Ricklefs, 2004; Field *et al.*, 2009; Newbold, 2012; Newbold *et al.*, 2014). At these scales questions like "how much habitat is enough?" (Fahrig, 2001) have often been asked (Francesco Ficetola & Denoël, 2009; Estavillo *et al.*, 2013), suggesting that land cover and suitable habitats could be important to species maintenance at these intermediate scales. The Lost-habitat model demonstrated that land cover is not only a good predictor of species variation (albeit not in the way that earlier literature suggests), but also how studies should precede to capture such variation at the landscape level.

Chapter 2 is entitled "Birds respond to habitat loss at the landscape-level, but not much to fragmentation". In this manuscript I tested predictions regarding the widespread belief that habitat fragmentation leads to loss of species diversity, more so when habitat amount remaining in the landscape is low (Villard *et al.*, 1999; Betts *et al.*, 2006; Fischer & Lindenmayer, 2007; Didham *et al.*, 2012). I examined whether habitat fragmentation *per se* affects species avian richness and species' probability of occurrence (p_{occ}) beyond the effect of loss of habitat area using 991 landscapes of 100km^2, varying and amount of habitat and fragmentation, in southern Ontario.

This manuscript adds an important contribution to the current debate about the independent roles of habitat fragmentation and habitat amount on species' ecological responses at the landscape level (Hanski, 2011; Fahrig, 2013, 2015, 2017; Haddad *et al.*, 2017). For the last 50 years or so (Fahrig, 2017), conservation practitioners have fostered corridors, passages on roads, reforestation to connect fragments, among others conservation measurements to protect species. Theses premises are measurements are heavily based on the "belief" that fragmentation is always detrimental on species' ecological responses. Corridors, for example, have become a feature of many ecological management strategies worldwide, yet evidence for their effectiveness is slim (Simberloff *et al.*, 1992; Beier & Noss, 1998; Debinski & Holt, 2000). However, Damschen *et al.* (2006) claimed that corridors increased plant species richness in ~50ha experimental landscapes, because connected *patches* retain more native plant species than isolated ones, with the difference increasing. Other observational and experimental studies have shown that diversity increased in larger and more connected *patches* (Kattan *et al.*, 1994; Villard *et al.*, 1999; Stouffer *et al.*, 2011; Hanski *et al.*, 2013; With *et al.*, 2015; Haddad *et al.*, 2017). Hence, it seems that there is little doubt about the detrimental effect of habitat fragmentation at the *patch scale*. However, in a literature recent review, Fahrig (2017) showed that most studies have shown *positive*, rather than *negative*, effect of habitat fragmentation after controlling for habitat amount at the landscape level. My Chapter 2 provides a strong test, with high statistical power, of the habitat fragmentation predictions at the landscape level.

Chapter 3 is entitled "Avian species-level' responses to land cover at the southern- and northern-margin of their distributions". In this manuscript, I tested a hypothesis stating that species' abilities to colonize landscapes at northern extremes (i.e. the northern edge of southerly species' ranges) may be limited by habitat loss and fragmentation (Pearson *et al.*, 2009; Thomas, 2010, Opdam & Wascher, 2004). I looked whether avian populations at the northern and southern margins of their geographical ranges respond differently to the amount of natural land cover remaining in the landscape. More specifically, I compared the species' probability of occurrence of three distinct groups: i) those whose northern range limit falls within the study area, ii) those whose southern range limit is in the study area, and iii) those whose ranges cover the entire study area (southern Ontario).

Chapter 3 has a direct impact on the climate change literature. Climate change studies often hypothesise that habitat loss and fragmentation may pose a barrier to species tracking warmer temperatures (Opdam & Wascher, 2004; Manning *et al.*, 2009; van de Pol *et al.*, 2010; Mantyka-Pringle *et al.*, 2012; Oliver *et al.*, 2015; Selwood *et al.*, 2015). Mechanistically, as species' ranges expand northward (e.g. Hill et al., 2002; Parmesan & Yohe, 2003; Coristine & Kerr, 2015), or in other directions (Currie & Venne, 2016), the lack of landscape features used by the species as habitat could, in principle, prevent species from moving to new, climatically suitable areas (Hill *et al.*, 2001; Travis, 2003; Opdam & Wascher, 2004; Robillard *et al.*, 2015). At the global scale, the effects of habitat loss and fragmentation seem to be greatest in areas with high temperatures (Mantyka-Pringle *et al.*, 2012). Alternatively, warming climate may also provide new habitat opportunities for populations at the cold-edge of their distributions (i.e. the northern edge of species' ranges) (Thomas *et al.*, 1999; Lennon *et al.*, 2002; Oliver *et al.*, 2012). Therefore, Chapter 3 provides an empirical test of whether partial conversion of natural land cover to human-dominated poses a serious barrier to the colonization of areas that become climatically suitable due to global climate change.

Chapter 4 asks an important conservation biology question: "Would conserving natural land cover in landscapes conserve biodiversity?" The question refers back to the general hypothesis of this thesis: habitat loss causes species loss. A corollary of the hypothesis is that conserving natural land cover (first approximation of habitat) will conserve biodiversity. I tested whether the relationship between avian species richness and natural land cover is independent of the data type: fine-grained occupancy data, versus coarser-grain range map data, sampled in grid cells of varying size.

The literature assumes that the relationship between avian species richness and natural land cover is the same using fine-grained species' distributions (Tilman *et al.*, 1994; Findlay & Houlahan, 1997; Drapeau *et al.*, 2000) and coarser-grained species' ranges (Pimm & Raven, 2000; Brooks *et al.*, 2002; Pimm *et al.*, 2006, 2014; Hubbell *et al.*, 2008; Betts *et al.*, 2017). Alternatively, since continental-scale studies of richness based on range maps have generally observed strong richness-climate relationships (Algar *et al.*, 2008; Field *et al.*, 2009), richness patterns generated from range maps may be more strongly related to temperature than to land cover, even over regional extents. In contrast, one might expect that a stronger effect of land cover would be detected on richness patterns generated from finer-grained atlas' distributions. I also tested whether these relationships depend on the grain size (cell sizes) at which species are recorded (25-km^2, 100-km^2 and 900-km^2) Finally, to test the consistency of our results, we compare fitted models from separate datasets covering southern Ontario and New York State.

This final chapter has a direct impact on a substantial body of the conservation literature that relates species' distributions to land cover features (i.e., forest cover, fragmentation, land-use intensity, etc), at national or global scales, in order to draw conclusions on the effect of habitat loss to biodiversity. It raises the question whether conservation should be looking at land cover amounts in order to develop its strategies and planning.

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CHAPTER 1

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TITLE

An empirical investigation of why species – area relationships overestimate species losses

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ABSTRACT

It is generally assumed that, when natural habitat is converted to human-dominated land cover, such habitat is "lost" to its native species. Most literature assumes that species richness should vary as a function of remaining natural area, following the well-known species-area relationship (i.e. Classic-SAR). However, Classic-SARs have consistently over-estimated species losses resulting from conversion of natural forested land cover to human-dominated landscapes. Moreover, richness is sometimes a peaked function of remaining natural habitat. Recent studies propose modified SAR models based on species' utilization of multiple habitat types, yet none fully explains a peaked species-area relationship. Here we evaluate the responses of total avian richness, forest bird richness, and open-habitat bird richness to remaining natural land cover within 991 quadrats, each 100 km^2, across southern Ontario, Canada. Total bird species richness peaks at roughly 50% natural land cover. Richness of forest birds varies as a classic power function of forested area. In contrast, richness of birds that prefer open habitats does not increase monotonically with either natural- or human-dominated land cover. Richness of open-habitat species can be predicted when we partition human-dominated land cover into an "available human-dominated" component and "lost" habitat. Distinguishing three land cover types (natural, available human-dominated, and lost) can thus permit accurate predictions of species richness in landscapes with differing levels of natural habitat conversion.

INTRODUCTION

Consider natural, mainly forested landscapes, in which some fraction of the forest is cleared for human use (e.g. logging, agriculture, buildings). What will be the effect on species richness? It has been broadly assumed that forest converted to human-dominated land covers is "lost" as habitat for biodiversity, and that species losses must ensue (Heywood & Stuart, 1992; Pimm and Raven 2000). This expectation derives from Island

Biogeography theory (MacArthur and Wilson 1967) and the empirical observation that species richness increases with island area. Forest patches in a matrix of human-dominated land can be viewed analogously (Pimm et al. 1995). In both cases, the Species-Area Relationship (hereafter called Classic-SAR) has often been modelled as a power function (Arrhenius 1921, Preston 1962):

$$S = cA^z \tag{1}$$

where S=species richness, A=habitat area, and c and z are empirical constants. Other model forms have been studied (e.g., Tjørve 2003; Mathews et al. 2014). In all of them, richness is a monotonic positive function of habitat area.

Area-based models such as eq. 1 are by far the most common method used to predict species extirpations should happen as natural habitat is converted to other land covers (Stork 2009, Pereira et. al 2010). For example, Koh and Ghazoul (2010) use eq. 1 to argue that, if the area of habitat in a landscape is originally A, and a subarea a is converted to human-dominated cover, then a decrease in richness can be predicted from the proportion of remaining original habitat:

$$\frac{S_{A-a}}{S_A} = \left(\frac{A-a}{A}\right)^z. \tag{2}$$

However, two empirical problems have been noted. Confirmed extinctions are generally smaller than predictions made by Classic-SARs (Budiansky 1994, Pimm and Askins 1995, Stork 2009, He and Hubbell 2011; Pereira et al. 2012). Second, Desrochers et al. (2011) observed a peaked relationship between avian richness and remaining natural land cover in human-modified landscapes in the southern part of Ontario, Canada.

This observation suggests that conversion of some natural forest to human-dominated land cover may actually increase richness.

One clear problem with the application of Classic-SARs to human-modified landscapes is the assumption that natural land cover that has been converted to human-dominated cover is "lost": no species persist there (Pereira and Daily 2006). Yet some species clearly do occupy human-dominated land covers. Among these are species associated with humans *per se.* Avian examples include House Sparrow (*Passer domesticus*), House Finch (*Haemorhous mexicanus*), Rock Dove (*Columba livia*), and a few others (Lowther and Cink 2006). Human-dominated habitats are also used by species that prefer early-successional or open habitats, which disturbances, anthropogenic or natural, create. Examples relevant to this study include: Carolina Wren (*Thryothorus ludovicianus*) and Blue-winged Warbler (*Vermivora cyanoptera*).

In this study, we hypothesize that, in landscapes where natural forest is converted to human-dominated land cover, the expected change in richness can be parsimoniously modelled as follows. Habitat conversion produces three functional categories of land cover (or habitats), to a first approximation: areas that support forest species, areas with species that prefer open or early successional habitats, and areas that support no unique species. Classic-SARs may over-estimate species losses because they neglect the fact that some proportion of human-dominated land cover supports species not found in forested habitat. The remaining human-dominated cover supports no species that are not found elsewhere in the landscape.

Forest bird species richness and open-habitat bird species richness should obey their own relationships with area of each corresponding land cover in a landscape:

$$S_{Forest} = cA_{Forest}{}^{z}$$

$$S_{Open} = cA_{Human}{}^{z} \tag{3}$$

where A_{Forest} is forested land cover, and A_{Human} is human kind cover.

The area of forest cover in a landscape can be directly assessed by remote sensing. The amount of human-dominated cannot be assessed directly, since these covers are only partly available. We hypothesize, therefore, that human-dominated cover (A_{Human}) can be divided into two classes: available human-dominated (A_{Human_avail}) land cover, which provides habitat for open-habitat species, and "unavailable human-dominated areas" (A_{Human_lost}), which are effectively "lost" as avian habitat. We further hypothesize that lost human-dominated area varies with total human-dominated area. Therefore, if open-habitat richness varies as a function of available human-dominated land cover, we obtain:

$$S_{Open} = c * \left(A_{human} - A_{Human\_lost}\right)^{z}$$

$$S_{Open} = \mathrm{c} * (A_{human} - c'(A_{human})^{z'})^{z} \tag{4}$$

(see *Appendix A* for details of the derivation of this equation). The constants *c, c', z and z'* are empirically derived.

Competing models

We test our multi-habitat model, which we shall call the Lost-Habitat SAR (eq. 4, LH-SAR), against the main competing area-based models currently available in the literature.

Single-habitat models

Classic-SAR: This model estimates species losses from eq.1 by calculating expected richness in two areas: the original forested area *A*, and the area of forest remaining after area *a* has been converted to human-dominated land cover (eq. 2).

Endemic-Area relationship (EAR): He and Hubbell (2011), in contrast, pointed out that species are lost from a landscape only when all of their individuals are endemic to the converted habitat. Based on sampling theory, they used the EAR to predict the number of species endemic to area *a*, and therefore the number expected to be lost if area *a* is converted from forest to human-dominated cover. The expected number of species to be lost by the EAR is also given by a power function:

$$\frac{S_a}{S_A} = 1 - \left(1 - \frac{a}{A}\right)^{z_{ear}} \qquad (5)$$

where S_a is the number of species found *only* in area *a* and not anywhere else in the landscape of area *A*; S_A is the number of species found in *A;* and z_{ear} is a constant that is necessarily smaller than z_{sar} (i.e. the exponent of the Classic-SAR). The z_{ear} can be derived from the Classic-SAR exponent z_{sar} by the formula (Harte & Kinzig, 1997; Kinzig & Harte, 2000):

$$z_{ear} = -\ln(1 - 1/2^{z_{sar}})/\ln(2) \qquad (6)$$

Multi-habitat models

Countryside-SAR: A second set of recent models proposes that species richness in modified landscapes depends upon habitat heterogeneity (Tjørve, 2003; Triantis *et al.*, 2003; Pereira & Daily, 2006a; Koh & Ghazoul, 2010). Among those, Pereira and Daily (2006) proposed the countryside-SAR model. Their model proposes that a landscape contains n different habitat types. A given group i of species has a particular affinity for each habitat type. The estimated species richness in group i is:

$$S_i = c_i\left(\sum_{j=1}^{n} h_{ij}\, A_j\right)^{z_i} \tag{7}$$

where S_i is the number of species in group i, h_{ij} is the affinity of group i to habitat j, A_j is the area covered by habitat j, and n is the number of habitat types. The power model parameters, c_i and z_i, are species-group dependent. The total number of species in the landscape is then given by the sum of the number of species in each of m species-groups:

$$S = \sum_{i=1}^{m} S_i \tag{8}$$

The countryside model predicts richness more accurately than the Classic-SAR models in plants (Proença & Pereira, 2013). Recently, Guilherme and Pereira (2013) showed that the countryside-SAR model predicts bird diversity better than Classic-SAR in abandoned farmlands in Portugal.

Two-habitat SAR: Desrochers et al. (2011) proposed a model in which total avian richness (in landscapes of 100 km^2) is modelled as the sum of two classic species-area relationships: A) forest-dwelling species as a Classic-SAR of natural (primarily forested) land cover, and B) open-habitat richness as a Classic-SAR of human-dominated land cover. These two land covers together account for 100% of the area. Therefore, total richness is given by:

$$S_{total} = S_{Forest} + S_{Human} = c_1 {A_{Forest}}^{y} + c_2 {A_{Human}}^{r} \tag{9}$$

where S_{total} is total species richness, and c_1, c_2, y and r are empirical constants.

Desrochers et al (2011) show that the sum of these two habitat Classic SARs predicts a peaked relationship between total richness and remaining forest cover, which can be approximated by a quadratic function of natural area:

$$S_{total} = a + bA_{Forest} + cA_{Forest}^{2} \quad (10)$$

where a, b, and c are regression coefficients.

Lost-Habitat SAR (LH-SAR): Our three-land cover model (eq. 4) differs from the Countryside model in postulating that two operationally defined species clades each respond to a particular habitat type, rather than to all habitat types. It differs from the Two-habitat SAR model by including "lost" land cover.

METHODS

To test whether the LH-SAR provides a better fit than competing models we extended the analysis of Desrochers et al (2011) to more fully explore variation in forest bird species richness, and total avian richness, as functions of the amount of forested land cover remaining in 991 quadrats, each 100 km^2, in southern Ontario, Canada. We similarly examined open-habitat bird species richness as a function of human-dominated land cover. The underlying data used in this study are the same as those used by Desrochers et al. (2011).

Study Area

Our study area covers southern Ontario, Canada (41º – 44º N and 84º – 74º W, ~ 200,000 km^2, Fig. 1). Historically, southern Ontario was mainly forested. Natural land cover was heavily altered during European settlement in the 18th – 19th centuries (Warwick 1980). Agriculture and logging removed relatively little natural forest in southern Ontario after the mid 20th century, as government programs began promoting selective harvesting and silviculture on private woodlots (Thompson et al. 2000, p. 84; Ontario Ministry of Natural Resources 2013).

Species richness

To determine species richness, we used bird species distributions in southern Ontario (Canada) reported in the 2005 Ontario Breeding Bird Atlas (BBA) (Cadman et al. 2007). The BBA was based upon surveys of breeding bird species in 10 km x 10 km quadrats, defined on the Universal Transverse Mercator (UTM) grid system (Fig. 1). We excluded wedge-shaped UTM quadrats, and quadrats with more than 10% lake area, to minimize variation in area among quadrats. We also excluded quadrats with <10 hours of sampling effort (Cadman et al. 2007). This left 991 BBA quadrats in our analysis.

We calculated species richness by tallying the number of species for which evidence of breeding was observed in each 100 km^2 quadrat. We excluded very rare species (detected in <10 quadrats), as well as apparent vagrants (26 species excluded, Cadman et al. 2007, www.natureserve.org). Therefore, for the purpose of this study, we considered 202 bird species as for total species richness. We categorized 89 of these as forest species and 113 as open-habitat species, based on the species accounts in the BBA and in Ehrlich et al. (1988). A complete list of the species we included and excluded in this study is in *Appendix B*.

Land cover

Land cover data were obtained from the Ontario provincial-scale data set produced by the Ontario Ministry of Natural Resources (2002) at 25m resolution, which distinguished 28 land cover classes. We grouped these classes into natural land covers (including all forested classes, wetlands and alvar) and human-dominated covers (including recent cutovers, mine tailings, quarries, bedrock outcrops, settlement and developed land, pasture and abandoned field, and cropland). There are a small number of coniferous plantations in the study area; we included these in natural cover. We excluded water and unclassified categories. Five other classes in the original land-cover classification did not occur in the study area.

Within the natural land cover category, forests constitute 97% of the total area of quadrats in the study area, while natural wetlands correspond to 3%. Therefore, in this study, natural land cover is approximately synonymous with forested areas. Within human-dominated areas, 76% is cropland (row crops, hay, or open soil), while the rest (24%) corresponds mainly to recent cutovers, mining, urban areas and pastures. Initial investigations suggested that distinguishing the components of human-dominated cover (e.g., the amounts of crop vs. open soil) did not improve predictions of species richness.

Note that, everywhere below, we expressed forest cover as a proportion of the total quadrat area. This is equivalent to re-scaling total area to a value of 1.0, since all landscapes in our study have the same total area (100 km^2). The present study does not address the effects of changing landscape area.

Statistical analysis

The five models we compare are all power functions or variations thereof (as described in the equations above). Three of the models we examine predict that total species richness, and/or its components are monotonic positive power functions of natural area, while two other models predict peaked functions of natural area. To test for the peaked shape, we fitted second-degree ordinary least-squares regressions (GLM function in R; R Development Core Team, 2008).

We added sampling effort as a covariate in our models, given that the number of census hours varied among BBA squares, and that richness may increase with sample effort. We excluded two quadrats in which sampling effort was much higher than in all other quadrats (>1200 hours, versus 10 h – 430 h in other quadrats) because these two quadrats had very high leverage in the regression models. Although sampling effort influences richness-area relationships, models retested without sampling effort led to the same qualitative conclusions. We compared the model fits using corrected Akaike information criterion (AICc) and the change in adjusted R^2 (R^2_{adj}). We also examined residuals for evidence of lack-of-fit or heteroscedasticity.

Finally, we asked whether it is possible to distinguish the available human-dominated land cover from "lost" land cover, based on satellite land cover images. To do this, we first estimated the area of lost cover by fitting eq. 4. We then used multiple regression to estimate of "lost" cover with the area of each of the remotely sensed classes of human-dominated land cover (recent cutovers, mining, urban areas, abandoned pastures and croplands).

RESULTS

Patterns in species richness

Total bird species richness per quadrat peaked at 53% forest cover (Fig. 2, Table 1, R^2= 0.45) as, described by the polynomial:

$$S_{Total} = 30.30 + 109.5\, A_{Forest} - 94.35\, A_{Forest}{}^{2} + 25.90 log_{10} E \qquad (11)$$

where S_{total} is total species richness, A_{Forest} is forested area in each BBA quadrat, and $log_{10}E$ is the log transformed sampling effort.

Forest bird species richness fits a quadratic function of forest cover (Fig. 3, R^2_{adj} =0.59, eq. 12). Nonetheless, forest richness is better fitted by a Classic-SAR and by the Countryside models than described by the polynomial function (Table 1).

$$S_{Forest} = 7.25 + 53.08A_{Forest} - 28.70{A_{Forest}}^2 + 11.60log_{10}E \qquad (12)$$

Open-habitat bird species richness initially increases with human-dominated land cover (i.e., 1.0 minus forested areas; Fig 4), and then declines. Open-habitat species richness peaks at 58% human-dominated area (with the peak significantly within the domain of the data: Mitchell-Olds & Shaw test; Fig. 4, $R^2_{adj} = 0.58$). The polynomial relationship that describes the relationship is:

$$S_{Open} = 13.81 + 74.89(1 - A_{Forest}) - 65.66(1 - A_{Forest})^2 + 14.27log_{10}E \qquad (13)$$

where $1\text{-}A_{Forest}$ represents human-dominated in each100km^2 landscapes.

Tests of the Classic-SAR and EAR

The polynomial relationship accounts for significantly more of the variance in total species richness ($R^2_{adj} = 0.45$, Table 1) than does either the Classic-SAR ($R^2_{adj}= 0.33$) or the EAR ($R^2_{adj} = 0.32$). The peaked form of the observed relationship is incompatible with both these models, and with any other model in which richness is a monotonic positive function of remaining natural habitat across a gradient from fully-forested to human-dominated landscapes (Koh & Ghazoul, 2010; Proença & Pereira, 2013; Pereira *et al.*, 2014).

The Classic-SAR explains well the variance in avian richness of forest birds with forest cover (Fig. 3, 89 forest species, $S_{Forest} = 33.75{A_{Forest}}^{0.37} + 11.09\ log_{10}E$, R^2_{adj} = 0.60, Table 1). However, the exponent of the power function (0.37) is much higher than values for total richness on continents, which typically vary from 0.10 and 0.25 (Ney-

Nifle and Mangel 2000, He and Hubbell 2011). In other words, forest birds are lost more quickly than the Classic-SAR model usually predicts, not less, as He and Hubbell (2011) have suggested. Moreover, in our analysis EAR underestimates the number of species gained as forest cover increases (Fig. 3, $S_{Forest} = 36.32A_{Forest}^{0.30}+9.17log_{10}E$). We reject the Classic-SAR and the EAR as descriptors of forest species richness in landscapes in which forest has been partially converted to human-dominated cover.

Test of the Countryside model

When we fitted forest- and open-habitat richness with the Countryside model (eq. 8, Pereira & Daily 2006), we found that the habitat-affinities for the non-preferred habitat of each guild is essentially 0 (see *Appendix C*). In other words, the model reduces to a Classic-SAR function of forest cover to predict the richness of forest birds, and a Classic-SAR function of human-dominated cover for open-habitat birds (Table 1, i.e. see Classic-SAR curves shown in Figures 3 and 4). Nonetheless, the countryside model fails to predict to peaked shape of the relationship between open-habitat species richness and human-dominated land cover. We reject the Countryside model.

Test of the Two-habitat SAR

The Two-habitat SAR (Desrochers et al. 2011) postulated that forest bird richness is a Classic-SAR function of forest cover, and that open-habitat bird richness is a Classic-SAR function of human-dominated cover. Nonetheless, we noticed two problems with their model: 1) open-habitat richness is, in fact, a peaked function of human-dominated cover (and, therefore, of forest cover as well, Fig. 4), and 2) the Two-habitat SAR model was tested with only a subset of forest- and open-habitat obligate species, rather than the majority of species present in Ontario split in two guilds, as we propose here. Thus, while the Two-habitat SAR correctly captures the peaked variation of total richness as a function of forest cover (Desrochers et al. 2011), it is inconsistent with the peaked relationship observed in open-habitat species. We therefore reject the Two-habitat SAR.

Test of the Lost-habitat SAR

The Lost-habitat SAR predicts that forest bird richness varies as a Classic-SAR function of forest cover, that open-habitat bird richness varies as a peaked function of human-dominated cover (i.e., 1.0-A_{forest}), and that total richness is a peaked function of forest cover. All three of these predictions are consistent with the data (Table 1). The nested power function (eq. 4), which postulates that a portion of human-dominated areas is "lost" area, provides the strongest statistical descriptor of the variation of open-habitat bird species richness as a function of the human-dominated cover in a landscape (Table 1). The fitted model, which explains 59% of the variance in open-habitat birds (Table, 2113 open-habitat species), is: $S_{open} = 47.06((1- A_{Forest})-0.90(1- A_{Forest})^{2.18})^{0.33} + 15.50\log_{10}E$). The sum of open- and forest-bird richness yields total richness. Again, the Lost-Habitat-SAR provides the strongest prediction of total richness (Table 1).

What is the "lost" land cover in the Lost-Habitat SAR?

In landscapes where small amounts of forest have been converted to human-dominated land cover, richness is greater than in 100% forest. Humans create habitat that supports additional species. Yet, when greater proportions of forest are converted to human-dominated cover, both open-habitat species richness and total richness decrease. The exponent z'=2.18 in our empirical LH-SAR model indicates that, as greater amounts of forest are converted, an increasing proportion of the human-dominated cover is "lost". The absolute amount of available human-dominated habitat (A_{human_avail}) peaks at 61%

human-dominated area (Fig. 5a, $A_{human\text{-}avail} = (1- A_{Forest})-0.90(1- A_{Forest})^{2.18}$). Thus, our LH-SAR model suggests that, when small amounts of forested landscape are converted to human-dominated cover, habitat becomes available to bird species not found in closed forest (Fig. 5a). When larger amounts of natural habitat are converted, an increasing proportion of the human-dominated land is "lost" (as well as forested cover), leading to low species richness of both forest- and open-habitat species (Fig. 5b).

Do these available and unavailable human-dominated land covers correspond to specific remotely-sensed habitat categories? The amount of human-dominated area that is available for birds covaries positively with the amount of remotely-sensed land cover in all human-dominated classes (Table D1, *Appendix D*). Cropland is the main contributor to human-dominated land cover that is used by bird species (see Beta-coefficients, Table D1, *Appendix D*). However, "lost" land cover was not unequivocally related to a particular type of remotely-sensed land use.

Does richness relate to land use differently in different biomes?

Our study area included two biomes: a northerly boreal biome on the Laurentian Shield (i.e., mainly coniferous forest with some mixed-wood forest) that has more remaining natural forest, but a smaller avian species pool, and a more southerly Mixed-wood Plains biome (with some influence of Carolinian forest), which has experienced greater forest loss, but has a larger avian species pool. To address possible differences between the biomes, we analysed the relationships between bird species richness and forest cover in the two biomes separately (*Appendix E*). We found that the biome *per se* increases the variance explained in total richness by only 1% over forest amount in

$100km^2$ (RSS=148,062, AICc=7786, R^2_{adj}=0.46). The equation best describing the relationship is:

$$S_{total}=-12.64+105.30A_{Forest}-80A_{Forest}^{2}+24.53\log10E+3.25Biome$$

where Biome is a categorical variable representing Laurentian (boreal) Shield and Mixed-wood Plains biomes (see *Appendix E*).

There are too few mainly forested quadrats in the Mixed-wood Plains, and too few mainly deforested quadrats in the Laurentian (boreal) Shield biome to convincingly describe the complete peaked richness-forest cover relationship in each of the two biomes. However, the critical distinction between our model and previous models is the higher richness in partially deforested quadrats, compared to fully forested quadrats (see *Appendix E*). This pattern is clearly evident in quadrats present in the Laurentian Shield, which are very well sampled in the range of 80%-100% forest cover (see Fig. E1, *Appendix E*). Although there are few mainly deforested quadrats in the Laurentian Shield biome, there is little doubt that richness would decline if sufficient forest were removed. There is also little doubt that richness is very low in mainly deforested quadrats in the Mixed-wood Plains. However, there is an insufficient number of forested quadrats in the Mixed-wood Plains to show unequivocally that quadrats with 100% forest cover have fewer species than partly deforested quadrats.

DISCUSSION

Previous studies that attempted to predict species losses from habitat modification were generally either: a) based on theoretical explorations of species-area relationships (e.g. based on sampling theory), as opposed to empirical observations of observed changes in richness following habitat loss (Pimm *et al.*, 1995, 2006, Brooks *et al.*, 1999, 2002; Ney-Nifle & Mangel, 2000; Pimm & Raven, 2000; He & Hubbell, 2011); or b) patch-based models focusing on richness in remaining patches of natural habitat of varying area, as opposed to richness in entire landscapes that contain a mixture of land covers (Kinzig and Harte 2000, Rybicki and Hanski 2013, Hanski et al. 2013). Relatively few studies have studied richness in a series of landscapes that have varying amounts of habitat conversion (Drapeau *et al.*, 2000; Desrochers *et al.*, 2011; Mayor *et al.*, 2012).

Our first important result (also noted by Desrochers et al. 2011) is that total richness does not decline monotonically over a gradient of conversion of natural forest to human-dominated covers. Avian species richness in 100km^2 quadrats in southern Ontario cannot be adequately described by any monotonic function of remaining natural cover: e.g., Classic species-area or Endemic-area relationships, nor by the Countryside model (*Appendix C*). Specifically, this result is inconsistent with He & Hubbell's (2011) proposed explanation of why Classic-SARs over-estimate species losses. Their EAR is an elegant theoretical model, based on sampling individuals that are distributed in space according to stated assumptions. Given the aggregation of species in real communities, the EAR model predicts that the number of extinctions rises more gradually with increasing habitat loss than predicted by the 'backwards' Classic-SAR. However, both EAR and Classic-SARs over-estimate species extirpation caused by habitat loss, we argue, because they predict that richness will vary as a monotonic positive function of forest cover. Empirically, we found that total richness is a peaked function of forest cover. Thus, Classic-SAR and EAR fail because they do not account for the open habitat that human-dominated cover provides.

Our second important result is that, in landscapes with large amounts of human-dominated habitat, richness of both forest- and open-habitat species declines. The Lost-habitat model is a modified Classic-SAR that: 1) accounts for the (often early-successional) species that use human-dominated land covers, and 2) accounts for area that supports few, if any, species. Thus, at least for bird species in southern Ontario, a coarse classification of two guilds (open-habitat and forest species) and three land cover types (forest, available human-dominated, and lost areas) predicts the observed monotonic positive relationship between forest-bird richness and forest cover, and the peaked relationships of open-habitat and total bird species richness and forest cover.

Other hypotheses have been proposed to explain over-estimation of species losses by Classic-SAR (Smith 2010, Kinzig and Harte, 2000). "Extinction debt" is one possibility (Tilman *et al.*, 1994; Halley *et al.*, 2013): a ‘‘relaxation" time between the destruction of a habitat and the time when species go extinct (Tilman *et al.*, 1994). As pointed out by Desrochers et al. (2011), conversion of natural area to human-dominated land-cover occurred predominantly in the 19th century. Thus, extinction debt could only be important in this study if it occurs over very long time periods. This seems unlikely in a relative vagile group such as birds. Extinction debt might affect the slope of a Classic-SAR (Halley et al. 2013), but it would not lead to a peaked relationship between richness and natural land cover. A second hypothesis about the failure to accurately predict species loss from habitat conversion is that habitat destruction itself could change the values of the parameters of the power function, c and/or z (Pimm and Askins 1995, Lewis 2006, Halley et al. 2013). Classic-SARs account only for the total amount of forested cover in a landscape, and not its configuration (Hanski et al. 2013). However, recent evidence suggests that species richness appears to respond only to the amount of habitat in a landscape, irrespective of the size, shape or configuration of the remaining fragments (Fahrig, 2013).

A third hypothesis is that habitat quantity *per se* may be a less important predictor of species richness than other factors (Ibáñez et al. 2006). For example, Gibbs et al. (2009) found that loss of imperilled species in Canada was more closely related to the use of pesticides than to habitat loss alone. The south-western part of our study area, where forest loss has been greatest, is currently dominated by a very intense agriculture with extensive crop fields. The southern and western areas are also where pesticide use has been greatest (McGee et al. 2003). We suspect that intensive agriculture (with more pesticides, greater mechanical disturbance, fewer hedgerows, etc.) is mainly responsible for the increasing proportion of unavailable ("lost") human-dominated land as the more natural cover is removed (Fig. D1, *Appendix D*). Total bird species richness is lower in agriculturally intensive south-western Ontario than it is in the most urbanized parts of the province (Cadman et al 2007, Figs. 3.3 and 3.4).

It is important to note several methodological limitations to this study. First, the grain of the species richness data – the area over which birds were determined to be present or absent – is constant at 100 km^2. It is possible that the richness-natural area relationship might be different at a different spatial grain. Second, we do not know if similar relationships would be observed in other biomes. Third, the amount of "lost land cover" was estimated from the fit of richness to a hypothesized functional relationship. Fourth, although we did not find that distinguishing between urban and agricultural components of human-dominated cover improved predictions of richness in southern

Ontario, we do not know if this would be true elsewhere. It is possible that different types of human land use might be more (or less) detrimental to avian richness. We had hoped that we could estimate lost cover from the classified satellite land cover images, but no clear relationship emerged. A more direct means of estimating the land cover that is unavailable for species' use would definitely be useful.

We nevertheless propose that a model with two bird guilds (forest and open) and three habitats (natural, available human-dominated, and lost area) is sufficient to produce unbiased predictions of richness, without the demands of models with greater complexity. In southern Ontario the amount of available human-dominated habitat reaches a maximum when 61% of forested habitat is converted to human-dominated landscapes (Fig. 5a). Thus, in landscapes with ~39% forest cover, there is nearly as much available habitat in human-dominated cover as in forest (Fig. 5b). It is not surprising that Classic-SARs based on forest cover overestimate species losses.

Our findings have some important implications about habitat conversion and species loss. It seems likely that human suppression of natural disturbances, as well as use of more open areas for cultivation, may have artificially reduced the availability of open, early successional habitats in many landscapes. Our results suggest that, at least for bird species in southern Ontario, conversion of up to 50% natural forest to human-dominated cover does not have negative consequence on species richness. Relatively little - only ~15% - of the human-dominated cover is truly lost at this level of forest conversion (Fig. 5b).

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Table 1. Total species richness, and richness of forest and open-habitat birds in southern Ontario landscapes. c, c’, z, and z’ and d are coefficients of the models in test. RSS is the residuals sum of the squares from the nonlinear regression; AICc is the corrected Akaike information criterion; R2adj is the adjusted R2, and w is the Akaike weight calculated by $w = e^{\Delta AIC/2} \sum_i e^{\Delta AIC_i/2}$, where ΔAIC is the difference between the AIC of that model and the best model.

	c	*c’*	*z*	*z’*	*d*	RSS	ΔAICc	*w*	R^2_{adj}
Forest species richness									
Countryside*	27.77		0.37		11.12	38,878	0	1	0.60
Classic-SAR	33.75		0.37		11.09	38,861	3	0.16	0.60
EAR	36.32		0.30		9.17	39,337	13	<0.001	0.59
Polynomial	†					39,369	18	<<0.001	0.59
Two-habitat SAR	The same as Classic-SAR								
LH-SAR	The same as Classic-SAR								
Open-habitat richness									
LH-SAR	47.06	0.90	0.33	2.18	15.50	67,608	0	1	0.59
Polynomial	†					69,254	21	<0.0001	0.58
Countryside*	33.15		0.17		14.57	78,132	137	<<0.0001	0.53
Classic-SAR	32.26		0.17		14.55	78,132	139	<<0.0001	0.53
EAR	35.15		0.13		12.50	79,601	155	<<0.0001	0.52
Two-habitat SAR	The same as Classic-SAR								
Total richness									
LH-SAR **						150,109	0	1	0.46
Polynomial	†					152,419	15	<0.0001	0.45
Two-habitat SAR***						167,115	100	<<0.0001	0.40
Classic-SAR	46.43		0.12		30.95	187,336	218	<<0.0001	0.33
EAR	48.82		0.08		29.03	188,274	221	<<0.0001	0.32
Countryside	38.90		0.34		30.46	200,276	284	<<0.0001	0.28

† - Coefficients and full equations for polynomial functions are provided in the body text.

* Habitat affinities estimates of the countryside model are presented in *Appendix C.*

** Parameters are the same as LH-SAR for forest- and open richness.

*** Parameters are the same as Classic-SAR for forest- and open- richness.

FIGURES

Chapter 1

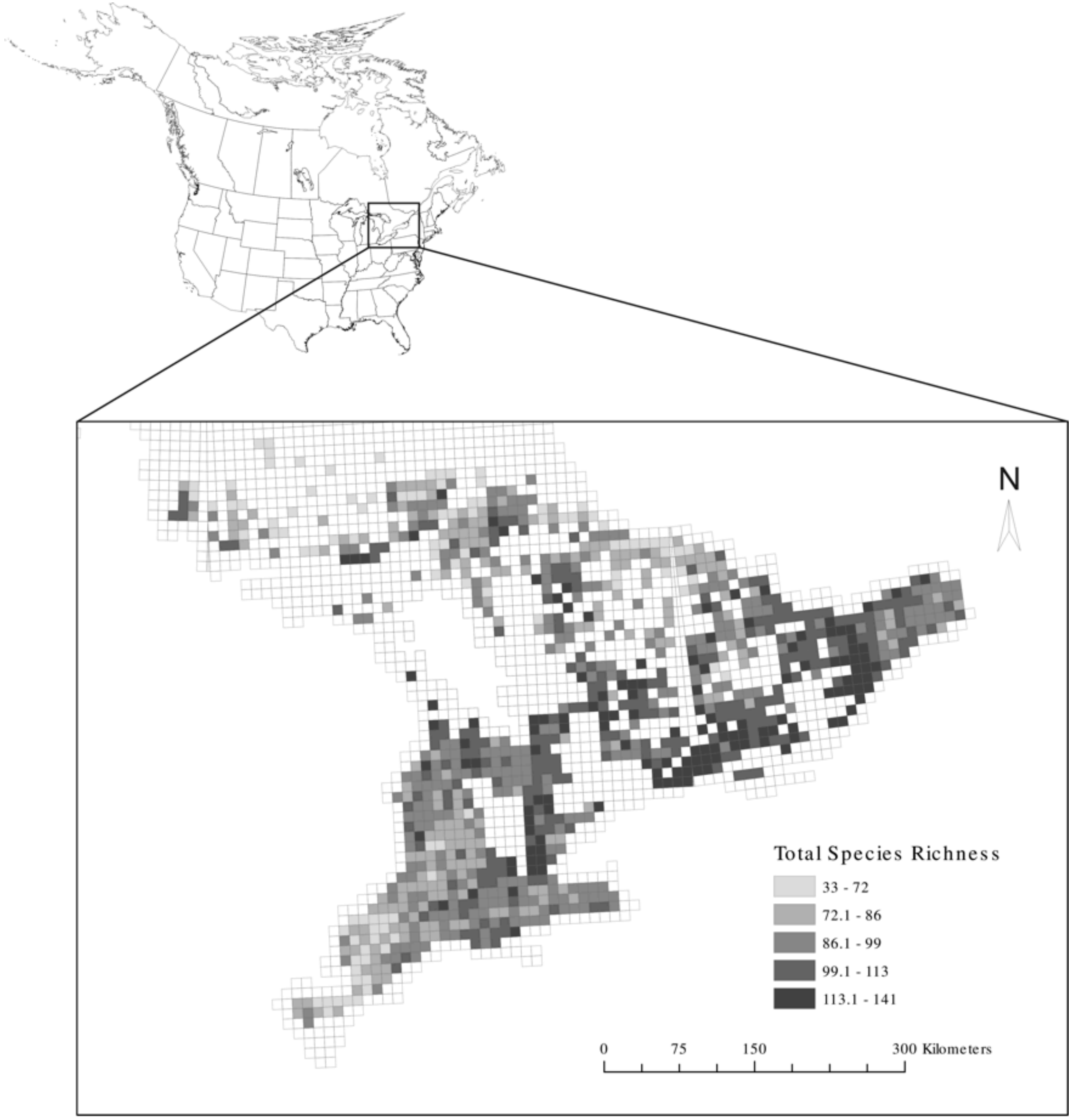

Figure 1. Avian species richness in southern Ontario. Breeding Bird Atlas squares are shown in a grid array. Unshaded squares, which were excluded from the analysis, had either <10h of sampling effort and/or >10% area covered by water. The projection is Lambert conformal conic.

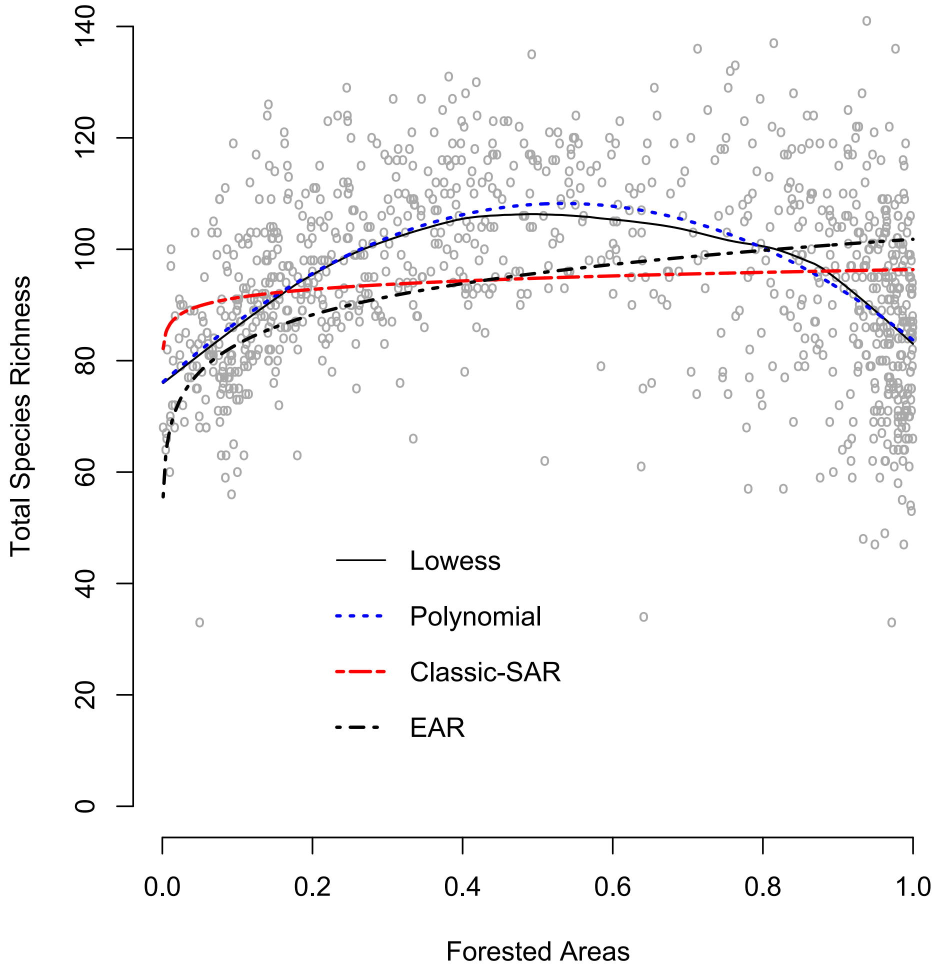

Figure 2. A comparison of a model free (lowess, solid line) relationship between total avian richness and forest cover with the Classic-SAR (dashed line), EAR (dot and dashed line) and a polynomial model (dotted line). All curves are based upon 202 species in 991 Breeding Bird Atlas squares.

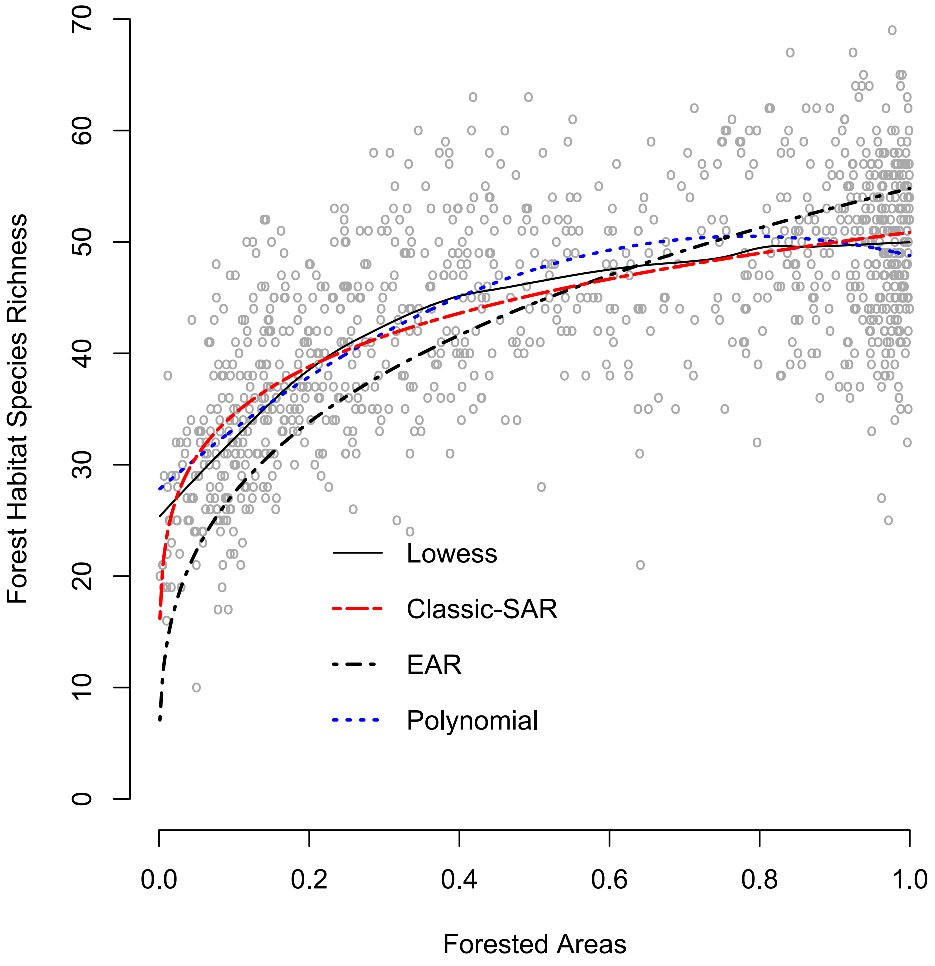

Figure 3. A comparison of the lowess (solid line) relationship between forest bird species richness and forest cover fitted Classic-SAR (dashed line), polynomial function (dotted line), and endemic-area relationship model (EAR model, dot and dashed line). N=991 BBA squares across the southern portion of Ontario.

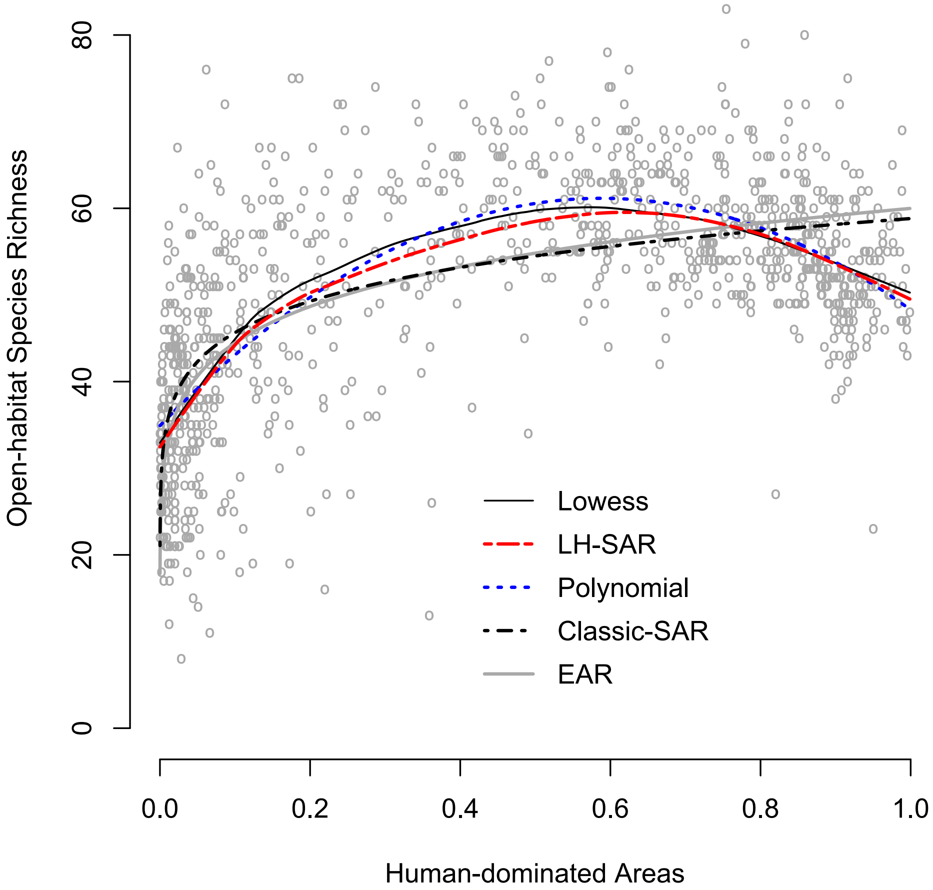

Figure 4. Richness of open-habitat bird species as a function of human-dominated area (1.0 minus forested cover). The long dashed and dotted line represents the Lost-Habitat SAR model (LH-SAR, R^2=0.59, n=991 squares). Dark solid line: lowess curve; dotted line: quadratic function of forested areas (Polynomial Model); dashed line: Classic-SAR model fitting; light grey solid line: EAR model. N=991 BBA squares across the southern portion of Ontario.

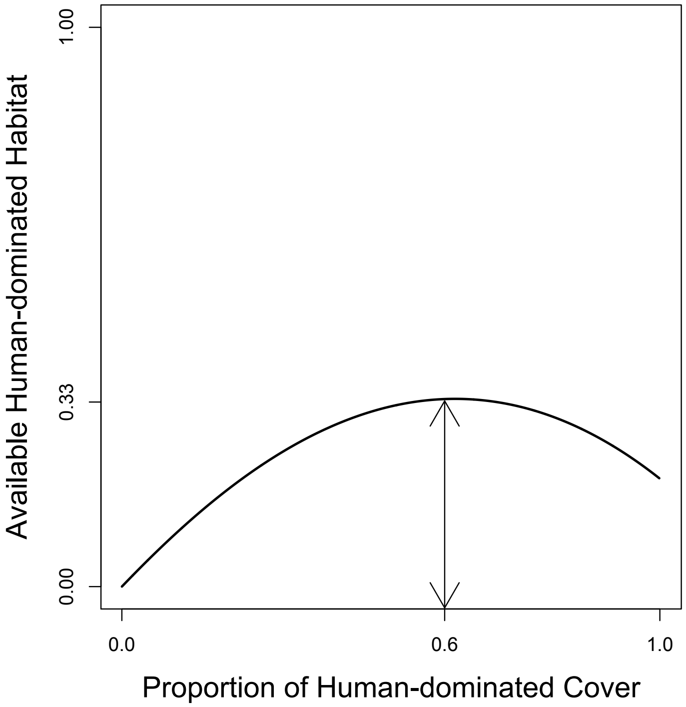

Figure 5a. The amount of available habitat modelled as function of human-dominated landscapes (one minus the proportion of natural land cover present in each square). The arrow indicates the maximum amount of available human-dominated area.

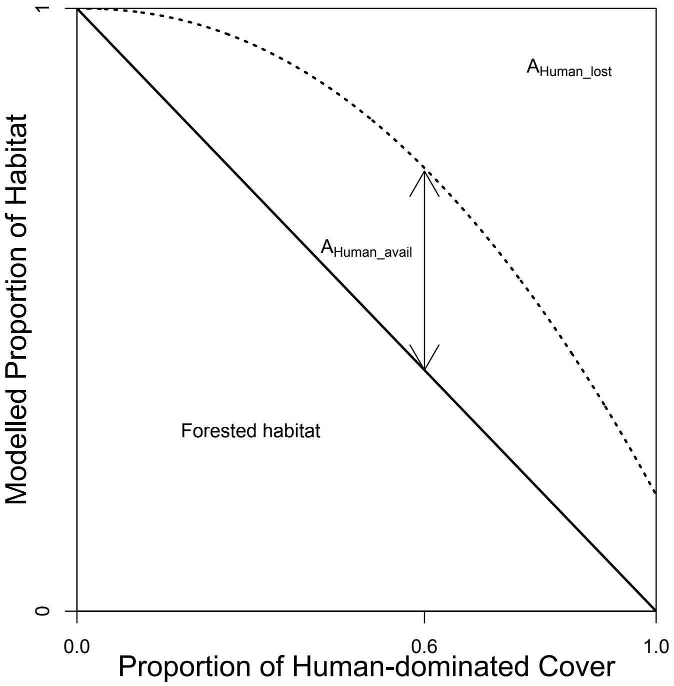

Figure 5b. Proportion of habitats modelled as function a gradient of human-dominated land cover. A_{Human_lost} is the empirically derived proportion of habitat that is lost for open-habitat bird species, and A_{Human_avail} is the modelled remaining of human-dominated landscapes that is available for bird species.

APPENDICES

Appendix A

Mathematical derivation of the Lost-habitat SAR model (LH-SAR).

Appendix B

List of the bird species names included in this study.

Appendix C

The empirical test of the Countryside Model.

Appendix D

The proportion of human-dominated land cover that is available for bird species explained by remote-sensed land cover types.

Appendix E

The effects of the two biomes (Laurentian Shield and Mixed-wood plains) on patterns of species richness.

Appendix F

The peaked relationship between total avian species richness and the proportion of natural land cover reconstructed by the sum of two derived species-area models.

Appendix A: The mathematical derivation of the Lost-Habitat SAR model (LH-SAR).

In contrast to earlier work, we posit that, as landscapes are converted to human-dominated land cover, a portion of the human-dominated area is “available” and part is “lost”. Lost areas could include buildings, paved areas, intensive agriculture, or other human infrastructure. Human-dominated available habitats could include recent cutovers, pastures and abandoned fields. Therefore, suppose that human-dominated cover (A_{human}) can be divided, to a first approximation, into two classes: available human-dominated (A_{Human_avail}) landscapes, which provides habitat for open-habitat species, and “unavailable human-dominated areas” (A_{Human_lost}) that is truly "lost" as avian habitat:

$$A_{Human} = A_{Human\_lost} + A_{Human\_avail} \qquad \text{(A.1)}$$

Since the proportion of A_{Human} in a landscape is one minus proportion of forested areas (A_{Forest}):

$$A_{human} = 1 - A_{Forest} \qquad \text{(A.2)}$$

Then the proportion of A_{Human_lost} would be:

$$A_{Human\_lost} = (1-A_{Forest}) - A_{Human\_avail} \qquad \text{(A.3)}$$

It seems reasonable to assume that, as the proportion of the landscape that is dominated by humans increases, the amount of human-dominated land cover that is inhospitable to birds would also increase. We hypothesize that A_{Human_lost} increases with human-dominated cover ($1-A_{Forest}$) following another power function:

$$A_{Human\_lost} = c' \, (1-A_{Forest})^{z'} \qquad \text{(A.4)}$$

where c' and z' are empirical constants.

If $z'=1$, then lost habitat is a constant proportion of the amount of human-dominated cover. If $z'>1$, then lost habitat is an increasing proportion of the human-dominated cover in landscapes with progressively more human-dominated cover. If $z'<1$, then lost habitat is a decreasing proportion of human-dominated cover in landscapes with progressively more human-dominated cover. Combining eq.(A.3) and (A.4) yields:

$$A_{Human\_avail} = (1- A_{Forest}) - c' (1- A_{Forest})^{z'} \tag{A.5}$$

Open-habitat species should respond to available open habitat (A_{Human_avail}) as according to a power relationship:

$$S_{open} = c\ (A_{Human\_avail})^{z} + d \log_{10} E \tag{A.6}$$

where c and z are derived constants and E is the log of sampling effort measured in hours. Combining eq.(A.5) and (A.6), we have the “lost habitat model”:

$$S_{open} = c((1- A_{Forest}) - c' (1- A_{Forest})^{z'})^{z} + d \log_{10} E \tag{A.7}$$

Therefore, we fitted eq. (A.7), the Lost-Habitat model, to open-habitat species richness as function of the amount of human-dominated landscape in each 100km^2. The constants c' and z were empirically derived from the data, d is a coefficient of the model. The disadvantage of this function is that non-linear functions with many free parameters can be impossible to fit. For example, we wanted to test whether the species pool (i.e. bird species obtained from course range maps) may contribute to explain the variance in species richness in each BBA quadrats once richness varies as a function of abiotic factors (e.g. Temperature). However, when we included the number of species in the species pool as a covariate in the “lost habitat model” (eq. A.7), the models failed to converge.

Appendix B: List of common and scientific bird names included in the study.

Table B1. The common and scientific names for the Ontario breeding bird species included in this study. Species are grouped by land cover type where they are usually found, according to the Atlas of the Breeding Bird of Ontario (ABBO; Cadman et al., 2007).

English Name	**Scientific Name**	**Land Cover Species Type**
Acadian Flycatcher	*Empidonax virescens*	Forest
American Redstart	*Setophaga ruticilla*	Forest
American Woodcock	*Scolopax minor*	Forest
Bald Eagle	*Haliaeetus leucocephalus*	Forest
Baltimore Oriole	*Icterus galbula*	Forest
Black-and-white Warbler	*Mniotilta varia*	Forest
Bay-breasted Warbler	*Dendroica castanea*	Forest
Black-backed Woodpecker	*Picoides arcticus*	Forest
Barred Owl	*Strix varia*	Forest
Blue-gray Gnatcatcher	*Polioptila caerulea*	Forest
Blackburnian Warbler	*Dendroica fusca*	Forest
Boreal Chickadee	*Poecile hudsonica*	Forest
Brown Creeper	*Certhia americana*	Forest
Black-throated Blue Warbler	*Dendroica caerulescens*	Forest
Black-throated Green Warbler	*Dendroica virens*	Forest
Broad-winged Hawk	*Buteo platypterus*	Forest
Canada Warbler	*Wilsonia canadensis*	Forest
Cerulean Warbler	*Dendroica cerulea*	Forest
Chipping Sparrow	*Spizella passerina*	Forest
Cape May Warbler	*Dendroica tigrina*	Forest
Cooper's Hawk	*Accipiter cooperii*	Forest
Common Merganser	*Mergus merganser*	Forest
Common Raven	*Corvus corax*	Forest
Common Tern	*Sterna hirundo*	Forest
Downy Woodpecker	*Picoides pubescens*	Forest
Eastern Screech-Owl	*Megascops asio*	Forest

Table B1. Continued…

English Name	**Scientific Name**	**Land Cover Species Type**
Eastern Wood-Pewee	*Contopus virens*	Forest
Evening Grosbeak	*Hesperiphona vespertina*	Forest
Great Blue Heron	*Ardea herodias*	Forest
Great Crested Flycatcher	*Myiarchus crinitus*	Forest
Golden-crowned Kinglet	*Regulus satrapa*	Forest
Great Horned Owl	*Bubo virginianus*	Forest
Gray Jay	*Perisoreus canadensis*	Forest
Green Heron	*Butorides virescens*	Forest
Green-winged Teal	*Anas crecca*	Forest
Hairy Woodpecker	*Picoides villosus*	Forest
Hermit Thrush	*Catharus guttatus*	Forest
Hooded Merganser	*Lophodytes cucullatus*	Forest
Hooded Warbler	*Wilsonia citrina*	Forest
Least Flycatcher	*Empidonax minimus*	Forest
Long-eared Owl	*Asio otus*	Forest
Louisiana Waterthrush	*Seiurus motacilla*	Forest
Magnolia Warbler	*Dendroica magnolia*	Forest
Merlin	*Falco columbarius*	Forest
Mourning Warbler	*Oporornis philadelphia*	Forest
Nashville Warbler	*Vermivora ruficapilla*	Forest
Northern Flicker	*Colaptes auratus*	Forest
Northern Goshawk	*Accipiter gentilis*	Forest
Northern Parula	*Parula americana*	Forest
Northern Waterthrush	*Seiurus noveboracensis*	Forest
Northern Saw-whet Owl	*Aegolius acadicus*	Forest
Orchard Oriole	*Icterus spurius*	Forest
Olive-sided Flycatcher	*Contopus cooperi*	Forest
Ovenbird	*Seiurus aurocapilla*	Forest
Pied-billed Grebe	*Podilymbus podiceps*	Forest
Philadelphia Vireo	*Vireo philadelphicus*	Forest
Pine Siskin	*Carduelis pinus*	Forest
Pine Warbler	*Dendroica pinus*	Forest
Pileated Woodpecker	*Dryocopus pileatus*	Forest
Purple Finch	*Carpodacus purpureus*	Forest
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Forest
Red-breasted Nuthatch	*Sitta canadensis*	Forest
Red-bellied Woodpecker	*Melanerpes carolinus*	Forest
Ruby-crowned Kinglet	*Regulus calendula*	Forest

Table B1. Continued…

English Name	**Scientific Name**	**Land Cover Species Type**
Red Crossbill	*Loxia curvirostra*	Forest
Red-eyed Vireo	*Vireo olivaceus*	Forest
Red-headed Woodpecker	*Melanerpes erythrocephalus*	Forest
Red-shouldered Hawk	*Buteo lineatus*	Forest
Ruby-throated Hummingbird	*Archilochus colubris*	Forest
Ruffed Grouse	*Bonasa umbellus*	Forest
Scarlet Tanager	*Piranga olivacea*	Forest
Spruce Grouse	*Falcipennis canadensis*	Forest
Sharp-shinned Hawk	*Accipiter striatus*	Forest
Swainson's Thrush	*Catharus ustulatus*	Forest
Tennessee Warbler	*Vermivora peregrina*	Forest
Tufted Titmouse	*Baeolophus bicolor*	Forest
Veery	*Catharus fuscescens*	Forest
Warbling Vireo	*Vireo gilvus*	Forest
White-breasted Nuthatch	*Sitta carolinensis*	Forest
Wild Turkey	*Meleagris gallopavo*	Forest
Winter Wren	*Troglodytes troglodytes*	Forest
Wood Duck	*Aix sponsa*	Forest
Wood Thrush	*Catharus mustelinus*	Forest
Whip-poor-will	*Caprimulgus vociferus*	Forest
White-winged Crossbill	*Loxia leucoptera*	Forest
Yellow-bellied Flycatcher	*Empidonax flaviventris*	Forest
Yellow-bellied Sapsucker	*Sphyrapicus varius*	Forest
Yellow-rumped Warbler	*Dendroica coronata*	Forest
Yellow-throated Vireo	*Vireo flavifrons*	Forest
American Black Duck	*Anas rubripes*	Open Habitat
Alder Flycatcher	*Empidonax alnorum*	Open Habitat
American Bittern	*Botaurus lentiginosus*	Open Habitat
American Coot	*Fulica americana*	Open Habitat
American Crow	*Corvus brachyrhynchos*	Open Habitat
American Goldfinch	*Carduelis tristis*	Open Habitat
American Kestrel	*Falco sparverius*	Open Habitat
American Robin	*Turdus migratorius*	Open Habitat
American Wigeon	*Anas americana*	Open Habitat
Bank Swallow	*Riparia riparia*	Open Habitat
Barn Swallow	*Hirundo rustica*	Open Habitat
Black-billed Cuckoo	*Coccyzus erythropthalmus*	Open Habitat
Black-capped Chickadee	*Poecile atricapillus*	Open Habitat

Table B1. Continued…

English Name	**Scientific Name**	**Land Cover Species Type**
Black-crowned Night-Heron	*Nycticorax nycticorax*	Open Habitat
Belted Kingfisher	*Megaceryle alcyon*	Open Habitat
Brown-headed Cowbird	*Molothrus ater*	Open Habitat
Blue Jay	*Cyanocitta cristata*	Open Habitat
Black Tern	*Chlidonias niger*	Open Habitat
Bobolink	*Dolichonyx oryzivorus*	Open Habitat
Brewer's Blackbird	*Euphagus cyanocephalus*	Open Habitat
Brown Thrasher	*Toxostoma rufum*	Open Habitat
Brewster's Warbler	*Hybrid*	Open Habitat
Bufflehead	*Bucephala albeola*	Open Habitat
Blue-winged Teal	*Anas discors*	Open Habitat
Blue-winged Warbler	*Vermivora pinus*	Open Habitat
Canada Goose	*Branta canadensis*	Open Habitat
Carolina Wren	*Thryothorus ludovicianus*	Open Habitat
Caspian Tern	*Sterna caspia*	Open Habitat
Clay-colored Sparrow	*Spizella pallida*	Open Habitat
Cedar Waxwing	*Bombycilla cedrorum*	Open Habitat
Chimney Swift	*Chaetura pelagica*	Open Habitat
Cliff Swallow	*Petrochelidon pyrrhonota*	Open Habitat
Common Goldeneye	*Bucephala clangula*	Open Habitat
Common Grackle	*Quiscalus quiscula*	Open Habitat
Common Loon	*Gavia immer*	Open Habitat
Common Moorhen	*Gallinula chloropus*	Open Habitat
Common Nighthawk	*Chordeiles minor*	Open Habitat
Wilson's Snipe	*Gallinago delicata*	Open Habitat
Common Yellowthroat	*Geothlypis trichas*	Open Habitat
Chestnut-sided Warbler	*Dendroica pensylvanica*	Open Habitat
Double-crested Cormorant	*Phalacrocorax auritus*	Open Habitat
Dark-eyed Junco	*Junco hyemalis*	Open Habitat
Eastern Bluebird	*Sialia sialis*	Open Habitat
Eastern Kingbird	*Tyrannus tyrannus*	Open Habitat
Eastern Meadowlark	*Sturnella magna*	Open Habitat
Eastern Phoebe	*Sayornis phoebe*	Open Habitat
European Starling	*Sturnus vulgaris*	Open Habitat
Field Sparrow	*Spizella pusilla*	Open Habitat
Gadwall	*Anas strepera*	Open Habitat
Gray Catbird	*Dumetella carolinensis*	Open Habitat
Great Egret	*Ardea alba*	Open Habitat

Table B1. Continued…

English Name	**Scientific Name**	**Land Cover Species Type**
Gray Partridge	*Perdix perdix*	Open Habitat
Grasshopper Sparrow	*Ammodramus savannarum*	Open Habitat
Golden-winged Warbler	*Vermivora chrysoptera*	Open Habitat
Herring Gull	*Larus argentatus*	Open Habitat
House Finch	*Carpodacus mexicanus*	Open Habitat
Horned Lark	*Eremophila alpestris*	Open Habitat
House Sparrow	*Passer domesticus*	Open Habitat
House Wren	*Troglodytes aedon*	Open Habitat
Indigo Bunting	*Passerina cyanea*	Open Habitat
Killdeer	*Charadrius vociferus*	Open Habitat
Le Conte's Sparrow	*Ammodramus leconteii*	Open Habitat
Least Bittern	*Ixobrychus exilis*	Open Habitat
Lesser Scaup	*Aythya affinis*	Open Habitat
Lincoln's Sparrow	*Melospiza lincolnii*	Open Habitat
Loggerhead Shrike	*Lanius ludovicianus*	Open Habitat
Mallard	*Anas platyrhynchos*	Open Habitat
Marsh Wren	*Cistothorus palustris*	Open Habitat
Mourning Dove	*Zenaida macroura*	Open Habitat
Mute Swan	*Cygnus olor*	Open Habitat
Northern Bobwhite	*Colinus virginianus*	Open Habitat
Northern Cardinal	*Cardinalis cardinalis*	Open Habitat
Northern Harrier	*Circus cyaneus*	Open Habitat
Northern Mockingbird	*Mimus polyglottos*	Open Habitat
Northern Pintail	*Anas acuta*	Open Habitat
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	Open Habitat
Northern Shoveler	*Anas clypeata*	Open Habitat
Osprey	*Pandion haliaetus*	Open Habitat
Peregrine Falcon	*Falco peregrinus*	Open Habitat
Prairie Warbler	*Dendroica discolor*	Open Habitat
Purple Martin	*Progne subis*	Open Habitat
Ring-billed Gull	*Larus delawarensis*	Open Habitat
Red-breasted Merganser	*Mergus serrator*	Open Habitat
Ring-necked Pheasant	*Phasianus colchicus*	Open Habitat
Ring-necked Duck	*Aythya collaris*	Open Habitat
Rock Pigeon	*Columba livia*	Open Habitat
Red-tailed Hawk	*Buteo jamaicensis*	Open Habitat

Table B1. Continued…

English Name	**Scientific Name**	**Land Cover Species Type**
Rusty Blackbird	*Euphagus carolinus*	Open Habitat
Ruddy Duck	*Oxyura jamaicensis*	Open Habitat
Red-winged Blackbird	*Agelaius phoeniceus*	Open Habitat
Sandhill Crane	*Grus canadensis*	Open Habitat
Savannah Sparrow	*Passerculus sandwichensis*	Open Habitat
Short-eared Owl	*Asio flammeus*	Open Habitat
Sedge Wren	*Cistothorus platensis*	Open Habitat
Sora	*Porzana carolina*	Open Habitat
Solitary Sandpiper	*Tringa solitaria*	Open Habitat
Song Sparrow	*Melospiza melodia*	Open Habitat
Spotted Sandpiper	*Tringa macularia*	Open Habitat
Swamp Sparrow	*Melospiza georgiana*	Open Habitat
Tree Swallow	*Tachycineta bicolor*	Open Habitat
Trumpeter Swan	*Cygnus buccinator*	Open Habitat
Turkey Vulture	*Cathartes aura*	Open Habitat
Upland Sandpiper	*Bartramia longicauda*	Open Habitat
Vesper Sparrow	*Pooecetes gramineus*	Open Habitat
Virginia Rail	*Rallus limicola*	Open Habitat
Western Meadowlark	*Sturnella neglecta*	Open Habitat
Willow Flycatcher	*Empidonax traillii*	Open Habitat
Wilson's Phalarope	*Steganopus tricolor*	Open Habitat
Wilson's Warbler	*Wilsonia pusilla*	Open Habitat
White-throated Sparrow	*Zonotrichia albicollis*	Open Habitat
Yellow-breasted Chat	*Icteria virens*	Open Habitat
Yellow-billed Cuckoo	*Coccyzus americanus*	Open Habitat
Yellow Warbler	*Dendroica petechia*	Open Habitat

Appendix C: Countryside model

The Countryside model (Pereira & Daily, 2006b) is a species-area model proposed to account for variation in species richness among human-dominated landscapes. In essence, the model proposes that landscapes are composed of multiple habitats, and that species assemblages in those landscapes are composed of multiple guilds. Guilds show differing degrees of affinity for different habitat types. Species richness of a given guild *i* varies as a power function of the sum of affinity *h* of the guild for each habitat type *j*, times the area of that habitat *Aj*:

$$S_i = c_i\left(\sum_j h_{ij}A_j\right)^z \tag{C.1}$$

where c_i and z are empirical constants. Total richness S_{Total} is the sum of the richness of all guilds:

$$S_{Tot} = \sum_i S_i \tag{C.2}$$

The model has been validated in agricultural landscapes with birds (Guilherme & Miguel Pereira, 2013) and plants (Proença & Pereira, 2013).

In our study, we proposed that total richness is composed of two general guilds – forest birds and open-habitat birds – which respond to two habitat types: forest, and human-dominated land cover.

We fitted the countryside model (eq. C.1) to the richness of these two guilds, allowing *z* and two *h* constants (i.e., the affinities for each habitat) to be free parameters. We also included a term to account for variation in the logarithm of sampling effort among quadrats. The resulting fitted model yielded parameter estimates that reduce to Classic-SARs (Table C1): for each guild, the affinity for the non-preferred habitat type is essentially 0. Therefore richness in each guild is a Classic-SAR, a power function of the area of the preferred habitat (i.e. the SAR curves shown in Figures 2 and 3 in the main text). The countryside model in this case becomes identical to the model of Desrochers et al. (2011). The countryside model (and the Desrochers model) predicts a peaked relationship between total species richness and forest cover. However, these two models fail to predict the peaked relationship between richness of open-habitat birds and forested (or human-dominated) land cover.

The difference between our approach and the countryside model is the exclusion of unavailable habitat – “lost” area - from human-dominated areas. We assume that such lost area increases as a power function of the proportion of human-dominated areas in each 100km^2.

Table C1. Nonlinear regression results from the fitted countryside model for total, forest and open-habitat species richness in 100km^2 quadrats localized in southern Ontario. $h_{o,F}$ is the habitat affinity of open-habitat birds to forest cover; $h_{o,HD}$ is the habitat affinity of open-habitat birds to human-dominated landscapes; $h_{f,\mathrm{F}}$ is the habitat affinity of forest birds to forest area; $h_{f, HD}$ is the habitat affinity of forest birds to human-dominated area; c and z and d are empirical constants. Total richness model constants, c and z, were obtained by fitting the model using the habitat affinities from forest and open-habitat models. d is the coefficient of an additive term accounting for the logarithm of the number of hours spent censusing each quadrat. *RSS* is the residual sum of the squares from the nonlinear regression; *AICc* is the corrected Akaike information criterion; and R^2_{adj} is the adjusted R^2.

	c	$h_{o,F}$	$h_{o,HD}$	$h_{f,F}$	$h_{f,HD}$	z	d	RSS	AICc	$\mathrm{R}^2_{\mathrm{adj}}$
Forest birds	27.77			1.67	0.001	0.37	11.12	38,878	6452	0.60
Open-habitat birds	33.15	0.000	0.867			0.17	14.57	78,132	7146	0.53
Total Richness	38.90	0.000	0.867	1.67	0.001	0.340	30.46	200,276	8081	0.28

Appendix D. The proportion of human-dominated land cover that is available for bird species explained by remote-sensed land cover types.

Our analysis showed that there is an important amount of habitat that is available to open-habitat bird species in a landscape of 100km^2 in southern Ontario. The available habitat is positively correlated with the amount of remotely sensed land cover in all human-dominated classes (Table D1). Cropland land cover, which corresponds to 34% of the total land cover in southern Ontario and to 76% of the human-dominated land cover, is the main contributor to the availability of human-dominated habitat used by bird species (see Beta-coefficients, Table D1). The amount of cropland in each BBA quadrat is responsible for 45% of the variability found in the proportion of habitat that is available for birds (linear regression, F = 820.6, R^2_{adj}= 0.45, p<0.0001). However, the relationship between human-dominated habitat that is available and cropland amount is peaked (Fig. D1).

Table D1. The results of a multiple regression predicting the proportion of human-dominated habitat (A_{human_avail}) that is available for bird species in 100km^2 quadrants southern Ontario (estimated empirically from the species richness of open-habitat birds) as a function of the amount of remotely-sensed land cover in various categories (R^2=0.85, n=991 squares). All coefficients are statistically significant, p<0.0001.

A_{human_avail} categories	Coefficients	Beta-coefficients	t-value
Recent cutovers	0.64	0.14	11.00
Mining tailings	0.49	0.24	19.62
Urban Areas	0.14	0.09	7.44
Pasture and fields	0.87	0.63	50.00
Croplands	0.25	0.75	57.5

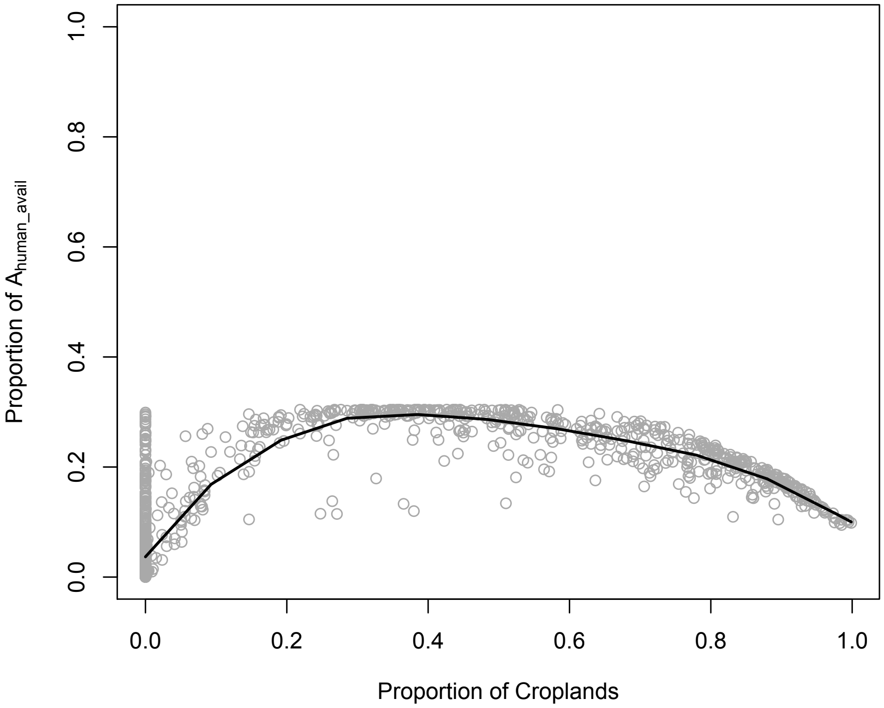

Figure D1. The peaked relationship between the proportions of habitat that is available for avian species and human-dominated (A_{human}) land cover that is composed by crops fitted with a lowess smoothing line.

Appendix E: Avian species richness across biomes in southern Ontario.

In the main text, we hypothesized that the peaked relationship between total richness and forest cover is due the amount of habitat that is available for bird species in human-dominated areas. In this supplementary material we ask: might the peaked shape of the richness-forest-cover relationship be the result of combining data from two biomes? To answer this question, we present the relationships between total avian species richness and the proportion of natural land cover (forest) in the Mixed-wood Plains and the Laurentian (boreal) Shield biomes separately (Fig. E1). The classification of the biomes follows the map distribution of the cited biomes in Cadman et al., 2007 (Fig. E2).

Total species richness has a peaked relationship with natural land cover in quadrats located on the Laurentian Shield (open circles, Fig. E1). However, richness increases monotonically with forest cover in the (mixed-wood) quadrats off the Shield. The monotonic positive relationship between total avian richness and natural forest cover in the Mixed-wood Plains biome may simply be a sampling artifact. There are very few quadrats in the Mixed-wood Plains covered by a high proportion of forest. Those quadrats are often surrounded by agriculture. The forest in those quadrats is almost certainly fragmented by roads, houses, etc, at a scale too small to be detected in remote sensing. Consequently, a fully-forested quadrat in the south is likely to contain small patches of habitat for open-habitat species (and therefore to have higher than usual species richness). In contrast, forested quadrats on the Laurentian Shield are typically within large tracts of continuous forest, with much less fine-scale human intrusion, and less fine-grained habitat for open-habitat species.

We cannot totally exclude the possibility that combining richness-area relationships in two biomes may have affected the peaked pattern observed between richness and forest cover in southern Ontario. The poor representation of quadrats with high forest cover in the Mixed-wood Plains data may bias the shape of the relationship at low percentages of forest cover. In contrast, fully forested quadrats are abundant on the Laurentian Shield. There, the peaked pattern of richness-area relationship emerges, as in the total data set.

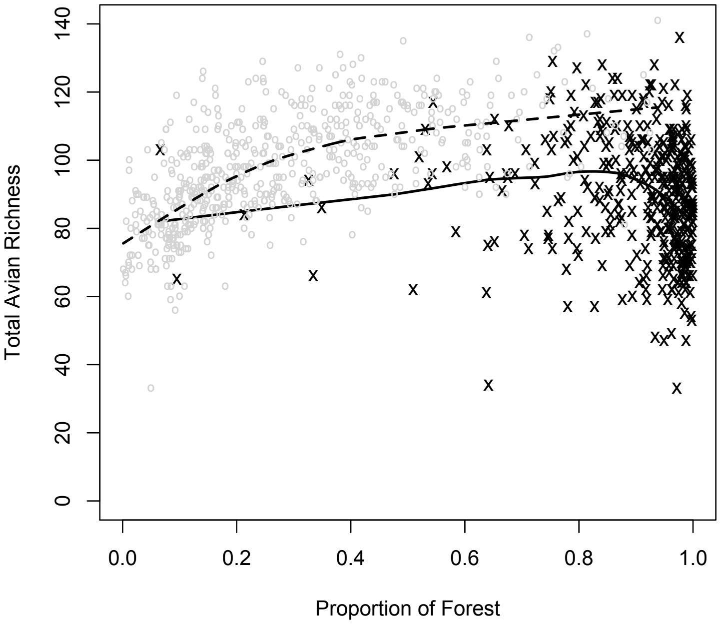

Figure E1. The relationships between total avian species richness and the proportion of forested land cover in both Mixed-wood plains and Laurentian Shield biomes. Empty circles represent the BBA squares located on Mixed-wood plains. The “x” dots represent the squares on Laurentian Shield biome. The black lines are the LOESS curve for both relationships.

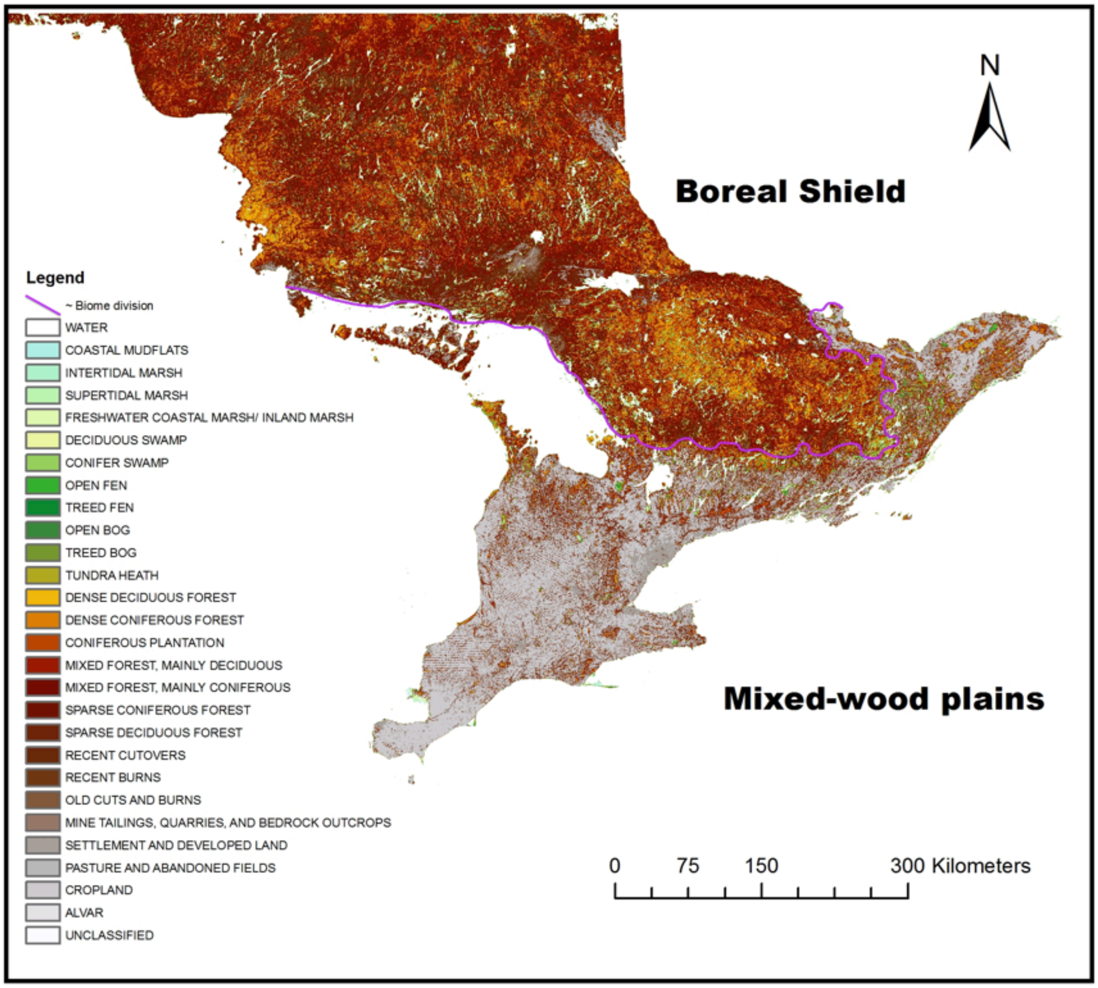

Figure E2. Laurentian Boreal Shield and Mixed-wood plains biomes represented in southern Ontario, Canada. Map source: Ontario Provincial-Scale Land Cover data set produced by the Ontario Ministry of Natural Resources (2002) from Landsat ThematicMapper (TM) scenes captured primarily in the 1990s (resampled to a 25-m resolution).

Appendix F. The peaked relationship between total avian species richness and the proportion of natural land cover reconstructed by the sum of two derived species-area models.

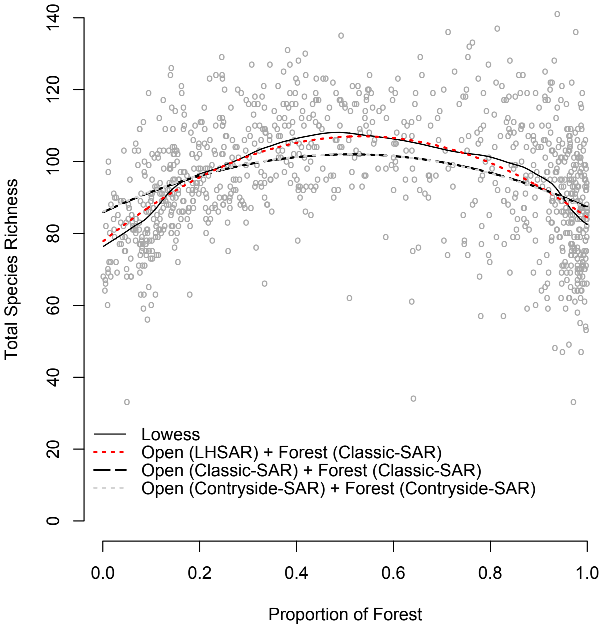

Figure F1. The pattern of total avian richness as function of forest cover reconstructed with different multi-habitat models approaches. Open circles represent observed total richness in 991 quadrats in southern Ontario (solid line, LOWESS curve). Open models represent open-habitat richness modeled as a function of human-dominated landscapes, and forest models fit forest richness as function of forest cover. Dotted-line: the sum of the best-fitting species-area relationships for open-habitat species richness (LH-SAR) and forest species richness (Classic-SAR). Long-dashed line represent the sum of two Classic-SAR models (Desrochers et al. 2011) fitted for open-habitat and forest richness. The sum of the two Countryside-SARs also predicts total richness as the sum of two Classic-SARs (dotted grey line over the long-dashed line). Model parameters and statistics are presented in the main text (Table 1).

CHAPTER 2

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TITLE

Birds respond to habitat loss at the landscape-level, but not much to fragmentation.

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ABSTRACT

Aim: It is usually thought that habitat fragmentation acts negatively on species survival, and consequently, on biodiversity. Recent literature challenges whether habitat fragmentation *per se* affects species richness, beyond the effect of loss of habitat area. Theoretical studies have suggested that fragmentation may matter most when the amount of available habitat is small or at intermediate levels. However, a recent review suggests that the effect of fragmentation on species richness is usually positive. Here, we dissect the richness-fragmentation relationship. What is the effect size? Does it depend upon the amount of habitat cover? How do individual species react to fragmentation?

Methods: Applying a macroecological approach, we empirically related avian richness and the probability of occurrence (p_{occ}) of individual species to fragmentation (number of patches), after controlling for habitat amount in 991 landscapes, each 100-km^2, in southern Ontario, Canada.

Results: Species richness was strongly related to total habitat amount, but habitat fragmentation had no detectable additional effect. Individual species' p_{occ} related strongly to habitat amount. For some species, p_{occ} also related secondarily to habitat fragmentation within landscapes. Logistic models revealed that p_{occ} related *significantly negatively* to fragmentation after controlling for habitat amount for only ~13% of forest- and 18% of open-habitat species bird species. However, p_{occ} related *significantly positively* to fragmentation for even greater proportions of species, including some red-listed species. Fragmentation effects were not stronger at low or intermediate levels of habitat amount within landscapes.

Conclusion: In earlier studies, negative effects of isolation were observed *at the patch level* in experimental manipulations. However, *at the landscape level*, avian species richness in Southern Ontario apparently responds primarily to habitat amount, and negligibly to fragmentation. We argue that the evidence is inconsistent with the hypothesis that reducing habitat fragmentation *per se* would be an effective conservation strategy for birds at the landscape level.

KEYWORDS

Habitat-amount-hypothesis, habitat fragmentation hypothesis, extinction threshold hypothesis, bird species richness, species' probability of occurrence, southern Ontario, forest cover, human-dominated land cover.

INTRODUCTION

The habitat fragmentation literature currently has a polarized discussion on the independent effects of habitat fragmentation and of habitat amount on species richness and species' probability of occurrence (Fahrig, 2017, Haddad et al., 2017, Fahrig, 2013). On one side, there is the widespread view that fragmentation of natural habitat creates small, isolated patches, which decreases the probability of survival of individual species, and thereby decreases biodiversity (Wilcox & Murphy, 1985; Andrén, 1994; Hanski, 1998, 2011). Following MacArthur & Wilson's (1967) theory of island biogeography, this view accumulated much empirical and theoretical support from studies in which the units of analysis were individual patches. Experimental studies at the patch-scale (e.g. square meters to hundreds of square meters) showed that the spatial configuration of habitats can negatively affect plant diversity (Quinn & Robinson, 1987), the stability of predator-prey interactions (Kareiva, 1987), parasitism (Kruess & Tscharntke, 1994), pollination (Groom, 1998), and the dispersal and demography of mammals (Dooley & Bowers 1998). Consequently, habitat fragmentation and its effect on biodiversity attract attention from ecologists and conservationists alike (e.g. see the Fragmentation special issue of *Ecography*, January 2017, Volume 40, Issue 1, Pages 1 – 237).

In contrast, studies at the landscape-scale have shown that the slope of the relationship between biological variables (i.e. richness, abundance, probability of occurrence) and habitat fragmentation can be either positive or negative (Trzcinski et al., 1999; Fahrig, 2003, 2013; Mortelliti et al., 2010; Smith et al., 2011; Reino et al., 2013; Rueda et al., 2013; Haddad et al., 2017). The SLOSS (**S**ingle **L**arge **O**r **S**everal **S**mall) debate (Diamond, 1975), which focused on richness in sets of parks (habitat patches), illustrated the uncertainty of landscape-level response to habitat fragmentation. Fahrig (2013) argued that, at the landscape level, species respond primarily to the total habitat amount, which captures both the effects of habitat patch size and isolation. Therefore, habitat amount can replace patch size and isolation (i.e. the "habitat amount hypothesis", Fahrig, 2013). Moreover, when fragmentation effects are detectable, they are more often positive than negative (Fahrig, 2017).

The importance of fragmentation may depend upon the total habitat amount in a landscape. Metapopulation models (Hanski, 1998) suggest that fragmentation is particularly important when habitat fragments are small enough to reduce the viability of the local populations they contain, which occurs when the total amount of habitat in the landscape is below 20-30% (the "fragmentation threshold hypothesis": (Andrén 1994; Pardini et al., 2010; Swift & Hannon, 2010; Martensen et al., 2012). In contrast, Villard & Metzger (2014) argued that fragmentation effects should be most apparent at intermediate amounts of habitat, where fragmentation potentially has the greatest variability, and the collinearity between habitat amount and fragmentation measurements is smallest (see also Pardini et al., 2010). Interestingly, at the landscape level, but at rather small scale, With (2016) found predominantly positive effects of fragmentation at low habitat amount.

Here, we tested predictions of the habitat amount hypothesis (versus habitat amount + habitat fragmentation) and the fragmentation threshold hypotheses. We specifically addressed the following predictions: 1) after controlling for total habitat amount, biotic responses are unrelated to measures of fragmentation, and 2) fragmentation effects are stronger when habitat amount is low or at intermediate level within a given landscape. We test these predictions using breeding birds in 991 landscapes, each 100 km^2, across a ~750 km x 250 km swath of southern Ontario, Canada. We chose this spatial grain because it is a scale at which management of biodiversity generally occurs (Desrochers et al. 2011).

METHODS

Predictors: Habitat amount and fragmentation metrics

We utilized the proportions of *forest* and *human-dominated* land covers as first proxy of habitats for *forest-* and *open-habitat-* bird species (description below), respectively, in 991 landscapes, 100-km^2 each, in southern Ontario, Canada (Fig. S1-1, Appendix S1). Remote-sensed land cover was obtained from Landsat 7 Thematic Mapper (https://landsat.gsfc.nasa.gov/the-thematic-mapper/) scenes captured primarily in the 1990s (resampled to a 30-m resolution), classified into 28 land cover classes. Details about the *landscapes and habitat quality* can be found in Appendix S1.

We used the number of patches of these two cover types within each landscape (100-km^2) as our measure of fragmentation. We used the number of *forest patches* for forest birds, and the number of *human-dominated land cover patches* for open-habitat birds. Villard & Metzger (2014) suggested that the number of patches per landscape is independent of habitat amount at intermediate values of habitat amount, offering an opportunity to separate the separate effects of the two (Fig. 1). The spatial configuration and isolation of the habitat remaining within landscapes are strongly correlated with number of patches. The analyses we present below do not distinguish between the former; however, we also considered other fragmentation measurements (e.g., average patch size and edge-density) in our statistical analysis (see section "*Tests of other fragmentation measurements*", in Appendix S1). The qualitative conclusions did not depend upon the fragmentation metric.

Species richness of functional groups

We evaluated how both avian *species richness* and individual bird *species' probability of occurrence* vary as functions of the landscape metrics habitat amount and fragmentation. Bird species' presences and absences in each100-km2 UTM landscapes in southern Ontario are reported in the *Atlas of the Breeding Birds of Ontario* (hereafter ABBO: Cadman et al. 2007, see details of the "Bird distribution data" in Appendix S1).

Testing predictions regarding the effects of fragmentation beyond that of habitat amount rests on an appropriate definition of habitat. The most common approach is to link species to their published local habitat use. However, species-habitat affiliations depend upon scale. A species such as the Sandhill Crane (*Grus canadensis*) forages in patches of open habitat (grasslands and wetlands (Cadman et al. 2007) that occur in primarily forested landscapes with little human disturbance (Currie, pers. obs.). Thus, the Sandhill Crane is an "open-habitat species" at the patch scale, but a "forest species" at the landscape scale.

In this landscape-level study, we empirically defined two functional groups of bird species at the landscape scale: "forest" and "open-habitat". To assign each species to one of these groups, we fitted a logistic regression of presence/absence as a function of forested land cover. We considered a species to be absent from a 100-km^2 landscape only if that landscape fell within 20 km of a landscape where the species was present. Otherwise, the landscape was excluded from analysis for that species, since the landscape may simply be out of the species' range due to factors other than land cover. Thus, our analyses focus on occupied landscapes and neighbouring unoccupied landscapes.

Among the initial 202 bird species, the probability of occurrence of 69 species (including the Sandhill Crane) increased as monotonic positive functions of forest cover. These were classified as forest species. Seventy-nine species responded negatively to forest cover, and were classified as open-habitat species (i.e., n=148 species retained for analyses, Table S2-1, *Appendix S2*). We tallied species richness for these two functional groups in each landscape. Presence/absence of the remaining 54 remaining species was either independent, or a peaked function, of forest amount and habitat fragmentation. Therefore, we did not consider these species as a group, since the distinction between habitat and non-habitat for them is unclear, and their response to fragmentation is irrelevant. We have also ran our analyses with a group of species empirically defined as fragmentation-sensitive. Finally, we repeated our analyses species defined as “forest” and “open-habitat” according to their local habitat use, as defined in published sources (e.g., Cadman et al, 2007); see Appendix S2).

Probability of occurrence of individual species

Using logistic regressions, we tested whether individual species’ probability of occurrence in a landscape depend upon fragmentation (number of patches), in addition to total habitat amount. For this analysis, we eliminated species that occurred in <10% or >90% of the landscapes in the study area (i.e. very rare or nearly ubiquitous species), because the probability of occurrence of these species is nearly invariant among landscapes (Jiménez-Valverde et al., 2008). We carried out this analysis for the 58 forest and 61 open-habitat species.

Other variables: confounding factors

The number of species present within a landscape presumably depends upon the size of the regional species pool, i.e., the number of species whose range limits overlap the study area. Therefore, we extracted breeding ranges from range maps of BirdLife International http://www.birdlife.org/, accessed in May 2016), and we tallied the number of bird species (among the 148 bird species retained for analysis) whose geographic ranges overlap each landscape. We defined this as the landscape’s species pool. Richness may also be influenced by sampling effort. Therefore, we used the number of species in the species pool and the log-transformed number of observer hours in each ABBO landscape as covariates in the regression models.

Statistical Analyses

Habitat amount hypothesis: species richness

The habitat amount hypothesis states that species richness is independent of the size and isolation of habitat patches, after accounting for the amount of habitat available in the landscape (Fahrig, 2013). The competing hypothesis, which we will call the "habitat fragmentation hypothesis", proposes that fragmentation has an independent, *negative* effect on richness. We tested these hypotheses by fitting an Ordinary Least Squares model (OLS) for the two species groups, forest- and open-habitat birds, in 991 landscapes:

$$SR_i = c_0 + c_1A_i + c_2A_i^2 + c_3N_i + c_4P_i + c_5\log E \qquad (1)$$

where SR_i is species richness in guild *i* (i.e. forest species, open-habitat species, fragmentation-sensitive species), A is habitat area of guild *i*, N_i is the number of patches of habitat type *i*, P_i is the species pool of guild *i*, E is the number of observer hours, and c_0 to c_5 are regression coefficients. We included a quadratic term for habitat area because richness typically increases as a decelerating function of habitat area (Tjørve, 2003). We tested whether the outcome of this model depends on whether species were classified according to local habitat affiliation versus landscape affiliation. We also ran models controlling for spatial autocorrelation (See section "*Extra Statistical Analyses",* Appendix S1).

Tests of the fragmentation threshold hypothesis using species richness

We further tested whether the effect of fragmentation depends upon the total amount of habitat in the landscape. First, in the model cited above, we included an interaction term between land cover amount and fragmentation to test whether the strength of fragmentation effects depends upon habitat amount, as proposed by Hanski (2015 and references therein), Villard & Metzger (2014) and others.

We repeated the analysis using the subset of the data that included landscapes with amounts of habitat (i.e., forest cover for forest birds, or human-dominated cover for open-habitat birds) below 30%, as proposed by Andrén (1994) (Fig. 1a). To test the sensitivity of the 30% threshold, we also fitted piecewise regression models, allowing the threshold to be a free parameter in the model. Finally, following Villard & Metzger (2014), we also repeated the analyses while restricting the data to *intermediate* amounts of habitat, where the collinearity between habitat amount and fragmentation is the lowest, and the variance of fragmentation is high (Fig. 1).

Tests of the habitat amount hypothesis and fragmentation threshold on individual species' probability of occurrence

For each individual species, we modelled probability of occurrence (p_{occ}) within 100-km^2 landscapes as a logistic function of habitat amount (forest or human-dominated land cover), fragmentation (number of patches), log-transformed effort, and species pool. We then tallied the frequencies of significant positive and negative functions of the number of patches (fragmentation), as well as strength of these relationships measured by the pseudo-r^2 (Nagelkerke R^2) obtained from the fitted models. Nagelkerke represents the likelihood of the models, but it does not reflect the amount of variance that is explained in the response variable, which is characteristic of r-squares from OLS models.

To address the predictions of the fragmentation threshold hypothesis, we included an interaction term between habitat amount and number of patches in the logistic models cited above. We also repeated the statistical analysis with subsets of the database (see Fig. 1).

RESULTS

Avian species richness: habitat amount hypothesis

As earlier studies observed (De Camargo & Currie, 2015), avian richness in both forest and open-habitat species groups (groups defined empirically at the landscape level) increases with the amount of habitat within landscapes (uncorrected for any other variables: Fig. 2a and 2c). However, the relationship with fragmentation, uncorrected for any other variables, is not straight-forward. Forest species richness has a ⊃ shaped relationship with the number of forest patches (Fig. 2b), whereas open-habitat species richness has a peaked relationship (Fig. 2d). Richness is less strongly related to other measures of habitat fragmentation (Tables S1-1,2, *Appendix S1*). The richness of fragmentation-sensitive species (also defined empirically at the landscape level) is also strongly related to forest amount and *not* statistically related to number of patches (Table S1-3, Fig. S1-2e-f, *Appendix S1*).

In multiple regression models, both forest- and open-habitat species richness relate positively to total habitat amount, but neither one relates significantly to number of patches after controlling for total habitat amount, effort and species pool (Table 1). The results do not depend upon whether species were classified to guilds based on their local habitat affiliation, or their landscape level affiliation (cf. Table 1 and *Appendix S1,* Table S1-3). The same multiple regressions fitted with edge-density instead of number of patches showed fragmentation marginally statistically significant (Table S1-2, Appendix S1); however, its effect size is tiny. These results are consistent with the habitat amount hypothesis. We also fitted non-linear regressions with sampling effort corrected as proposed by Link & Sauer (1999); this also did not qualitatively alter the conclusions of the analysis (Table S1-4, *Appendix S1*). Models correcting for spatial autocorrelation explained slightly more variance in richness and had lower AIC values (Table S1-5, *Appendix S1*). However, once again, richness was related most strongly to habitat amount and was independent of any additional effect of fragmentation.

Avian species richness: fragmentation threshold hypothesis

Without any threshold (i.e. no data trimming, Fig. 1), the interaction between habitat amount and fragmentation on species richness is not statistically significant (Table S1-6, *Appendix S1*). Fragmentation effects do not depend linearly upon the amount of habitat cover.

Using data trimmed to ≤30% habitat cover within landscapes, simple linear relationships show showed that richness (forest- and open-habitat species) increases with both habitat amount and fragmentation (Fig. 3). Note that fragmentation is usually hypothesized to have a *negative* effect on richness at low habitat amounts. When the richness-fragmentation relationship is controlled for habitat amount, log-transformed effort and species pool, we did find a nearly significant ($p=0.053$) *negative* relationship for forest birds, but the effect size is very small: the number of patches increases explained variance by <1% (*Appendix S1,* Tables S1-7). For open-habitat species, there is a significantly ($p=0.031$) *positive* relationship between richness and number of patches, after controlling for total habitat amount (Table S1-7, *Appendix S1*). Empirically defined thresholds (break-point models) did not qualitatively alter the conclusions (Table S1-8, *Appendix S1*).

At intermediate levels of habitat amount, where total forest cover and the number of patches are uncorrelated, all relationships become weak or non-significant (Fig. S1-3, Table S1-9, *Appendix S1*). This is inconsistent with Villard & Metzger's (2014) suggestion that fragmentation should be strongest at intermediate amounts of habitat in the landscape.

Species' probability of occurrence (pocc): habitat amount hypothesis and fragmentation threshold hypothesis

Is it possible that individual species' $\underline{p_{occ}}$ is affected by fragmentation, even though this is not evident at the level of total species richness? Only a few species' p_{occ} show a significantly negative effect of fragmentation, after controlling for habitat area. Most species are either more likely to occur in landscapes with greater fragmentation, or their p_{occ} is independent of fragmentation (Fig 4a, b).

When data are constrained to less than 30% habitat cover, even fewer species'

p_{occ} relates significantly negatively to fragmentation (Fig. 4c, d). Using the subset of data with intermediate habitat amount yielded similar results (Fig. 4e, f). No difference was detected in the average likelihood of the logistic models grouped by species showing *significant* or *insignificant* p-values of the slope of number of patches (positive or negative) (Fig. S1-4, Appendix S1).

Four forest- and four open-habitat bird species in our dataset are classified as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). None of these species' p_{occ} was significantly negatively related to number of patches (Fig. 4, Appendix S1, Table S1-10). The only significant relationship was positive.

For a few individual bird species, the fragmentation effect was negative and stronger when habitat amount is low, as predicted by the fragmentation threshold hypothesis. The interaction term in the logistic models identified 5 out of 58 forest birds, and 5 out of 61 open-habitat species for which p_{occ} was significantly *negatively* related to the number of patches, with a significantly *positive* interaction term between land cover amount and fragmentation (Table S1-11, *Appendix 1*). The results for these species are consistent with the notion that the fragmentation effect is negative, and that its effect is stronger when habitat amount is low. For about 20% of species (13 in each group) the interaction term is positive (i.e., in the predicted direction by the fragmentation threshold hypothesis), but there was no detectable signal of the number of patches (Table S1-10, *Appendix 1*). For the majority of species, the interaction between habitat fragmentation and habitat amount was either non-significant, or significant in the wrong direction (*Appendix S1,* Table S1-10).

DISCUSSION

A large part of the conservation-oriented literature over the last half-century has been concerned with identifying negative effects of habitat fragmentation on species' ecology (Harrison & Bruna, 1999; Hanski, 2011; Fahrig, 2013, 2017). Fahrig's (2017) recent review found that, measured independently of habitat amount, the effects of habitat fragmentation at the landscape level are more frequently positive than negative. This contradicts the premise that habitat fragmentation is a threat to species diversity, a widespread view in the conservation literature. These findings have fostered a polarised discussion about the independent role of habitat fragmentation from habitat amount on shaping species' ecological responses (Fahrig, 2017, Haddad et al., 2017, Hanski, 2015, Fahrig, 2013). For example, Haddad et al. (2017) unequivocally reject the habitat amount hypothesis, based on three experimental studies.

Our study is distinct from most of those reviewed by Fahrig (2017) in that we examined the natural variation in species richness, and the probabilities of occurrence of each individual species of birds, among a very large number (n=991) of landscapes. Each landscape encompassed a natural mix of habitat patches and intervening matrix, and birds were censused across the entire landscape (versus within patches, or at discrete points, e.g. Smith et al. 2011). Haddad et al (2015) argue that, "Observational studies [such as the present study] have limited ability to isolate the effects of fragmentation from concomitant habitat loss and degradation per se (4, 7, 22)." We have shown here that, with high statistical power, our study could isolate fragmentation effects in two ways: statistically (in multiple regressions), and by selecting data subsets in which fragmentation is highly variable, but habitat loss is not (Fig. 1). Haddad et al (2015, 2017) further argue that their experiments "mimic anthropogenic fragmentation" (Haddad et al 2015, p. 4), but this is an assumption that is true in some respects (creation of patches) and clearly false in others (e.g., the landscape context in which patches occur). Instead of studying patch-level mimics of anthropogenic fragmentation, our macroecological approach examines landscapes in which anthropogenic fragmentation actually occurred.

We found that richness varies among landscapes in a manner *consistent* with Fahrig's habitat amount hypothesis, and mostly *inconsistent* with the notion that habitat fragmentation poses an extra threat to biodiversity, beyond that posed by habitat loss. The probability of occurrence of individual forest bird species more often related positively to habitat fragmentation than negatively. The frequency of species showing positive or negative relationship with fragmentation beyond habitat amount is similar to open-habitat species. The majority of the bird species show no detectable response to fragmentation. These findings reject the notion that fragmentation significant threatens species independently of total habitat loss.

Experimental studies suggest a reason why some studies are consistent with the habitat amount hypothesis while others are not. With (2015) and Haddad et al. (2017) created experimental landscapes with multiple habitat patches, and they examined the species-area relationship (SAR) using individual habitat patches as the sampling units.

Both studies observed lower richness in small patches, and a steeper slope of the SAR when patches are more isolated. However, these studies actually addressed the effect of patch isolation on patch richness, not the effect of landscape fragmentation on landscape richness. In both With (2015) and Haddad et al. (2017), the steeper SAR slope in fragmented landscapes indicates that species turnover among patches is greater when patches are more isolated. Thus, fragmentation in their experiment led to landscapes with more isolated patches with lower richness, but greater species turnover among patches within landscapes (see the intersecting curves in Fig. 2a in With 2015 and in Fig. 1b in Haddad et al., 2017). The latter effect off-sets the former. The relative magnitudes of the two effects in different systems may explain why Fahrig (2017) observed some positive, and some negative, landscape-level associations between richness and fragmentation. In very homogeneous areas, with little species turnover among patches, fragmentation should reduce landscape richness. However, if landscape fragmentation isolates potential competitors from one another and leads to different species dominating different patches (e.g., Diamond's 1975 "checkerboard distributions"), then fragmentation may increase effective habitat heterogeneity and landscape-level richness.

Distinguishing the effects of habitat fragmentation from habitat amount is a common theme in the literature (Fahrig, 2003; Ewers & Didham, 2006; Didham et al., 2012; Villard & Metzger, 2014; Hanski, 2015). To a degree, it is impossible to disentangle the two: fragmentation must be zero when habitat cover is 0% or 100%, and it must peak at intermediate coverage (Fig. 1). In practice, habitat loss nearly invariably results in fragmented forest cover. In a theoretical study, Didham, et al. (2012) proposed that models attempting to disentangle the variance explained by habitat loss and fragmentation should detect a large chunk of variance related to the interdependence between the two stressors, and small effects of both habitat loss and fragmentation independently (see Fig. 2d in Didham, et al. 2012). Our results are not consistent with their model. The variance explained by habitat amount is always larger than by fragmentation (Figs. S1-5,6). At high forest cover, richness varies little (Fig. 2). At intermediate forest cover, where cover and fragmentation are not collinear, richness is independent of fragmentation (Appendix S1, Fig. S1-3). At low forest cover, the effect of fragmentation is apparently positive (Fig. 3). Overall, our multiple regression models (Table 1) are consistent with previous studies suggesting that the amount of habitat is the primary driver of species' ecological responses, when tested independently of fragmentation (Trzcinski et al., 1999; Fahrig, 2003, 2013; Prugh et al., 2008; Mortelliti et al., 2010; Smith et al., 2011; Reino et al., 2013; Rueda et al., 2013). Habitat amount also better predicts bird species' probability of occurrence; few species lower p_{occ} as fragmentation increases, after controlling for the habitat amount considered within landscapes (Fig. 4).

Fragmentation's effect measured when intermediate to low habitat amount is left in the landscape.

The fragmentation threshold hypothesis argues that the effect of fragmentation on species richness, and potentially on species occurrences, is stronger, and potentially only detectable, when the amount of habitat is reduced in a landscape below 30% (Andrén, 1994). Few empirical studies have found supportive evidence for the fragmentation threshold (Parker & Nally, 2002; Swift & Hannon, 2010; Fahrig, 2017). However, there is still a “belief” (Fahrig, 2015) that fragmentation poses an extra threat beyond habitat amount in habitat-depleted landscapes (Hanski, 2011, 2015; Rybicki & Hanski, 2013). Our analysis showed that forest bird richness is nearly significantly *negatively* related to fragmentation in landscapes with <30% forest (Table S1-7, *Appendix S1*), but statistical power is high and the effect size is tiny. Below 30% human-dominated land cover, open-habitat richness *increases* with fragmentation (Table S1-7, *Appendix S1*).

Rybicki and Hanski (2013) constructed a modified species-area model that predicted that species are more prone to go extinct when landscapes are highly fragmented and the amount of habitat remaining is below 20%. We do not contest that reduction of the *total amount of habitat* can reduce species richness and individual species’ persistence within individual forest fragments. However, our empirical results (Fig. 3) are inconsistent with their theoretical prediction of a negative effect of a greater number of habitat patches (their Fig. 6). This suggests that their model of area-dependent, stochastic patch occupancy and extinction fails to capture some critical aspect of habitat loss.

An important assumption of our analyses is that the probability of detection of birds is independent of habitat cover. Given that ABBO birders actively searched for birds (versus, for example, point counts), habitat-related sampling bias should be reduced. Moreover, we obtained consistent results analysing fragmentation effects over the full range of habitat cover, and in subsets of the range. However, to the extent that birds may be easier to detect in fragmented landscapes, this would tend to reduce apparent negative effects of fragmentation.

Our study has several methodological limitations. First, the grain of the species richness data (the area over which birds were determined to be present or absent) is constant at 100 km^2. It is likely that species' ecological responses to cover are scale-dependent. We have some evidence that they are strongest at fine spatial grains (De Camargo & Currie, see Chapter 4). At the landscape level, fragmentation is most likely to affect species richness positively (Fahrig, 2017). Moreover, at coarser spatial grain, diversity patterns is increasingly strongly related to abiotic factors (Field et al., 2009, De Camargo & Currie, unpublished).

Second, one might prefer some other index of fragmentation than the number of patches. After controlling for total habitat area, the number of patches is inversely proportional to average patch size. The results of our analyses with different indices of fragmentation were not sensitive to the choice of metric. For example, we also examined the effect of edge-density. Its effect on forests birds is negligible (Tables S1-1,2).

Finally, our analyses are obviously restricted to the response of bird species, which are highly vagile and have the capacity to adjust to environmental changes at a variety of spatial and temporal scales (Tingley et al., 2009). Our results cannot be extrapolated with certainty to any other taxa. Nonetheless, the standard null hypothesis would be that unobserved taxa behave similarly to taxa that have been studied. There are good reasons to speculate that different taxa may respond differently to habitat fragmentation at the landscape level. Pending tests of those speculations, there is not yet reason to limit the generality of our conclusions.

We conclude, in agreement with Fahrig (2017), that habitat fragmentation reduction is unlikely to be a useful tool to improve species diversity at the scale of 100 km^2 landscapes, at minimum for avian species in southern Ontario, and perhaps much more broadly than that. Given limited resources that are allotted to conservation, those should be based on strong scientific evidence. There is both experimental evidence, and comparative evidence among systems that habitat amount is a strong driver of species occurrences and diversity at the landscape level. The same cannot be said about fragmentation. Within a landscape, all habitat patches are potentially valuable (even the small and scattered ones) and policies that reflect this (instead of assigning higher values to large patches) could allow the conservation of more total habitat amount, and therefore more species, with a given investment.

BIOSKETCH

Rafael X. De Camargo is interested in analysing the underlying factors and processes driving species distributions (e.g. richness, occurrences, abundances) within meso-scale landscapes and across large regions. Author's webpage: www.rafaeldecamargo.com

Véronique Boucher Lalonde is a postdoc interested in general ecological patterns and their potential underlying mechanisms, as long as these are falsifiable.

David J. Currie is interested in the predictable properties of the distribution of life on earth (when he is thinking as a scientist) and the beautiful intricacies of nature (when he is not)

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TABLES

Chapter 2

Table 1. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (NP) in 100-km2 landscapes in southern Ontario (n=991). Habitat amount was represented by the area of forest Afor for forest birds, and by the area of human-dominated cover Ahd for open-habitat birds. Models included log-transformed effort and the number of species in the species pool.

Model	Standardised Coefficients	Confidential Intervals		t-values	p-values	R^2
		2.5%	97.5%			
Forest richness						
Intercept	0.00	-23.02	-17.30	-13.9	<0.001	0.85
A_{for}	1.10	0.39	0.54	13.1	<0.001	
A_{for}^2	-0.58	-0.001	-0.001	-6.4	<0.001	
N_P	-0.03	-0.13	0.003	-1.3	0.259	
$\log_{10}$ (effort)	0.14	5.40	7.90	10.4	<0.001	
Species pool	0.44	0.46	0.55	20.2	<0.001	
Open-habitat richness						
Intercept	0.00	-30.90	-24.38	-16.6	<0.001	0.86
A_{hd}	1.05	0.42	0.60	10.7	<0.001	
A_{hd}^2	-0.70	-0.004	-0.002	-8.15	<0.001	
N_P	-0.03	-0.01	0.003	-1.20	0.232	
$\log_{10}$ (effort)	0.20	8.62	11.42	14.00	<0.001	
Species pool	0.47	0.65	0.76	25.47	<0.001	

FIGURES

Chapter 2

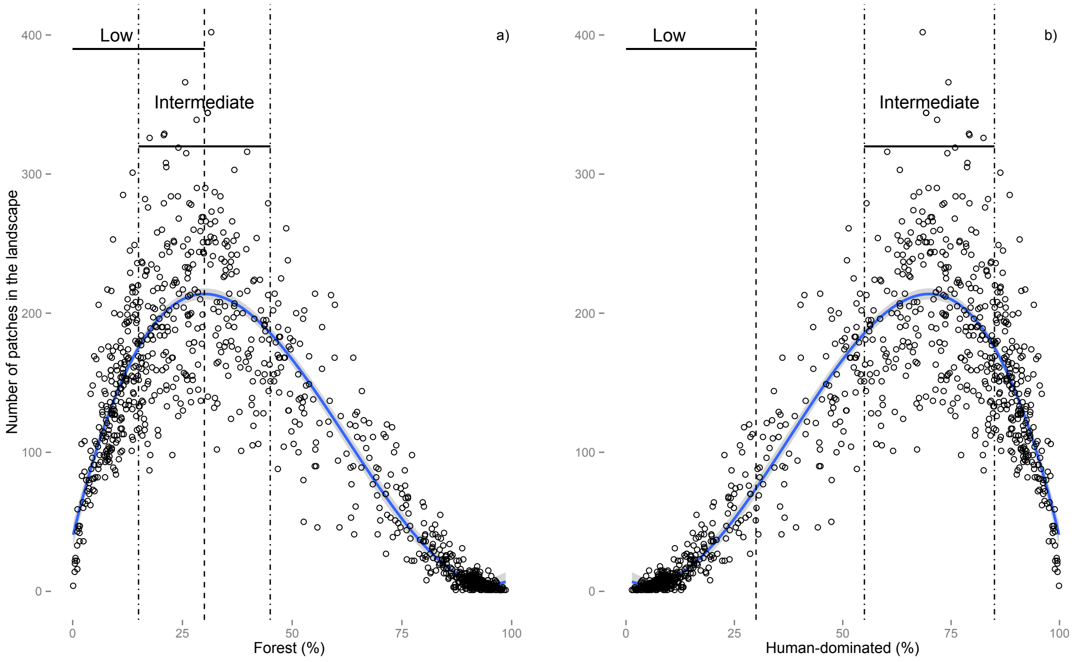

Figure 1. Relationship between number of habitat patches and total habitat amount in 991 landscapes (100-km2) across southern Ontario, measured for two habitat types: i) Forest or ii) Human-dominated cover. The solid blue curves represent third degree polynomials fitting the entire data range (best model: Np=A+A2+A3, R2=0.84, p<0.0001, where A = habitat amount). Dashed lines indicate two fragmentation thresholds: low habitat amount (A<=30% in both figures) following (Andrén, 1994); and intermediate habitat amount, where the number of patches at a given amount of habitat cover is most variable, and the collinearity between the two variables is smallest (between 15% and 45% cover in Fig. 1-a, and between 55% and 85% in Fig. 1-b), following Villard & Metzger (2014).

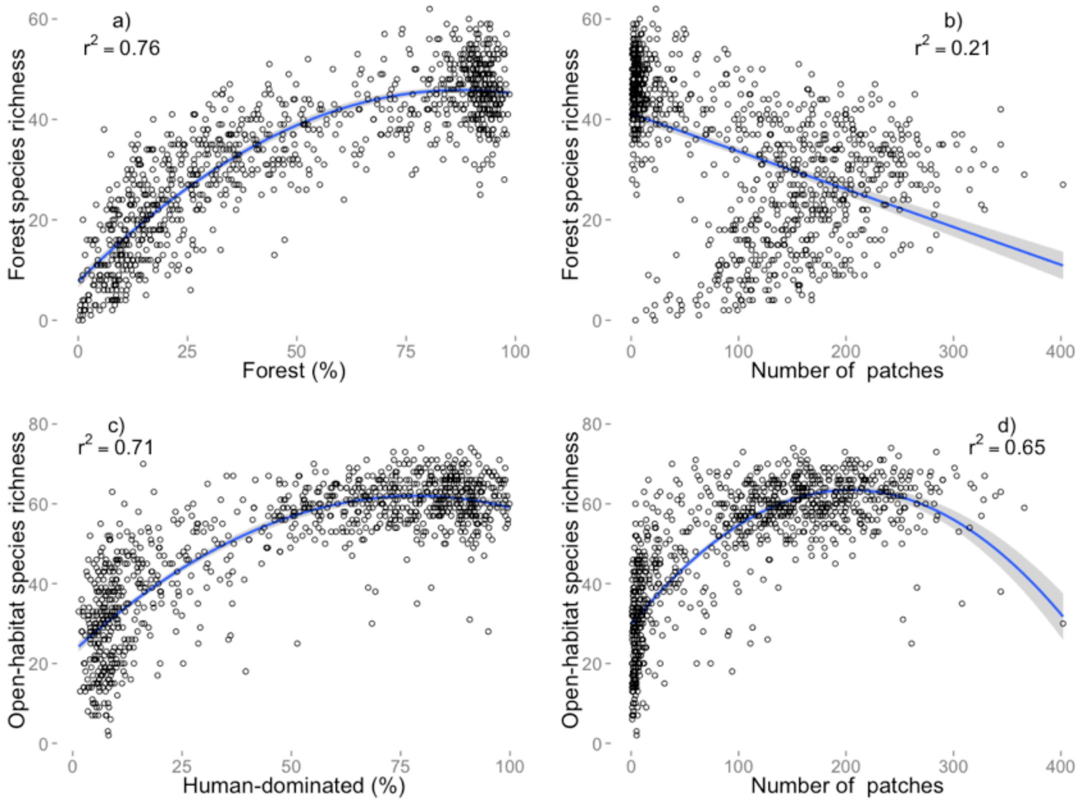

Figure 2. Simple bivariate relationships between bird species richness and habitat amount or fragmentation (number of patches) within 100-km2 landscapes in southern Ontario (n=991). Upper panels: forest bird species richness is shown as a function of (a) forest habitat cover (S_{for}=Afor+Afor2), and (b) number of patches (S_{for}=Np+Np2). Lower panels: open-habitat species richness is show as a function of (c) human-dominated habitat cover (S_{open}=Ahd+Ahd2), and (d) number of patches (S_{open}=Np+Np2). Models with quadratic terms were significantly better (ΔAIC<-2) than linear models.

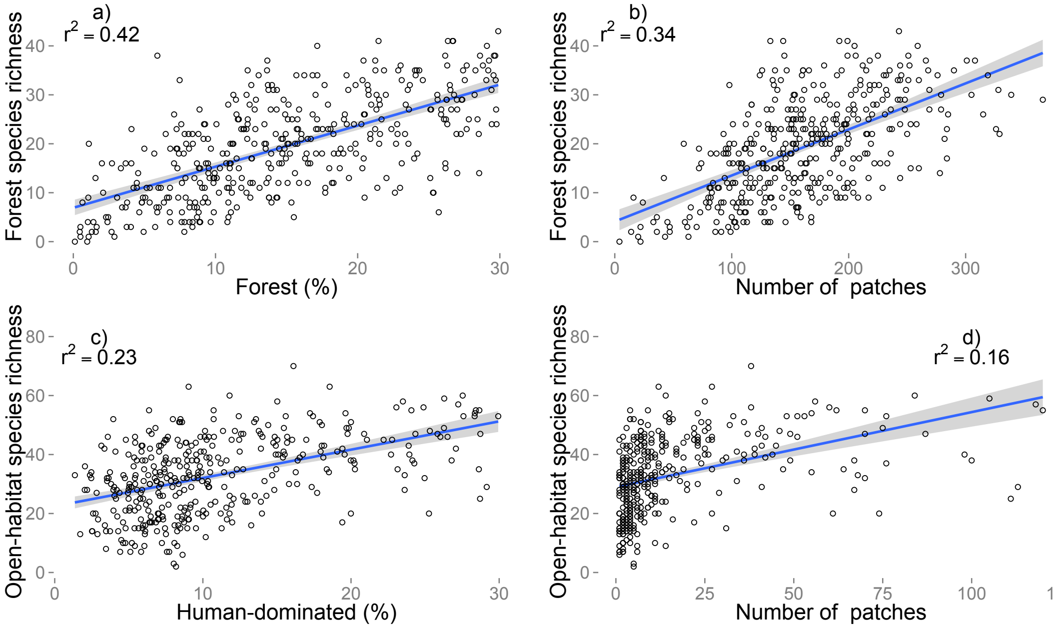

Figure 3. Simple bivariate relationships between bird species richness and habitat amount or fragmentation (number of patches) within 100-km2 landscapes in southern Ontario, restricting the data to landscapes with <30% forest cover. Upper panel: forest bird species richness regressed against a) forest habitat cover (S_{for}=6.92+0.83Afor), and b) number of patches (S_{for}=4.10+0.09Np) (n=397 landscapes). Lower panel: open-habitat species richness as a function of c) human-dominated cover (S_{open}=22.45+0.95Ahd), and d) number of patches (S_{open}=29+0.25Np) (n=382 landscapes).

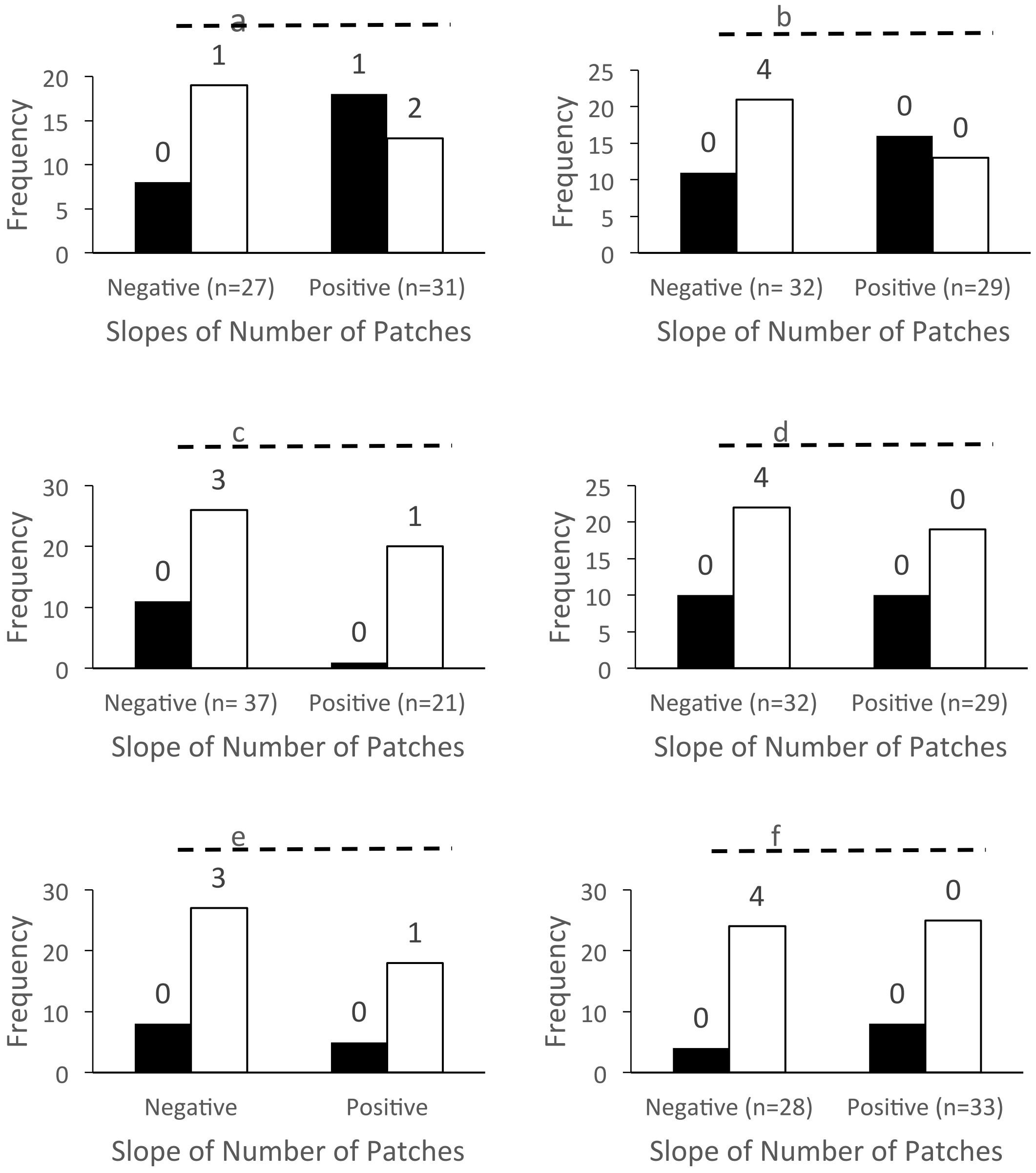

Figure 4. Numbers of forest bird species (a, c, e) and open-habitat bird species (b, d, f) whose probability of occurrence (pocc) is negatively or positively related to fragmentation in logistic regression models controlled for land cover amount, effort, and species pool size. Black bars represent models in which pocc is significantly related to the number of patches ($p<0.05$), whereas white bars represent non-significant relationships. Dashed lines indicate results that are inconsistent with the hypothesis that habitat fragmentation negatively affects species' probability of occurrence. Numbers above the bars represent the number of endangered listed species by COSEWIC (see species names on Table S1-10, Appendix S1). Panels a-b show models fitted using the entire dataset; c-d, the trimmed dataset with A<= 30%; and e-f, the trimmed dataset with intermediate area (see Fig. 2.1).

APPENDICES

Appendix S1: additional tables and figures providing supporting statistical analysis.

Study area

Our analysis is restricted to 991 landscapes of 100-km^2 each in southern Ontario, Canada (Fig. S1-1). Historically, southern Ontario was mainly forested. Natural land cover was heavily altered during European settlement in the 18th – 19th centuries (Warwick 1980). After the mid-20th century, government programs began promoting selective harvesting and silviculture on private woodlots in southern Ontario (Thompson et al. 2000, p. 84; Ontario Ministry of Natural Resources 2015). As a result, the amount of forest cover has been relatively stable for the last ~70 years.

Landscapes and habitat quality

Remote-sensed land cover was obtained from the Ontario Provincial-Scale Land Cover data set produced by the Ontario Ministry of Natural Resources (2002) from Landsat 7 Thematic Mapper (https://landsat.gsfc.nasa.gov/the-thematic-mapper/) scenes captured primarily in the 1990s (resampled to a 30-m resolution), which distinguished 28 land cover classes. We grouped these classes into *forested land* and *human-dominated covers*. Forested areas are composed by nine classes including older forest clear-cuts and forest fires, wetlands (seven classes) and alvar (dry grass- land found over limestone substrate with thin soils). Human-dominated land cover is composed by seven classes, including recent cutovers, mine tailings, quarries, bedrock outcrops, settlement and developed land, pasture and abandoned field, and cropland. We include some small portions of coniferous plantations as forested cover. We excluded water and unclassified categories. Five other classes in the original land-cover classification did not occur in the study area. Within forest land cover category, forests constitute 97% of the total area of landscapes in the study area, while natural wetlands correspond to 3%. Within human-dominated areas, 76% is cropland (row crops, hay, or open soil), while the rest (24%) corresponds mainly to recent cutovers, mining, urban areas and pastures.

Bird distribution data

We evaluated how both *avian species richness* and *individual bird species' probability of occurrence* vary as functions of the landscape metrics habitat amount and fragmentation. Bird species' presences and absences in each100-km^2 UTM landscapes in southern Ontario are reported in the *Atlas of the Breeding Birds of Ontario* (hereafter ABBO: Cadman et al. 2007). Data in northern Ontario, which are recorded at a coarser grain, were excluded from our analyses. To compile the ABBO, each volunteer "atlasser" was assigned to search a specific landscape as completely as possible for evidence of all species breeding in the landscape. Sampling was repeated over a five-year period, from 2000 to 2005, for 20-600 hours total sampling effort in most landscapess. Volunteers were instructed to search in particular for regionally rare species. Any species that was observed in a given landscape in 2000-2005 was considered present. Since atlassers specifically searched for birds (versus point counts), we treat the data as presence/absence (corrected for sampling effort), although "absence" operationally means absent or undetected.

We excluded wedge-shaped UTM landscapes and landscapes with more than 10% water area to minimize variation in land cover area among landscapes. We also excluded landscapes with <20 hours and > 600 hours of bird censusing effort (Cadman et al. 2007). This left 991 landscapes each in our analysis. Landscapes vary from nearly entirely forested to nearly entirely human-dominated land covers, and from low to high fragmentation (Fig. S1-1).

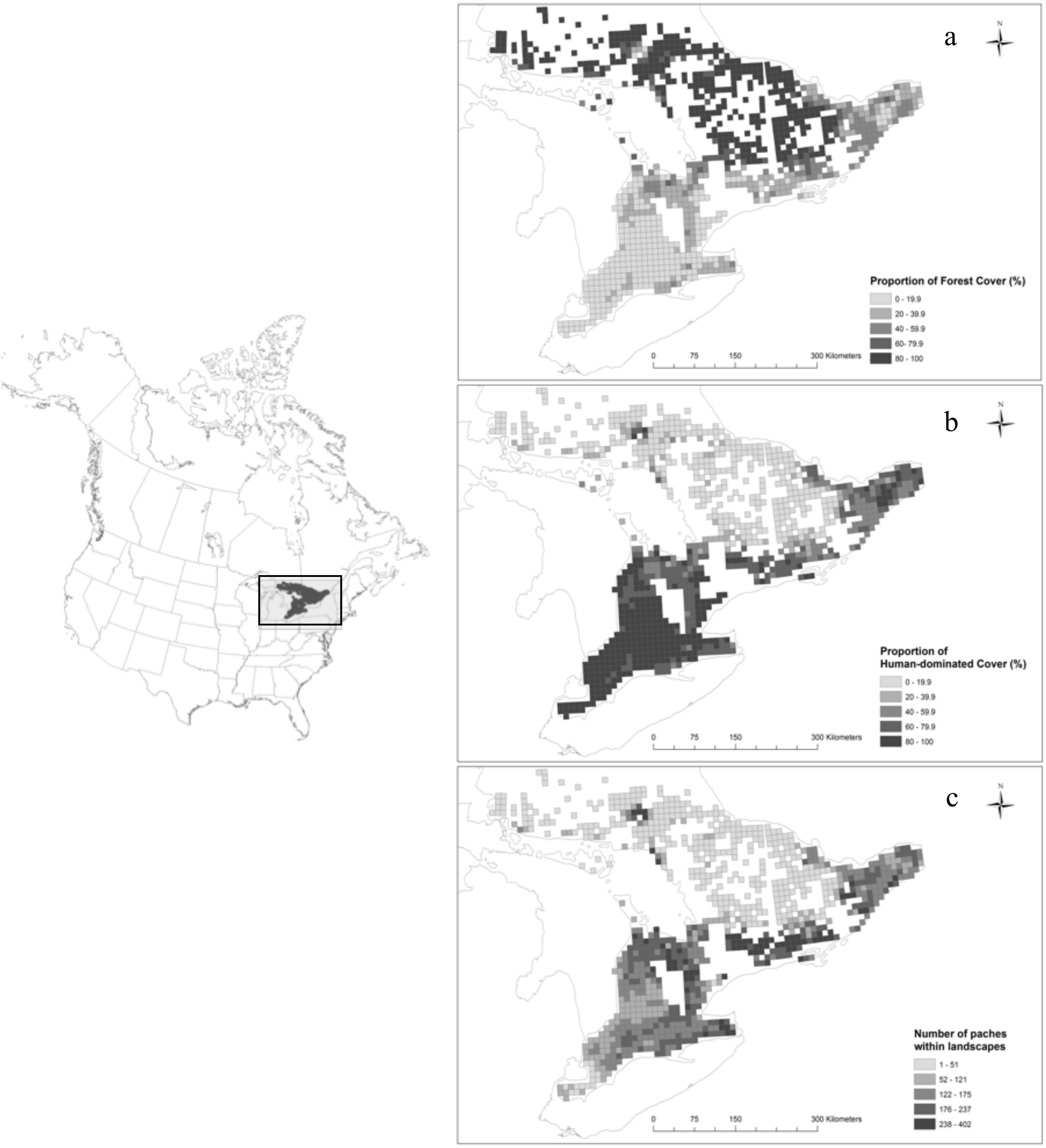

Fig. S1-1. Distribution of a) proportion of forest covers, b) proportion of human-dominated covers, and c) number of patches within each landscape of 100-km^2 in southern Ontario, Canada (41º – 44º N and 84º – 74º W, ~ 200,000 km^2).

Tests of other fragmentation measurements

In this section, we present statistical analyses utilizing other metrics of habitat fragmentation instead of number of patches. Our results were based on the number of patches because of its stronger statistical relationship with richness in comparison to the other fragmentation measurements (Table S1-1, *Appendix S1*). However, we also included edge density (i.e., the summation of perimeters of each and every patch within a landscape containing the habitat measured divided by the landscape area) as a habitat fragmentation metric in our statistical analysis. Edge density does not change qualitatively our conclusions (Table S1-2).

Table S1-1. Correlations between species richness of forest species and of open-habitat species richness, as functions of three fragmentation measurements. *Np* represents number of patches, *AvP* is the average patch size for each landscape, and *ED* is edge density.

Dependent	Independent variable	Slope	R^2
Forest species richness	N_p	-0.07	0.21
	AvP	0.32	0.16
	ED	14.83	0.02
Open-habitat species richness	Np	0.13	0.51
	AvP	-058	0.41
	ED	40.92	0.11

Table S1-2. Forest- and open-habitat bird species richness modelled as functions of habitat amount and **Edge Density (*ED*)** in 100-km^2 landscapes in southern Ontario (n=991). Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. Models included log-transformed effort and the number of species in the species pool.

Model	Standardised Coefficients	Confidential Intervals		t-values	p-values	R^2
		2.5%	97.5%			
Forest richness						
Intercept	0.00	-23.40	-17.70	-14.13	<0.001	0.85
A_{for}	1.34	0.44	0.69	8.95	<0.001	
A_{for}^2	-0.80	-0.001	-0.002	-5.28	<0.001	
ED	-0.06	-12.75	-0.51	-2.13	0.0335	
$\log_{10}$ (effort)	0.14	5.43	7.92	10.52	<0.001	
Species pool	0.44	0.45	0.55	20.84	<0.001	
Open-habitat richness						
Intercept	0.00	-30.64	-24.23	-16.67	<0.001	0.86
A_{hd}	1.14	0.42	0.68	8.46	<0.001	
A_{hd}^2	-0.78	-0.005	-0.002	-5.83	<0.001	
ED	-0.04	-11.86	1.72	-1.46	0.1440	
$\log_{10}$ (effort)	0.19	8.57	11.36	14.00	<0.001	
Species pool	0.48	0.65	0.76	25.44	<0.001	

Extra Statistical Analyses

We present below only the results obtained using the empirically-defined guilds, based on landscape-level habitat associations. Results with guilds defined using patch-level habitat associations were very similar (Table S1-3, Fig S1-2).

Link & Sauer (1999) showed that variation in sampling effort can affect the performance of statistical models using survey count data, but here we found that it did not affect our qualitative conclusions (see Table S1-4). Spatial autocorrelation can affect models coefficients in spatial analyses (Diniz-Filho et al., 2003). Hence, we also corrected the richness models for spatial autocorrelation by fitting simultaneous autoregressive error models (SARerr) proposed by Kissling & Carl (2007) in R (function “errorsarlm”, R Development Core Team, 2008) (Table S1-5).

Table S1-3. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario (n=991). Habitat amount was represented by the area of forest A_{for} for forest and fragmentation-sensitive bird species richness, and by the area of human-dominated cover A_{hd} for open-habitat species richness. **Here, forest- and open-habitat species were classified according to habitat affiliation from Cadman et al. (2007).** Fragmentation-sensitive species were empirically defined using our data (see Methods section in the main text). Models included log-transformed effort and the number of species in the species pool. Fragmentation (i.e., the number of patches) and its interaction with A_{for} increase explained variation by <1% for fragmentation sensitive richness.

Model	Estimates	t-values	p-values	R^2
Forest richness				
Intercept	-3.035	-1.810	0.007	0.63
A_{for}	0.595	8.010	<0.001	
A_{for}^2	-0.004	-6.570	<0.001	
N_P	0.005	0.750	0.454	
$\log_{10}$ (effort)	11.260	16.350	<0.001	
Species pool	0.280	9.70	<0.001	
A_{for}* N_P	-0.001	-2.475	0.013	
Open-habitat richness[a]				
Intercept	-9.835	-5.115	<0.001	0.70
A_{hd}	0.465	6.195	<0.001	
A_{hd}^2	-0.004	-5.955	<0.001	
N_P	0.020	1.095	0.274	
$\log_{10}$ (effort)	9.750	11.942	<0.001	
Species pool	0.550	16.485	<0.001	
A_{hd}*N_P	-0.001	-0.260	0.795	
Fragmentation-sensitive species[b]				
Intercept	-55.100	-7.856	<0.001	0.62
A_{for}	0.202	6.575	<0.001	
A_{for}^2	-0.001	-5.256	<0.001	
N_P	0.005	1.851	0.065	
$\log_{10}$ (effort)	3.650	12.680	<0.001	
Species pool	0.150	12.860	<0.001	
A_{for}* N_P	-0.001	-1.511	0.131	

a) Dropping the interaction term from the model makes the N_p marginally significant.
b) Dropping the interaction term from the model **does not** make the N_p significant.

Table S1-4. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario (n=991). Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. **Here, non-linear regressions included sampling effort transformations as proposed by Link & Sauer, (1999): $Effort_p = b(Effort^p -1)/p$, where b is a coefficient and p is empirically determined by the data**. Models were also corrected for the number of species in the species pool.

Model	Estimates	t-values	p-values	R^2
Forest richness				
Intercept	-13.700	-9.528	<0.001	0.85
A_{for}	0.556	8.157	<0.001	
A_{for}^2	-0.003	-4.977	<0.001	
N_P	0.001	0.213	0.831	
$Effort_p$	4.550	1.950	0.051	
Species pool	0.501	19.301	<0.001	
A_{for}* N_P	-0.0002	-1.458	0.1451	
p	1.641	1.950	0.051	
Open-habitat richness				
Intercept	-18.721	-10.437	<0.001	0.86
A_{hd}	0.521	7.897	<0.001	
A_{hd}^2	-0.003	-5.200	<0.001	
N_P	-0.010	-0.587	0.557	
$Effort^p$-1/p	14.840	3.047	0.002	
Species pool	0.700	24.891	<0.001	
A_{hd}*N_P	0.00001	0.304	0.761	
p	-0.306	0.525	0.599	

Table S1-5. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario (n=991). Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. **Here tested models included an extra term to correct for spatial autocorrelation, following** Kissling & Carl, (2007)**.**

Model	Estimates	t-values	p-values	R^2
Forest richness				
Intercept	-21.555	-11.172	<0.001	0.87
A_{for}	0.637	8.428	<0.001	
A_{for}^2	-0.003	-5.348	<0.001	
N_P	0.01	1.870	0.061	
$\log_{10}$ (effort)	6.950	10.554	<0.001	
Species pool	0.459	13.878	<0.001	
A_{for}* N_P	-0.00005	-2.642	0.008	
Open-habitat richness				
Intercept	-17.769	-8.671	<0.001	0.88
A_{hd}	0.493	6.901	<0.001	
A_{hd}^2	-0.003	-4.124	<0.001	
N_P	0.011	0.590	0.554	
$\log_{10}$ (effort)	8.828	12.304	<0.001	
Species pool	0.580	17.309	<0.001	
A_{hd}*N_P	-0.0001	-0.646	0.518	

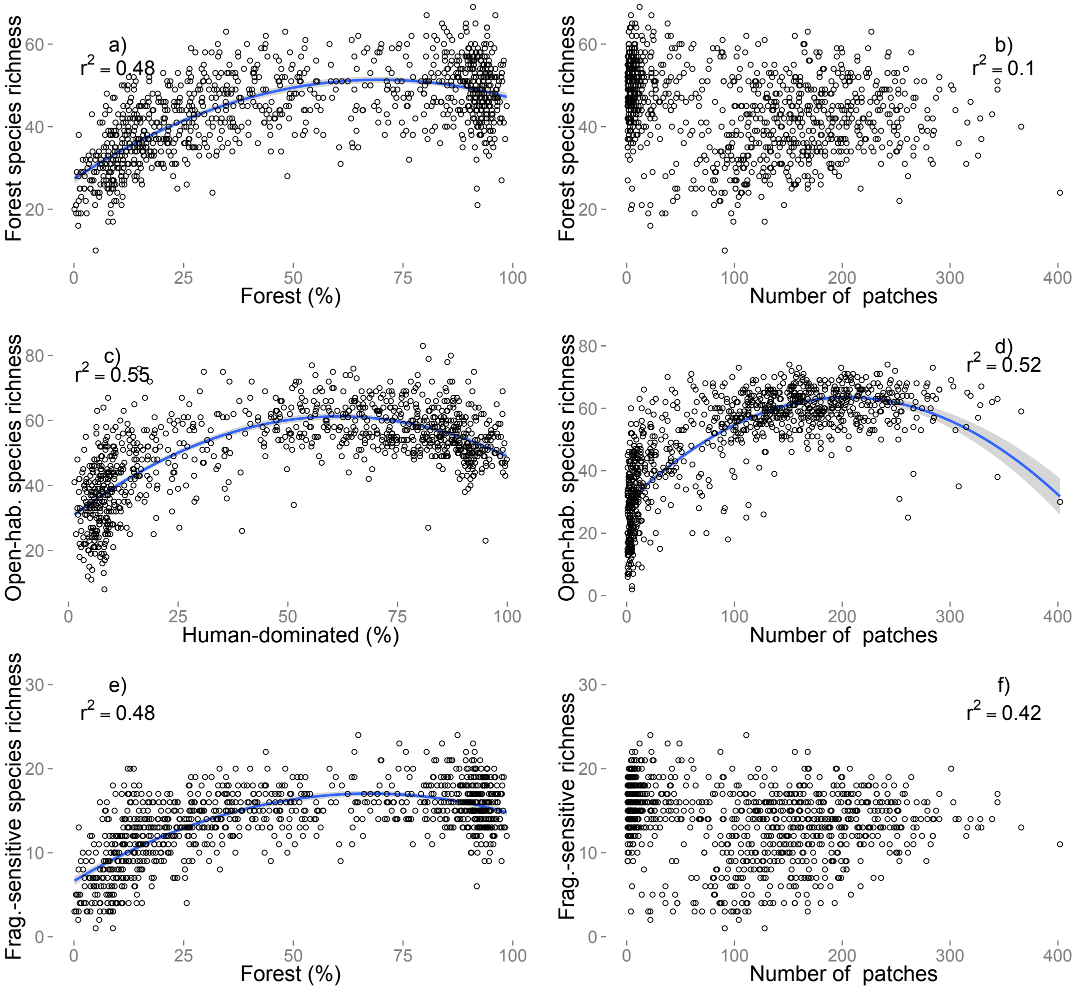

Fig. S1-2. Simple bivariate relationships between bird species richness and habitat amount or fragmentation (number of patches) within 100-km^2 landscapes in southern Ontario (n=991). **Here, forest- and open-habitat species are defined by their local habitat (patch-scale) affinity according to Cadman et al. (2007)**. **Fragmentation-sensitive species richness are empirically defined from our data.** Forest species richness is shown as a function of (a) forest habitat cover ($S_{for}=A_{for}+A_{for}^2$), and (b) number of patches ($S_{for}=Np+Np^2$). Open-habitat species richness is shown as a function of (c) human-dominated habitat cover ($S_{open}=A_{hd}+A_{hd}^2$), and (d) number of patches ($S_{open}=Np+Np^2$). Fragmentation-sensitive (defined empirically at the landscape level) species richness varies as function of e) forest habitat cover ($S_{for}=A_{for}+A_{for}^2$), and f) number of patches ($S_{for}= Np+Np^2$). Models with the quadratic terms performed better (higher r-squared) than models fitted with simple independent variables. Complete species list included in each species group available on *Appendix S2*.

Table S1-6. Forest- and open-habitat bird species richness modelled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario (n=991). **The interactions habitat amount and fragmentation are not significant**. Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. Models included log-transformed effort and the number of species in the species pool.

Model	Estimates	t-values	p-values	R^2
Forest richness				
Intercept	-20.960	-13.500	<0.001	0.85
A_{for}	0.553	8.132	<0.001	
A_{for}^2	-0.003	-4.935	<0.001	
N_P	0.001	0.254	0.779	
$\log_{10}$ (effort)	6.605	10.365	<0.001	
Species pool	0.501	19.302	<0.001	
A_{for}* N_P	-0.001	-1.475	0.141	
Open-habitat richness				
Intercept	-27.740	-16.420	<0.001	0.86
A_{hd}	0.525	7.984	<0.001	
A_{hd}^2	-0.003	-5.280	<0.001	
N_P	-0.105	-0.600	0.550	
$\log_{10}$ (effort)	10.000	13.945	<0.001	
Species pool	0.705	25.330	<0.001	
A_{hd}*N_P	0.001	0.300	0.766	

Table S1-7. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario. Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. Models included log-transformed effort and the number of species in the species pool. **To test the fragmentation threshold effect, only landscapes (quadrats) with habitat amount below 30%** were retained (see Fig. 1 main text). Fragmentation (i.e., the number of patches) and its interaction with A_{for} increase explained variation by <9% for open-habitat richness, but does not make a difference for forest richness. Models without the interactions terms made N_p statistically insignificant.

Model	Estimates	t-values	p-values	R^2
Forest richness (397 landscapes)				
Intercept	-18.000	-9.445	<0.001	0.72
A_{for}	0.274	2.808	<0.005	
N_P	-0.203	-1.941	0.053	
$\log_{10}$ (effort)	6.050	7.246	<0.001	
Species pool	0.540	18.077	<0.001	
A_{for}* N_P	0.001	1.680	0.094	
Open-habitat richness (382 landscapes)				
Intercept	-29.945	-10.185	<0.001	0.63
A_{hd}	0.550	4.462	<0.001	
N_P	0.230	2.160	0.031	
$\log_{10}$ (effort)	13.164	7.335	<0.001	
Species pool	0.630	15.505	<0.001	
A_{hd}*N_p	-0.001	2.590	0.010	

obs: removing the interaction term does not affect the results qualitatively, and Np continues to be statistically insignificant.

Table S1-8. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario. Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. Models included log-transformed effort and the number of species in the species pool. **Here models were tested using the empirical-defined thresholds (see methods) of 31.3% forest cover, and 45.5% of human-dominated cover for open-habitat birds.**

Model	Estimates	t-values	p-values	R^2
Forest richness (404 landscapes)				
Intercept	-17.761	-9.459	<0.001	0.73
A_{for}	0.232	2.512	<0.012	
N_P	-0.001	-1.917	0.056	
$\log_{10}$ (effort)	6.000	7.283	<0.001	
Species pool	0.537	18.000	<0.001	
A_{for}* N_P	0.0001	2.850	0.037	
Open-habitat richness (429 landscapes)				
Intercept	-30.000	-11.042	<0.001	0.69
A_{hd}	0.486	6.093	<0.001	
N_P	0.050	1.032	0.033	
$\log_{10}$ (effort)	13.312	8.104	<0.001	
Species pool	0.649	17.397	<0.001	
A_{hd}*N_p	-0.003	-1.835	0.067	

obs: removing the interaction term does not affect the results qualitatively, and Np continues to be statistically insignificant.

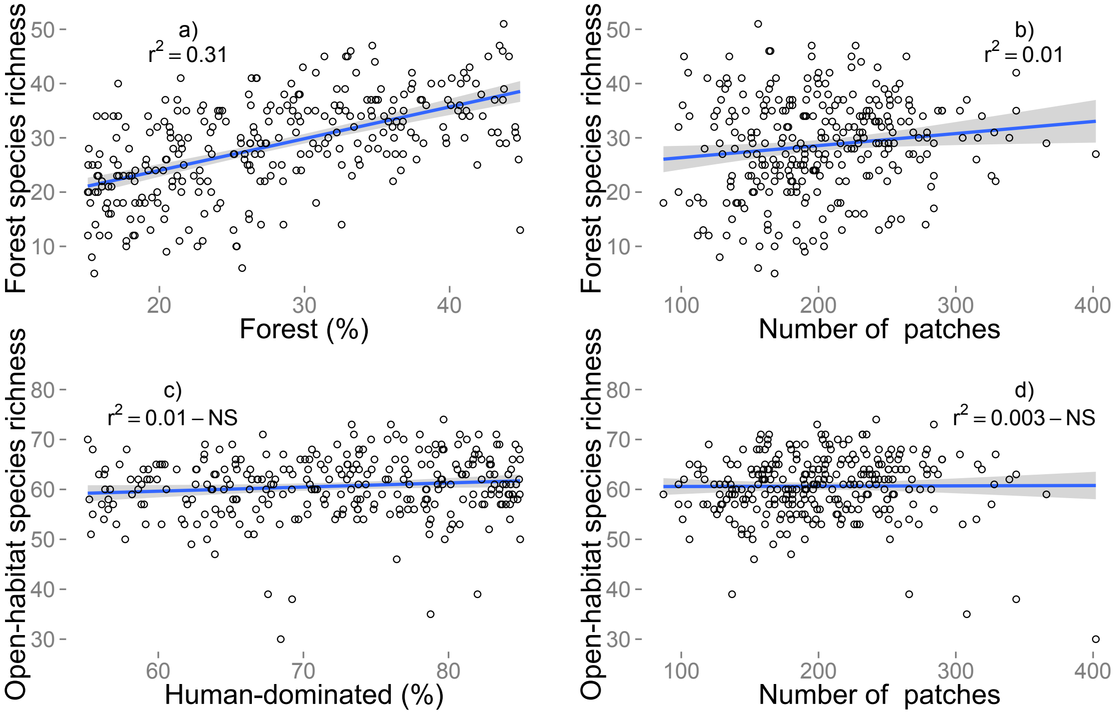

Fig. S1-3. Simple bivariate relationships between bird species richness and habitat amount or fragmentation (number of patches) within 100-km^2 landscapes in southern Ontario (n=287 landscapes), restricting the data to landscapes with **intermediate amount of habitat** (see Fig. 1 main text). Upper panel: forest species richness regressed against a) forest habitat amount ($S_{for}=12.286+0.585A_{for}$), and b) number of patches ($S_{for}=24.132+0.022Np$) (n=289 landscapes). Lower panel: open-habitat species richness varying with c) human-dominated habitat cover ($S_{open}=54.654+0.083A_{hd}$), and d) number of patches ($S_{open}=60.510+0.665Np$) (n=289 landscapes).

Table S1-9. Forest- and open-habitat bird species richness modeled as functions of habitat amount and number of patches (N_P) in 100-km^2 landscapes in southern Ontario. Habitat amount was represented by the area of forest A_{for} for forest birds, and by the area of human-dominated cover A_{hd} for open-habitat birds. Models included log-transformed effort and the number of species in the species pool. **Data here were trimmed to test intermediate fragmentation threshold effect, in which habitat amount is at intermediate levels within landscapes**.

Model	Estimates	t-values	p-values	R^2
Forest richness (289 landscapes)				
Intercept	-23.53	-5.504	<0.001	0.68
A_{for}	0.223	1.565	0.119	
N_P	-0.013	-0.773	0.440	
$\log_{10}$ (effort)	7.609	7.688	<0.001	
Species pool	0.658	17.330	<0.001	
$A_{for}*N_P$	0.0003	0.389	0.698	
Open-habitat richness (348 landscapes)				
Intercept	-35.630	-3.361	<0.001	0.51
A_{hd}	0.015	0.132	0.894	
N_P	-0.012	-0.259	0.795	
$\log_{10}$ (effort)	7.963	8.997	<0.001	
Species pool	1.088	11.265	<0.001	
$A_{hd}* N_P$	0.0002	0.301	0.763	

obs: removing the interaction term does not affect the results qualitatively, and Np continues to be statistically insignificant.

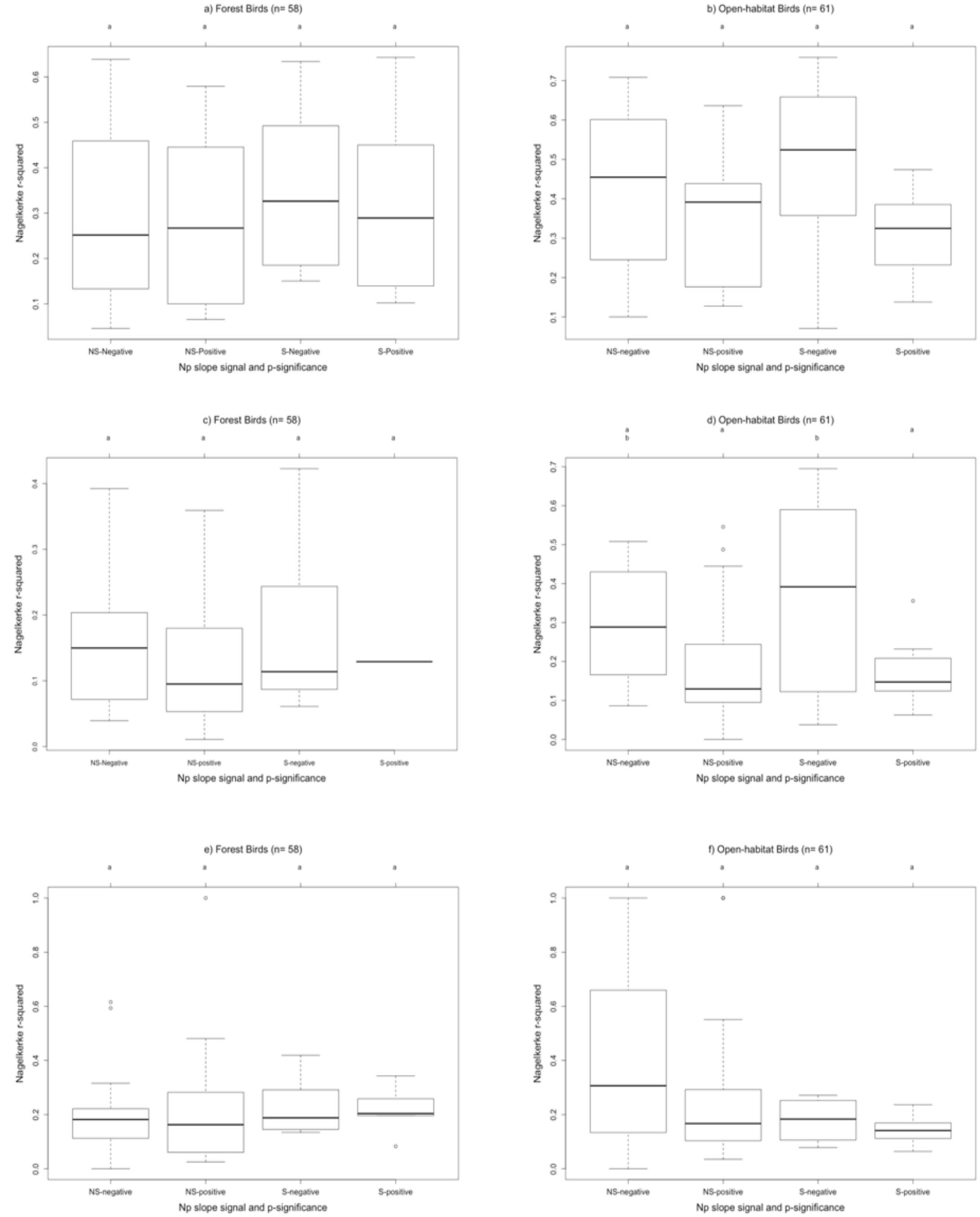

Fig. S1-4. Average Nagelkerke R-squared extracted from fitted logistic models with habitat amount (forest and human-dominated land cover), number of patches (fragmentation), log-transformed effort and species pool. Average was calculated for group of species that showed significant or insignificant p-values of the slope of number of patches (positive or negative). a, c, e correspond to forest birds, b, d, f – open-habitat bird species. a-b – entire dataset; c-d – A<= 30%; e-f – Intermediate amount of land cover within landscapes (see Fig. 1 in the main text). Different letters in the graphs represent statistical significant values among mean values. Stats for the ANOVA in d: df=3, SS=0.34, F=4.4, p<0.01).

Table S1-10. COSEWIC Red-listed bird species whose probability of occupancy is negative (-) or positively (+), significantly (S) or insignificantly (N.S) by habitat fragmentation (number of patches) within landscapes of southern Ontario (see Fig. 4 main text).

		Np-slope and p-significance		
Common Name	**Scientific Name**	**Entire dataset**	**A<=30 %**	**Intermediate Habitat Amount**
Forest birds				
Olive-sided Flycatcher	*Contopus cooperi*	N.S. (-)	N.S.(-)	N.S. (-)
Canada Warbler	*Wilsonia canadensis*	N.S. (+)	N.S.(-)	N.S. (+)
Whip-poor-will	*Caprimulgus vociferus*	N.S. (+)	N.S.(-)	N.S. (-)
Golden-winged Warbler	*Vermivora chrysoptera*	S (+)	N.S.(+)	N.S. (-)
Open-habitat birds				
Chimney Swift	*Chaetura pelagica*	N.S. (-)	N.S.(-)	N.S. (-)
Barn Swallow	*Hirundo rustica*	N.S. (-)	N.S.(-)	N.S. (-)
Red-headed Woodpecker	*Melanerpes erythrocephalus*	N.S. (-)	N.S.(-)	N.S. (-)
Eastern Meadowlark	*Sturnella magna*	N.S. (-)	N.S.(-)	N.S. (-)

Table S1-11. Statistical outcome of logistic regressions show the slopes of the model term and interpretations according to the predictions made by both habitat fragmentation (HF) and threshold hypotheses. Logistic models fitted with presence/ absences as a function of land cover amount (forest- and human-dominated), log-transformed effort, and species pool in 991 landscapes of 100-km^2 each in southern Ontario.

Np	**p-value**	**A*Np**	**p-value**	**# of species**	**Average Nagelkerke R^2**	**# Red-listed species**	**Consistent with**		**Interpretation of the effect of habitat fragmentation and its interaction with habitat amount**
							HF	**Threshold**	
					Forest birds				
-	S	+	S	5	0.28	1	Yes	Yes	Species significantly decrease p_{occ} in fragmented landscapes AND its effect is worse when forest cover is low
-	S	-	N.S.	1	0.10	0	Yes	No	Species significantly decrease p_{occ} in fragmented landscapes BUT there is no indication that its effect is worse when forest cover is low
-	S	+	N.S.	2	0.52	0	Yes	Yes	
-	N.S.	+	S	13	0.30	1	Yes	Yes	There is NO detectable signal of habitat fragmentation BUT fragmentation may negatively affect species p_{occ} when forest cover is high
+	N.S.	+	S	12	0.30	0	No	Yes	
-	N.S.	+	N.S.	6	0.46	0	Yes	No	There is NO detectable signal of habitat fragmentation NOR of fragmentation threshold
-	N.S.	-	N.S.	4	0.25	0	Yes	No	
+	N.S.	-	N.S.	3	0.25	0	No	No	
+	N.S.	+	N.S.	7	0.30	1	No	Yes	
+	S	+	S	2	0.30	1	No	Yes	Species increase p_{occ} in fragmented landscapes more so in fragmented landscapes with high forest cover
+	S	+	N.S.	3	0.30	0	No	Yes	Species increase p_{occ} in fragmented landscapes AND there is no indication of fragmentation effect when forest cover is low

Table S1-11. Continued…

Np	p-value	A*Np	p-value	# of species	Average Nagelkerke R^2	# Red-listed species	Consistent with		Interpretation of the effect of habitat fragmentation and its interaction with habitat amount
							HF	Threshold	
Open-habitat birds									
-	S	+	S	5	0.27	1	Yes	Yes	Species significantly decrease p_{occ} in fragmented landscapes AND its effect is worse when open-habitat cover is low
-	S	-	N.S.	1	0.66	0	Yes	No	Species decrease p_{occ} in fragmented landscapes BUT there is no indication that its effect is worse when open-habitat land cover is low
-	N.S.	+	S	13	0.40	1	Yes	Yes	There is NO detectable signal of habitat fragmentation BUT fragmentation may be worse when open-habitat land cover is low
+	N.S.	+	S	15	0.40	1	No	Yes	
-	N.S.	+	N.S.	4	0.50	0	Yes	Yes	There is NO detectable signal of habitat fragmentation NOR of fragmentation threshold
+	N.S.	-	N.S.	1	0.62	0	No	No	
+	N.S.	+	N.S.	1	0.60	1	No	Yes	
+	S	+	N.S.	6	0.48	0	No	Yes	Species increase p_{occ} in fragmented landscapes AND there is no indication of fragmentation effect when open-habitat land cover is low
+	S	+	S	15	0.30	0	No	Yes	Species increase p_{occ} in fragmented landscapes AND its effect is more pronounced when open-habitat land cover is low

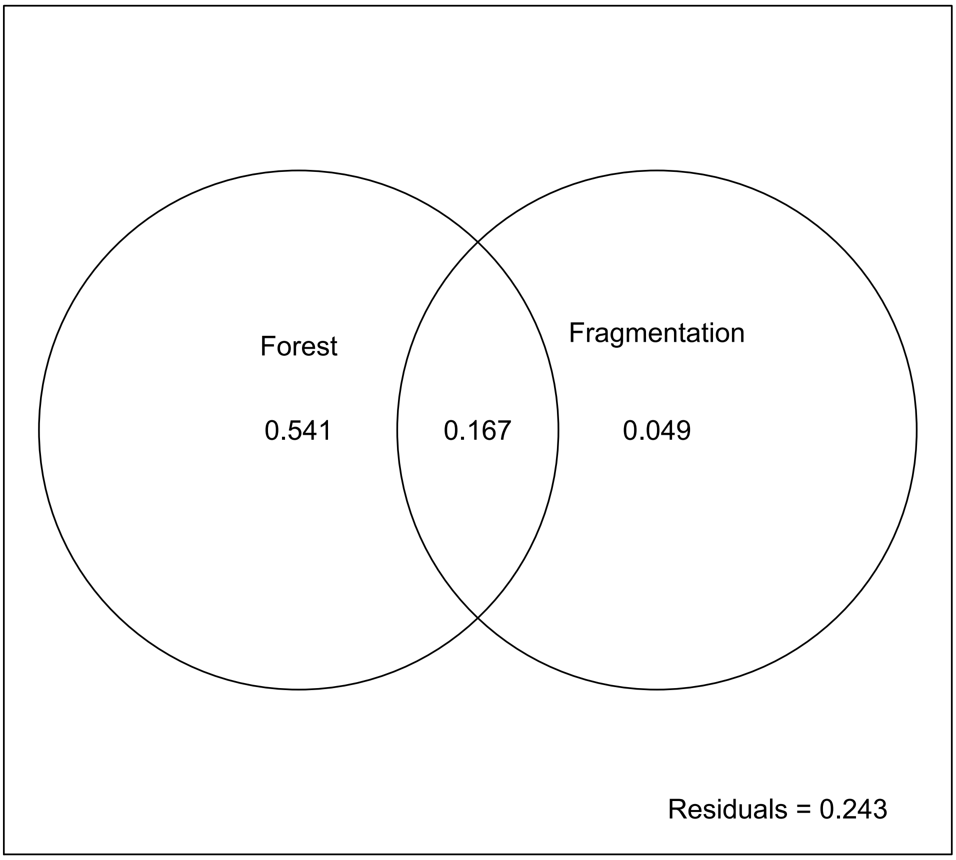

Fig. S1-5. Variation in **forest species** richness explained by the dependent variables number of patches (fragmentation) and forest habitat amount. Variance obtained from the model $S_{for} = a+A_{for}+Np$, where S_{for} is forest species richness; A_{for} represent the amount of forest habitat within landscapes, and Np is the number of patches within landscapes. (N=991 landscapes).

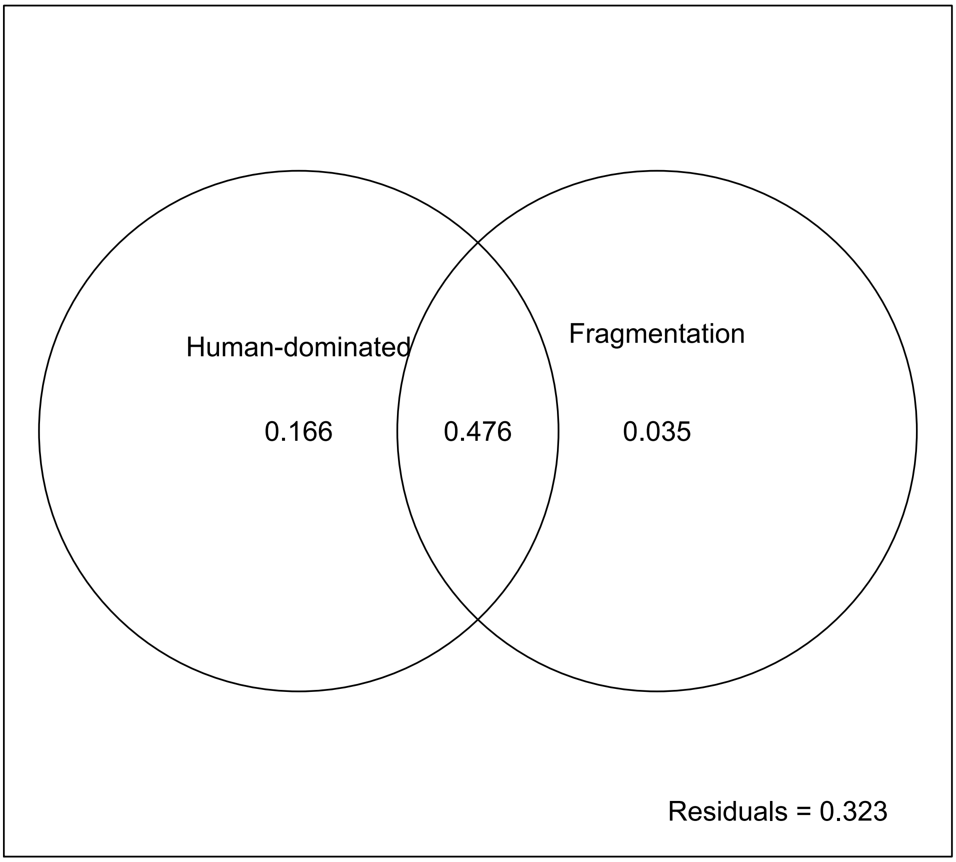

Fig. S1-6. Variation in **open-habitat** species richness explained by the dependent variables number of patches (fragmentation) and human-dominated habitat amount. Variance obtained from the model $S_{open} = a+A_{hd}+Np$, where S_{open} is open-habitat species richness; A_{hd} represent the amount of human-dominated habitat within landscapes, and Np is the number of patches within landscapes. (N=991 landscapes).

Appendix S2: list of species used to compose the species richness groups.

Definition of species groups

Our main analyses are based on forest- and open-habitat species defined empirically (main text). However, we similarly empirically defined a functional group of fragmentation-sensitive species: those for which presence is negatively related to fragmentation, obtained from fitted logistic models (i.e. n=41 species, Table S2-1).

We also tallied species richness of forest and open-habitat guilds based on local habitat affiliation, using the species accounts in the ABBO (Cadman et al., 2007). Using literature descriptions avoids using the same data both to assign species to functional groups and to calculate the dependent variable (species richness). Based on the ABBO descriptions, 89 species were categorized as forest species, and 113 as open-habitat species (Table S2-2).

Table S2-1. Empirical definition of the three functional species group: forest, open-habitat and fragmentation sensitive species. Forest species are those whose probability of occupancy (p_{occ}) significantly increases with forest cover within 100-km^2 landscapes (n=991); open-habitat species' p_{occ} significantly decrease with forest cover ; fragmentation-sensitive species' p_{occ} significantly decreases with number of forested patches within landscapes. Only statistically significant models included in the list (p<0.05).

FOREST SPECIES - Species whose probability of presence is a positive monotonic function of the amount of forest cover (n=69 species)							
Species	**English Name**	**Scientific Name**	**COSEWICK**	**NSQ**	**Coeff.**	**P**	**Nagelkerke_R.2**
ABDU	American Black Duck	Anas rubripes	Not_at_risk	370	0.01	0.00	0.05
ACFL	Acadian Flycatcher	Empidonax virescens	Endangered	28	0.04	0.05	0.03
ALFL	Alder Flycatcher	Empidonax alnorum	Not_at_risk	826	0.05	0.00	0.28
AMBI	American Bittern	Botaurus lentiginosus	Not_at_risk	502	0.02	0.00	0.14
AMRE	American Redstart	Setophaga ruticilla	Not_at_risk	912	0.04	0.00	0.16
BAWW	Black-and-white Warbler	Mniotilta varia	Not_at_risk	777	0.09	0.00	0.50
BBWA	Bay-breasted Warbler	Dendroica castanea	Not_at_risk	88	0.05	0.00	0.09
BBWO	Black-backed Woodpecker	Picoides arcticus	Not_at_risk	122	0.05	0.00	0.14
BCCH	Black-capped Chickadee	Poecile atricapillus	Not_at_risk	981	0.10	0.01	0.19
BDOW	Barred Owl	Strix varia	Not_at_risk	360	0.02	0.00	0.13
BLBW	Blackburnian Warbler	Dendroica fusca	Not_at_risk	529	0.06	0.00	0.55
BRCR	Brown Creeper	Certhia americana	Not_at_risk	602	0.02	0.00	0.09
BTBW	Black-throated Blue Warbler	Dendroica caerulescens	Not_at_risk	541	0.06	0.00	0.56
BTNW	Black-throated Green Warbler	Dendroica virens	Not_at_risk	708	0.07	0.00	0.48
BWHA	Broad-winged Hawk	Buteo platypterus	Not_at_risk	597	0.05	0.00	0.45
CAWA	Canada Warbler	Wilsonia canadensis	Threatened	516	0.04	0.00	0.37
CMWA	Cape May Warbler	Dendroica tigrina	Not_at_risk	140	0.02	0.00	0.06
COGO	Common Goldeneye	Bucephala clangula	Not_at_risk	74	0.02	0.00	0.05
COLO	Common Loon	Gavia immer	Not_at_risk	489	0.05	0.00	0.37
COME	Common Merganser	Mergus merganser	Not_at_risk	331	0.03	0.00	0.22
CORA	Common Raven	Corvus corax	Not_at_risk	613	0.07	0.00	0.48
COSN	Wilson's Snipe	Gallinago delicata	Not_at_risk	618	0.01	0.01	0.01
CSWA	Chestnut-sided	Dendroica	Not_at_risk	844	0.10	0.00	0.46

	Warbler	pensylvanica					
DEJU	Dark-eyed Junco	Junco hyemalis	Not_at_risk	308	0.04	0.00	0.25
EVGR	Evening Grosbeak	Hesperiphona vespertina	Not_at_risk	379	0.05	0.00	0.37
GCKI	Golden-crowned Kinglet	Regulus satrapa	Not_at_risk	445	0.04	0.00	0.39
GRAJ	Gray Jay	Perisoreus canadensis	Not_at_risk	202	0.05	0.00	0.12
GWWA	Golden-winged Warbler	Vermivora chrysoptera	Threatened	213	0.01	0.00	0.05
HAWO	Hairy Woodpecker	Picoides villosus	Not_at_risk	961	0.01	0.03	0.02
HERG	Herring Gull	Larus argentatus	Not_at_risk	218	0.03	0.00	0.20
HETH	Hermit Thrush	Catharus guttatus	Not_at_risk	583	0.07	0.00	0.58
HOME	Hooded Merganser	Lophodytes cucullatus	Not_at_risk	467	0.02	0.00	0.18
LEFL	Least Flycatcher	Empidonax minimus	Not_at_risk	912	0.03	0.00	0.11
LISP	Lincoln's Sparrow	Melospiza lincolnii	Not_at_risk	117	0.02	0.00	0.06
MAWA	Magnolia Warbler	Dendroica magnolia	Not_at_risk	606	0.07	0.00	0.57
MERL	Merlin	Falco columbarius	Not_at_risk	309	0.02	0.00	0.12
MOWA	Mourning Warbler	Oporornis philadelphia	Not_at_risk	750	0.02	0.00	0.09
NAWA	Nashville Warbler	Vermivora ruficapilla	Not_at_risk	725	0.08	0.00	0.49
NOGO	Northern Goshawk	Accipiter gentilis	Not_at_risk	187	0.01	0.04	0.01
NOPA	Northern Parula	Parula americana	Not_at_risk	158	0.03	0.00	0.10
NOWA	Northern Waterthrush	Seiurus noveboracensis	Not_at_risk	702	0.02	0.00	0.14
NSWO	Northern Saw-whet Owl	Aegolius acadicus	Not_at_risk	180	0.01	0.00	0.03
OSFL	Olive-sided Flycatcher	Contopus cooperi	Threatened	262	0.04	0.00	0.27
OSPR	Osprey	Pandion haliaetus	Not_at_risk	332	0.01	0.00	0.02
OVEN	Ovenbird	Seiurus aurocapilla	Not_at_risk	928	0.18	0.00	0.44
PBGR	Pied-billed Grebe	Podilymbus podiceps	Not_at_risk	351	0.00	0.05	0.01
PHVI	Philadelphia Vireo	Vireo philadelphicus	Not_at_risk	128	0.02	0.00	0.06
PISI	Pine Siskin	Carduelis pinus	Not_at_risk	235	0.02	0.00	0.11
PIWA	Pine Warbler	Dendroica pinus	Not_at_risk	619	0.02	0.00	0.09
PIWO	Pileated Woodpecker	Dryocopus pileatus	Not_at_risk	825	0.03	0.00	0.18
PUFI	Purple Finch	Carpodacus purpureus	Not_at_risk	688	0.06	0.00	0.48
RBNU	Red-breasted Nuthatch	Sitta canadensis	Not_at_risk	771	0.05	0.00	0.36
RCKI	Ruby-crowned Kinglet	Regulus calendula	Not_at_risk	274	0.04	0.00	0.33
RECR	Red Crossbill	Loxia curvirostra	Not_at_risk	64	0.02	0.00	0.07
RNDU	Ring-necked Duck	Aythya collaris	Not_at_risk	227	0.02	0.00	0.08

RSHA	Red-shouldered Hawk	Buteo lineatus	Not_at_risk	229	0.01	0.00	0.05
RUGR	Ruffed Grouse	Bonasa umbellus	Not_at_risk	839	0.04	0.00	0.18
SACR	Sandhill Crane	Grus canadensis	Not_at_risk	223	0.02	0.00	0.08
SWSP	Swamp Sparrow	Melospiza georgiana	Not_at_risk	893	0.05	0.00	0.24
SWTH	Swainson's Thrush	Catharus ustulatus	Not_at_risk	314	0.06	0.00	0.42
TEWA	Tennessee Warbler	Vermivora peregrina	Not_at_risk	103	0.02	0.03	0.02
VEER	Veery	Catharus fuscescens	Not_at_risk	906	0.12	0.00	0.41
WIWR	Winter Wren	Troglodytes troglodytes	Not_at_risk	699	0.05	0.00	0.40
WPWI	Whip-poor-will	Caprimulgus vociferus	Threatened	255	0.01	0.00	0.02
WTSP	White-throated Sparrow	Zonotrichia albicollis	Not_at_risk	791	0.13	0.00	0.54
WWCR	White-winged Crossbill	Loxia leucoptera	Not_at_risk	144	0.02	0.00	0.11
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris	Not_at_risk	187	0.05	0.00	0.24
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius	Not_at_risk	797	0.08	0.00	0.44
YRWA	Yellow-rumped Warbler	Dendroica coronata	Not_at_risk	689	0.08	0.00	0.55

OPEN-HABITAT SPECIES - Species whose probability of presence is a positive monotonic function of the amount of open land cover (n=79 species)							
Species	**English Name**	**Scientific Name**	**COSEWICK**	**NSQ**	**Coeff.**	**P**	**Nagelkerke_R.2**
AMCR	American Crow	Corvus brachyrhynchos	Not_at_risk	968	-0.07	0.00	0.20
AMGO	American Goldfinch	Carduelis tristis	Not_at_risk	949	-0.11	0.00	0.29
AMKE	American Kestrel	Falco sparverius	Not_at_risk	768	-0.05	0.00	0.36
AMWO	American Woodcock	Scolopax minor	Not_at_risk	742	-0.01	0.00	0.06
BANS	Bank Swallow	Riparia riparia	Not_at_risk	514	-0.03	0.00	0.28
BAOR	Baltimore Oriole	Icterus galbula	Not_at_risk	748	-0.09	0.00	0.59
BARS	Barn Swallow	Hirundo rustica	Threatened	856	-0.08	0.00	0.42
BBCU	Black-billed Cuckoo	Coccyzus erythropthalmus	Not_at_risk	708	-0.01	0.00	0.05
BGGN	Blue-gray Gnatcatcher	Polioptila caerulea	Not_at_risk	209	-0.04	0.00	0.14
BHCO	Brown-headed Cowbird	Molothrus ater	Not_at_risk	769	-0.08	0.00	0.55
BOBO	Bobolink	Dolichonyx oryzivorus	Not_at_risk	784	-0.07	0.00	0.48
BRTH	Brown Thrasher	Toxostoma rufum	Not_at_risk	793	-0.05	0.00	0.37
BWTE	Blue-winged Teal	Anas discors	Not_at_risk	344	-0.01	0.00	0.05
CAGO	Canada Goose	Branta canadensis	Not_at_risk	851	-0.04	0.00	0.28
CARW	Carolina Wren	Thryothorus ludovicianus	Not_at_risk	113	-0.03	0.00	0.08
CHSP	Chipping Sparrow	Spizella passerina	Not_at_risk	978	-0.13	0.04	0.22
CHSW	Chimney Swift	Chaetura pelagica	Threatened	439	-0.01	0.00	0.07
CLSW	Cliff Swallow	Petrochelidon pyrrhonota	Not_at_risk	565	-0.03	0.00	0.26
COGR	Common Grackle	Quiscalus quiscula	Not_at_risk	967	-0.06	0.00	0.17
COHA	Cooper's Hawk	Accipiter cooperii	Not_at_risk	409	-0.02	0.00	0.16
COTE	Common Tern	Sterna hirundo	Not_at_risk	36	-0.02	0.02	0.05
DOWO	Downy Woodpecker	Picoides pubescens	Not_at_risk	948	-0.03	0.00	0.09
EABL	Eastern Bluebird	Sialia sialis	Not_at_risk	677	-0.02	0.00	0.15
EAKI	Eastern Kingbird	Tyrannus tyrannus	Not_at_risk	909	-0.06	0.00	0.27
EAME	Eastern Meadowlark	Sturnella magna	Threatened	739	-0.07	0.00	0.52
EAPH	Eastern Phoebe	Sayornis phoebe	Not_at_risk	899	-0.03	0.00	0.14
EASO	Eastern Screech-Owl	Megascops asio	Not_at_risk	483	-0.06	0.00	0.46
EAWP	Eastern Wood-Pewee	Contopus virens	Not_at_risk	870	-0.05	0.00	0.27
EUST	European Starling	Sturnus vulgaris	Not_at_risk	844	-0.14	0.00	0.52
FISP	Field Sparrow	Spizella pusilla	Not_at_risk	596	-0.03	0.00	0.22
GADW	Gadwall	Anas strepera	Not_at_risk	57	-0.01	0.03	0.02
GCFL	Great Crested Flycatcher	Myiarchus crinitus	Not_at_risk	922	-0.05	0.00	0.24

GHOW	Great Horned Owl	Bubo virginianus	Not_at_risk	536	-0.03	0.00	0.29
GRCA	Gray Catbird	Dumetella carolinensis	Not_at_risk	842	-0.07	0.00	0.43
GRHE	Green Heron	Butorides virescens	Not_at_risk	514	-0.03	0.00	0.25
GRSP	Grasshopper Sparrow	Ammodramus savannarum	Not_at_risk	288	-0.01	0.00	0.03
HOFI	House Finch	Carpodacus mexicanus	Not_at_risk	551	-0.07	0.00	0.56
HOLA	Horned Lark	Eremophila alpestris	Not_at_risk	528	-0.09	0.00	0.64
HOSP	House Sparrow	Passer domesticus	Not_at_risk	658	-0.09	0.00	0.69
HOWR	House Wren	Troglodytes aedon	Not_at_risk	720	-0.07	0.00	0.57
INBU	Indigo Bunting	Passerina cyanea	Not_at_risk	883	-0.05	0.00	0.28
KILL	Killdeer	Charadrius vociferus	Not_at_risk	802	-0.08	0.00	0.49
MALL	Mallard	Anas platyrhynchos	Not_at_risk	878	-0.04	0.00	0.23
MODO	Mourning Dove	Zenaida macroura	Not_at_risk	849	-0.10	0.00	0.47
NOCA	Northern Cardinal	Cardinalis cardinalis	Not_at_risk	602	-0.08	0.00	0.65
NOHA	Northern Harrier	Circus cyaneus	Not_at_risk	661	-0.03	0.00	0.20
NOMO	Northern Mockingbird	Mimus polyglottos	Not_at_risk	174	-0.02	0.00	0.08
NRWS	Northern Rough-winged Swallow	Stelgidopteryx serripennis	Not_at_risk	545	-0.04	0.00	0.36
NSHO	Northern Shoveler	Anas clypeata	Not_at_risk	61	-0.01	0.02	0.02
OROR	Orchard Oriole	Icterus spurius	Not_at_risk	161	-0.04	0.00	0.11
PUMA	Purple Martin	Progne subis	Not_at_risk	283	-0.02	0.00	0.09
RBGR	Rose-breasted Grosbeak	Pheucticus ludovicianus	Not_at_risk	950	-0.02	0.00	0.06
RBWO	Red-bellied Woodpecker	Melanerpes carolinus	Not_at_risk	279	-0.06	0.00	0.27
RHWO	Red-headed Woodpecker	Melanerpes erythrocephalus	Threatened	172	-0.02	0.00	0.05
RIPH	Ring-necked Pheasant	Phasianus colchicus	Not_at_risk	169	-0.03	0.00	0.09
RODO	Rock Pigeon	Columba livia	Not_at_risk	752	-0.09	0.00	0.57
RTHA	Red-tailed Hawk	Buteo jamaicensis	Not_at_risk	813	-0.05	0.00	0.38
RTHU	Ruby-throated Hummingbird	Archilochus colubris	Not_at_risk	927	-0.01	0.00	0.03
RUDU	Ruddy Duck	Oxyura jamaicensis	Not_at_risk	45	-0.03	0.02	0.03
RWBL	Red-winged Blackbird	Agelaius phoeniceus	Not_at_risk	944	-0.09	0.00	0.27
SAVS	Savannah Sparrow	Passerculus sandwichensis	Not_at_risk	819	-0.11	0.00	0.53
SORA	Sora	Porzana carolina	Not_at_risk	339	-0.01	0.00	0.05
SOSP	Song Sparrow	Melospiza melodia	Not_at_risk	977	-0.30	0.01	0.28

SPSA	Spotted Sandpiper	Tringa macularia	Not_at_risk	761	-0.03	0.00	0.22
SSHA	Sharp-shinned Hawk	Accipiter striatus	Not_at_risk	524	-0.01	0.00	0.03
TRES	Tree Swallow	Tachycineta bicolor	Not_at_risk	932	-0.06	0.00	0.26
TUVU	Turkey Vulture	Cathartes aura	Not_at_risk	847	-0.02	0.00	0.08
UPSA	Upland Sandpiper	Bartramia longicauda	Not_at_risk	303	-0.02	0.00	0.07
VESP	Vesper Sparrow	Pooecetes gramineus	Not_at_risk	659	-0.04	0.00	0.39
WAVI	Warbling Vireo	Vireo gilvus	Not_at_risk	775	-0.07	0.00	0.50
WBNU	White-breasted Nuthatch	Sitta carolinensis	Not_at_risk	839	-0.03	0.00	0.18
WIFL	Willow Flycatcher	Empidonax traillii	Not_at_risk	518	-0.05	0.00	0.48
WITU	Wild Turkey	Meleagris gallopavo	Not_at_risk	543	-0.02	0.00	0.14
WIWA	Wilson's Warbler	Wilsonia pusilla	Not_at_risk	42	-0.03	0.01	0.07
WODU	Wood Duck	Aix sponsa	Not_at_risk	831	-0.02	0.00	0.06
WOTH	Wood Thrush	Catharus mustelinus	Not_at_risk	836	-0.05	0.00	0.31
YBCU	Yellow-billed Cuckoo	Coccyzus americanus	Not_at_risk	221	-0.02	0.00	0.09
YTVI	Yellow-throated Vireo	Vireo flavifrons	Not_at_risk	277	-0.01	0.01	0.01
YWAR	Yellow Warbler	Dendroica petechia	Not_at_risk	932	-0.18	0.00	0.37

Fragmentation-sensitive SPECIES - Species whose probability of presence is a negative monotonic function of the number of forest patches (n=41 species)

Species	English Name	Scientific Name	COSEWICK	NSQ	Coeff.	P	Nagelkerke_R.2
ABDU	American Black Duck	Anas rubripes	Not_at_risk	370	0.00	0.00	0.02
ALFL	Alder Flycatcher	Empidonax alnorum	Not_at_risk	826	0.00	0.03	0.01
AMBI	American Bittern	Botaurus lentiginosus	Not_at_risk	502	0.00	0.02	0.01
AMRE	American Redstart	Setophaga ruticilla	Not_at_risk	912	0.00	0.15	0.00
BAWW	Black-and-white Warbler	Mniotilta varia	Not_at_risk	777	-0.01	0.00	0.05
BLJA	Blue Jay	Cyanocitta cristata	Not_at_risk	986	-0.01	0.27	0.02
BOCH	Boreal Chickadee	Poecile hudsonica	Not_at_risk	40	-0.01	0.30	0.02
BRCR	Brown Creeper	Certhia americana	Not_at_risk	602	0.00	0.00	0.02
CATE	Caspian Tern	Sterna caspia	Not_at_risk	14	0.00	0.83	0.00
CERW	Cerulean Warbler	Dendroica cerulea	Endangered	42	0.00	0.40	0.00
CSWA	Chestnut-sided Warbler	Dendroica pensylvanica	Not_at_risk	844	0.00	0.00	0.02
DCCO	Double-crested Cormorant	Phalacrocorax auritus	Not_at_risk	58	0.00	0.08	0.01
GWWA	Golden-winged Warbler	Vermivora chrysoptera	Threatened	213	0.00	0.16	0.00
LCSP	Le Conte's Sparrow	Ammodramus leconteii	Not_at_risk	13	0.00	0.80	0.00
LESC	Lesser Scaup	Aythya affinis	Not_at_risk	20	0.00	0.91	0.00
LISP	Lincoln's Sparrow	Melospiza lincolnii	Not_at_risk	117	0.00	0.00	0.04
MOWA	Mourning Warbler	Oporornis philadelphia	Not_at_risk	750	0.00	0.00	0.04
NOBO	Northern Bobwhite	Colinus virginianus	Not_at_risk	16	0.00	0.76	0.00
NOWA	Northern Waterthrush	Seiurus noveboracensis	Not_at_risk	702	0.00	0.37	0.00
NSWO	Northern Saw-whet Owl	Aegolius acadicus	Not_at_risk	180	0.00	0.01	0.01
OROR	Orchard Oriole	Icterus spurius	Not_at_risk	161	0.00	0.04	0.01
PEFA	Peregrine Falcon	Falco peregrinus	Special Concern	19	0.00	0.64	0.00
PHVI	Philadelphia	Vireo	Not_at	128	0.00	0.0	0.04

	Vireo	philadelphicus	_risk			0	
PIWA	Pine Warbler	Dendroica pinus	Not_at_risk	619	0.00	0.00	0.03
PIWO	Pileated Woodpecker	Dryocopus pileatus	Not_at_risk	825	0.00	0.01	0.01
PRAW	Prairie Warbler	Dendroica discolor	Not_at_risk	16	0.00	0.21	0.02
RBME	Red-breasted Merganser	Mergus serrator	Not_at_risk	19	0.00	0.82	0.00
RBWO	Red-bellied Woodpecker	Melanerpes carolinus	Not_at_risk	279	0.00	0.01	0.02
RSHA	Red-shouldered Hawk	Buteo lineatus	Not_at_risk	229	0.00	0.03	0.01
RUBL	Rusty Blackbird	Euphagus carolinus	Special Concern	42	0.00	0.21	0.01
RUDU	Ruddy Duck	Oxyura jamaicensis	Not_at_risk	45	0.00	0.25	0.01
RUGR	Ruffed Grouse	Bonasa umbellus	Not_at_risk	839	0.00	0.04	0.01
SACR	Sandhill Crane	Grus canadensis	Not_at_risk	223	0.00	0.00	0.03
SOSA	Solitary Sandpiper	Tringa solitaria	LC	21	-0.01	0.21	0.04
SPGR	Spruce Grouse	Falcipennis canadensis	Not_at_risk	38	0.00	0.21	0.02
TEWA	Tennessee Warbler	Vermivora peregrina	Not_at_risk	103	-0.01	0.03	0.03
VEER	Veery	Catharus fuscescens	Not_at_risk	906	0.00	0.70	0.00
WEME	Western Meadowlark	Sturnella neglecta	Not_at_risk	12	0.00	0.71	0.00
WPWI	Whip-poor-will	Caprimulgus vociferus	Threatened	255	0.00	0.25	0.00
WTSP	White-throated Sparrow	Zonotrichia albicollis	Not_at_risk	791	-0.01	0.00	0.05
YBCH	Yellow-breasted Chat	Icteria virens	Endangered	13	0.00	0.67	0.00

Table S2-2. Forest and Open-habitat habitat species defined by the Atlas of Breeding Birds of Ontario (Cadman et al. (2007).

Forest Species (n=89 species)			
species	**species_english_name**	**Scientific_Name**	**Land Cover Type**
ACFL	Acadian Flycatcher	Empidonax virescens	Forest
AMRE	American Redstart	Setophaga ruticilla	Forest
AMWO	American Woodcock	Scolopax minor	Forest
BAEA	Bald Eagle	Haliaeetus leucocephalus	Forest
BAOR	Baltimore Oriole	Icterus galbula	Forest
BAWW	Black-and-white Warbler	Mniotilta varia	Forest
BBWA	Bay-breasted Warbler	Dendroica castanea	Forest
BBWO	Black-backed Woodpecker	Picoides arcticus	Forest
BDOW	Barred Owl	Strix varia	Forest
BGGN	Blue-gray Gnatcatcher	Polioptila caerulea	Forest
BLBW	Blackburnian Warbler	Dendroica fusca	Forest
BOCH	Boreal Chickadee	Poecile hudsonica	Forest
BRCR	Brown Creeper	Certhia americana	Forest
BTBW	Black-throated Blue Warbler	Dendroica caerulescens	Forest
BTNW	Black-throated Green Warbler	Dendroica virens	Forest
BWHA	Broad-winged Hawk	Buteo platypterus	Forest
CAWA	Canada Warbler	Wilsonia canadensis	Forest
CERW	Cerulean Warbler	Dendroica cerulea	Forest
CHSP	Chipping Sparrow	Spizella passerina	Forest
CMWA	Cape May Warbler	Dendroica tigrina	Forest
COHA	Cooper's Hawk	Accipiter cooperii	Forest
COME	Common Merganser	Mergus merganser	Forest
CORA	Common Raven	Corvus corax	Forest
COTE	Common Tern	Sterna hirundo	Forest
DOWO	Downy Woodpecker	Picoides pubescens	Forest
EASO	Eastern Screech-Owl	Megascops asio	Forest
EAWP	Eastern Wood-Pewee	Contopus virens	Forest
EVGR	Evening Grosbeak	Hesperiphona vespertina	Forest
GBHE	Great Blue Heron	Ardea herodias	Forest
GCFL	Great Crested Flycatcher	Myiarchus crinitus	Forest
GCKI	Golden-crowned Kinglet	Regulus satrapa	Forest
GHOW	Great Horned Owl	Bubo virginianus	Forest
GRAJ	Gray Jay	Perisoreus canadensis	Forest
GRHE	Green Heron	Butorides virescens	Forest

GWTE	Green-winged Teal	Anas crecca	Forest
HAWO	Hairy Woodpecker	Picoides villosus	Forest
HETH	Hermit Thrush	Catharus guttatus	Forest
HOME	Hooded Merganser	Lophodytes cucullatus	Forest
HOWA	Hooded Warbler	Wilsonia citrina	Forest
LEFL	Least Flycatcher	Empidonax minimus	Forest
LEOW	Long-eared Owl	Asio otus	Forest
LOWA	Louisiana Waterthrush	Seiurus motacilla	Forest
MAWA	Magnolia Warbler	Dendroica magnolia	Forest
MERL	Merlin	Falco columbarius	Forest
MOWA	Mourning Warbler	Oporornis philadelphia	Forest
NAWA	Nashville Warbler	Vermivora ruficapilla	Forest
NOFL	Northern Flicker	Colaptes auratus	Forest
NOGO	Northern Goshawk	Accipiter gentilis	Forest
NOPA	Northern Parula	Parula americana	Forest
NOWA	Northern Waterthrush	Seiurus noveboracensis	Forest
NSWO	Northern Saw-whet Owl	Aegolius acadicus	Forest
OROR	Orchard Oriole	Icterus spurius	Forest
OSFL	Olive-sided Flycatcher	Contopus cooperi	Forest
OVEN	Ovenbird	Seiurus aurocapilla	Forest
PBGR	Pied-billed Grebe	Podilymbus podiceps	Forest
PHVI	Philadelphia Vireo	Vireo philadelphicus	Forest
PISI	Pine Siskin	Carduelis pinus	Forest
PIWA	Pine Warbler	Dendroica pinus	Forest
PIWO	Pileated Woodpecker	Dryocopus pileatus	Forest
PUFI	Purple Finch	Carpodacus purpureus	Forest
RBGR	Rose-breasted Grosbeak	Pheucticus ludovicianus	Forest
RBNU	Red-breasted Nuthatch	Sitta canadensis	Forest
RBWO	Red-bellied Woodpecker	Melanerpes carolinus	Forest
RCKI	Ruby-crowned Kinglet	Regulus calendula	Forest
RECR	Red Crossbill	Loxia curvirostra	Forest
REVI	Red-eyed Vireo	Vireo olivaceus	Forest
RHWO	Red-headed Woodpecker	Melanerpes erythrocephalus	Forest
RSHA	Red-shouldered Hawk	Buteo lineatus	Forest
RTHU	Ruby-throated Hummingbird	Archilochus colubris	Forest
RUGR	Ruffed Grouse	Bonasa umbellus	Forest
SCTA	Scarlet Tanager	Piranga olivacea	Forest
SPGR	Spruce Grouse	Falcipennis canadensis	Forest
SSHA	Sharp-shinned Hawk	Accipiter striatus	Forest
SWTH	Swainson's Thrush	Catharus ustulatus	Forest

TEWA	Tennessee Warbler	Vermivora peregrina	Forest
TUTI	Tufted Titmouse	Baeolophus bicolor	Forest
VEER	Veery	Catharus fuscescens	Forest
WAVI	Warbling Vireo	Vireo gilvus	Forest
WBNU	White-breasted Nuthatch	Sitta carolinensis	Forest
WITU	Wild Turkey	Meleagris gallopavo	Forest
WIWR	Winter Wren	Troglodytes troglodytes	Forest
WODU	Wood Duck	Aix sponsa	Forest
WOTH	Wood Thrush	Catharus mustelinus	Forest
WPWI	Whip-poor-will	Caprimulgus vociferus	Forest
WWCR	White-winged Crossbill	Loxia leucoptera	Forest
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris	Forest
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius	Forest
YRWA	Yellow-rumped Warbler	Dendroica coronata	Forest
YTVI	Yellow-throated Vireo	Vireo flavifrons	Forest

Open-habitat Species (n=113 species)

species	**species_english_name**	**Scientific_Name**	**Land Cover Species Type**
ABDU	American Black Duck	Anas rubripes	Open Habitat
ALFL	Alder Flycatcher	Empidonax alnorum	Open Habitat
AMBI	American Bittern	Botaurus lentiginosus	Open Habitat
AMCO	American Coot	Fulica americana	Open Habitat
AMCR	American Crow	Corvus brachyrhynchos	Open Habitat
AMGO	American Goldfinch	Carduelis tristis	Open Habitat
AMKE	American Kestrel	Falco sparverius	Open Habitat
AMRO	American Robin	Turdus migratorius	Open Habitat
AMWI	American Wigeon	Anas americana	Open Habitat
BANS	Bank Swallow	Riparia riparia	Open Habitat
BARS	Barn Swallow	Hirundo rustica	Open Habitat
BBCU	Black-billed Cuckoo	Coccyzus erythropthalmus	Open Habitat
BCCH	Black-capped Chickadee	Poecile atricapillus	Open Habitat
BCNH	Black-crowned Night-Heron	Nycticorax nycticorax	Open Habitat
BEKI	Belted Kingfisher	Megaceryle alcyon	Open Habitat
BHCO	Brown-headed Cowbird	Molothrus ater	Open Habitat
BLJA	Blue Jay	Cyanocitta cristata	Open Habitat
BLTE	Black Tern	Chlidonias niger	Open Habitat
BOBO	Bobolink	Dolichonyx oryzivorus	Open Habitat
BRBL	Brewer's Blackbird	Euphagus cyanocephalus	Open Habitat
BRTH	Brown Thrasher	Toxostoma rufum	Open Habitat
BRWA	Brewster's Warbler	Hybrid	Open Habitat
BUFF	Bufflehead	Bucephala albeola	Open Habitat

BWTE	Blue-winged Teal	Anas discors	Open Habitat
BWWA	Blue-winged Warbler	Vermivora pinus	Open Habitat
CAGO	Canada Goose	Branta canadensis	Open Habitat
CARW	Carolina Wren	Thryothorus ludovicianus	Open Habitat
CATE	Caspian Tern	Sterna caspia	Open Habitat
CCSP	Clay-colored Sparrow	Spizella pallida	Open Habitat
CEDW	Cedar Waxwing	Bombycilla cedrorum	Open Habitat
CHSW	Chimney Swift	Chaetura pelagica	Open Habitat
CLSW	Cliff Swallow	Petrochelidon pyrrhonota	Open Habitat
COGO	Common Goldeneye	Bucephala clangula	Open Habitat
COGR	Common Grackle	Quiscalus quiscula	Open Habitat
COLO	Common Loon	Gavia immer	Open Habitat
COMO	Common Moorhen	Gallinula chloropus	Open Habitat
CONI	Common Nighthawk	Chordeiles minor	Open Habitat
COSN	Wilson's Snipe	Gallinago delicata	Open Habitat
COYE	Common Yellowthroat	Geothlypis trichas	Open Habitat
CSWA	Chestnut-sided Warbler	Dendroica pensylvanica	Open Habitat
DCCO	Double-crested Cormorant	Phalacrocorax auritus	Open Habitat
DEJU	Dark-eyed Junco	Junco hyemalis	Open Habitat
EABL	Eastern Bluebird	Sialia sialis	Open Habitat
EAKI	Eastern Kingbird	Tyrannus tyrannus	Open Habitat
EAME	Eastern Meadowlark	Sturnella magna	Open Habitat
EAPH	Eastern Phoebe	Sayornis phoebe	Open Habitat
EUST	European Starling	Sturnus vulgaris	Open Habitat
FISP	Field Sparrow	Spizella pusilla	Open Habitat
GADW	Gadwall	Anas strepera	Open Habitat
GRCA	Gray Catbird	Dumetella carolinensis	Open Habitat
GREG	Great Egret	Ardea alba	Open Habitat
GRPA	Gray Partridge	Perdix perdix	Open Habitat
GRSP	Grasshopper Sparrow	Ammodramus savannarum	Open Habitat
GWWA	Golden-winged Warbler	Vermivora chrysoptera	Open Habitat
HERG	Herring Gull	Larus argentatus	Open Habitat
HOFI	House Finch	Carpodacus mexicanus	Open Habitat
HOLA	Horned Lark	Eremophila alpestris	Open Habitat
HOSP	House Sparrow	Passer domesticus	Open Habitat
HOWR	House Wren	Troglodytes aedon	Open Habitat
INBU	Indigo Bunting	Passerina cyanea	Open Habitat
KILL	Killdeer	Charadrius vociferus	Open Habitat
LCSP	Le Conte's Sparrow	Ammodramus leconteii	Open Habitat
LEBI	Least Bittern	Ixobrychus exilis	Open Habitat
LESC	Lesser Scaup	Aythya affinis	Open Habitat

LISP	Lincoln's Sparrow	Melospiza lincolnii	Open Habitat
LOSH	Loggerhead Shrike	Lanius ludovicianus	Open Habitat
MALL	Mallard	Anas platyrhynchos	Open Habitat
MAWR	Marsh Wren	Cistothorus palustris	Open Habitat
MODO	Mourning Dove	Zenaida macroura	Open Habitat
MUSW	Mute Swan	Cygnus olor	Open Habitat
NOBO	Northern Bobwhite	Colinus virginianus	Open Habitat
NOCA	Northern Cardinal	Cardinalis cardinalis	Open Habitat
NOHA	Northern Harrier	Circus cyaneus	Open Habitat
NOMO	Northern Mockingbird	Mimus polyglottos	Open Habitat
NOPI	Northern Pintail	Anas acuta	Open Habitat
NRWS	Northern Rough-winged Swallow	Stelgidopteryx serripennis	Open Habitat
NSHO	Northern Shoveler	Anas clypeata	Open Habitat
OSPR	Osprey	Pandion haliaetus	Open Habitat
PEFA	Peregrine Falcon	Falco peregrinus	Open Habitat
PRAW	Prairie Warbler	Dendroica discolor	Open Habitat
PUMA	Purple Martin	Progne subis	Open Habitat
RBGU	Ring-billed Gull	Larus delawarensis	Open Habitat
RBME	Red-breasted Merganser	Mergus serrator	Open Habitat
RIPH	Ring-necked Pheasant	Phasianus colchicus	Open Habitat
RNDU	Ring-necked Duck	Aythya collaris	Open Habitat
RODO	Rock Pigeon	Columba livia	Open Habitat
RTHA	Red-tailed Hawk	Buteo jamaicensis	Open Habitat
RUBL	Rusty Blackbird	Euphagus carolinus	Open Habitat
RUDU	Ruddy Duck	Oxyura jamaicensis	Open Habitat
RWBL	Red-winged Blackbird	Agelaius phoeniceus	Open Habitat
SACR	Sandhill Crane	Grus canadensis	Open Habitat
SAVS	Savannah Sparrow	Passerculus sandwichensis	Open Habitat
SEOW	Short-eared Owl	Asio flammeus	Open Habitat
SEWR	Sedge Wren	Cistothorus platensis	Open Habitat
SORA	Sora	Porzana carolina	Open Habitat
SOSA	Solitary Sandpiper	Tringa solitaria	Open Habitat
SOSP	Song Sparrow	Melospiza melodia	Open Habitat
SPSA	Spotted Sandpiper	Tringa macularia	Open Habitat
SWSP	Swamp Sparrow	Melospiza georgiana	Open Habitat
TRES	Tree Swallow	Tachycineta bicolor	Open Habitat
TRUS	Trumpeter Swan	Cygnus buccinator	Open Habitat
TUVU	Turkey Vulture	Cathartes aura	Open Habitat
UPSA	Upland Sandpiper	Bartramia longicauda	Open Habitat
VESP	Vesper Sparrow	Pooecetes gramineus	Open Habitat
VIRA	Virginia Rail	Rallus limicola	Open Habitat

WEME	Western Meadowlark	Sturnella neglecta	Open Habitat
WIFL	Willow Flycatcher	Empidonax traillii	Open Habitat
WIPH	Wilson's Phalarope	Steganopus tricolor	Open Habitat
WIWA	Wilson's Warbler	Wilsonia pusilla	Open Habitat
WTSP	White-throated Sparrow	Zonotrichia albicollis	Open Habitat
YBCH	Yellow-breasted Chat	Icteria virens	Open Habitat
YBCU	Yellow-billed Cuckoo	Coccyzus americanus	Open Habitat
YWAR	Yellow Warbler	Dendroica petechia	Open Habitat

CHAPTER 3

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RUNNING TITLE

Land cover modification shapes edge-species

TITLE

Avian species-level' responses to land cover at the southern- and northern-margin of their distributions.

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ABSTRACT

Aim: Climate and habitat conditions are among the main drivers of species' occupancy in space and time. Potentially, climate change and habitat loss may interact: habitat loss may impede the colonization or movement of species whose ranges are shifting in response to climate. Here, we examined individual bird species' probability of occupancy of 100-km^2 landscapes in southern Ontario, Canada, as a function of the amount of remaining natural land cover.

Location: southern Ontario, Canada.

Time period: 2000-2005.

Major taxa studied: Birds.

Methods: Climate warming should push species northward. We compared three groups of species: i) those whose northern range limit falls within the study area, ii) those whose southern range limit is in the study area, and iii) those whose ranges cover the entire study area.

Results: We found that southern-edge species are *less* likely to occur in landscapes with reduced natural land cover (i.e. forest), while northern-edge species are *more* likely to occur in landscapes with reduced natural land cover.

Main Conclusions: The climate change literature often proposes that habitat loss at the leading edge of shifting ranges should inhibit movement. Our results suggest the contrary: at southern range edges, the dual stresses of climatic warming and habitat conversion are especially negative. However, at northern (potentially expanding) range edges, partially disturbed landscapes are more readily occupied than undisturbed landscapes.

KEYWORDS

Habitat loss, climate change, logistic regression, species' probability of occurrence, bird species, range limits, southern Ontario.

INTRODUCTION

As climate changes worldwide, rather than adapting *in situ*, species' ranges are expected to shift as a function of climatic suitability (Hill *et al.*, 2002). The question is whether species can colonize new environments beyond their current range boundaries, especially when habitat has been modified by human activities. Consequently, populations living at the margin of a species' range are likely to be most sensitive to the environmental changes (Sexton *et al.*, 2009) and may offer opportunities to study the effects of combinations of environmental stressors on those species (Hampe & Petit, 2005).

Species' capacity to adapt to environmental changes could be determined by responses of populations living at range margins (Sexton *et al.*, 2009; Thomas, 2010; Sultaire *et al.*, 2016). Marginal populations are likely to experience greater variability in survival and reproduction due to limiting factors (Sexton *et al.*, 2009). For example, marginal populations might be more prone to extinction due to habitats or climates that exceed individual species' preferences (Kirkpatrick & Barton, 1997), which ultimately determine limits of a species' niche (Brown, 1984; Parmesan *et al.*, 2005). Increased extinction proneness could be due to lower genetic variability in edge-populations in comparison to central ones (e.g. "central-marginal" hypothesis, Eckert et al., 2008), driven by spatial isolation, habitat fragmentation or heterogeneity that reduces gene flow (Eckert *et al.*, 2008). Yet whether or not marginal populations have higher probability of extinction than those from the centre has been challenged (Channell & Lomolino, 2000; Sagarin & Gaines, 2002; Vucetich & Waite, 2003).

Warmer temperatures may threaten the survival of species at warm-edge range boundaries (i.e. the southern edge of northern hemisphere species' ranges) (Pearson *et al.*, 2009; Thomas, 2010), but warming may also provide new habitat opportunities for populations at the cold-edge of their distributions (i.e. the northern edge of species' ranges) (Thomas *et al.*, 1999; Lennon *et al.*, 2002; Oliver *et al.*, 2012). If northern-edge populations have been limited by their cold thermal limits, climatic warming should lead to larger population sizes and range expansion (Thomas *et al.*, 2001; Davies *et al.*, 2006). On the other hand, southern range edges should retract poleward when hit by warmer temperatures (Hampe & Petit, 2005; Anderson *et al.*, 2009; Sunday *et al.*, 2012).

Species' colonization and extinction rates at range boundaries may depend upon habitat availability (Opdam & Wascher, 2004). It has often been argued that habitat loss and modification might accelerate regional species extinction, and create barriers to range shifts (Robillard *et al.*, 2015). Opdam & Wascher (2004) theoretically argue that landscape with low levels of spatial cohesion due to natural habitat loss or fragmentation may inhibit the movement of species tracking climate change. Alternatively, species colonizing novel areas may actually do better in partially disturbed environments, perhaps due to reduced "biotic resistance" (Guo *et al.*, 2012; González-Moreno *et al.*, 2015). For instance, Collingham & Huntley (2000) using simulation models showed that migration rates of the wind-dispersed tree *Tilia cordata* is reduced when habitat availability fell below 25% of the landscape area, especially in landscapes composed of fewer larger patches.

Here we test whether avian populations at the northern and southern margins of their geographical ranges respond differently to the amount of natural land cover remaining in the landscape. Most studies of northern and southern range edges have considered a fixed set of species in different geographic regions. Here, we use a complementary approach: to avoid the confounding effects of environmental variables other than land cover that may also differ between southern-edge and northern-edge boundaries, we examined a single region, in which a large number of both northern and southern range species' range limits occur. (i.e. the southern edge of northerly species, and the northern edge of southerly species).

METHODS

Study Area

Our study area covers southern Ontario, Canada (41º – 44º N and 84º – 74º W, ~ 200,000 km^2, see Fig. 1 in De Camargo and Currie 2015). Historically, southern Ontario was mainly forested. Natural land cover was heavily altered during European settlement in the 18th – 19th centuries (Warwick 1980). After the mid 20th century, government programs began promoting selective harvesting and silviculture on private woodlots in southern Ontario (Thompson et al. 2000, p. 84; Ontario Ministry of Natural Resources 2015). As a result, the amount of forest cover has been relatively stable for the last 70 years. Landscapes vary from entirely forested to entirely human-dominated land covers.

Bird species distributions

We used 100-km^2 UTM (Universal Transverse Mercator) quadrats (i.e., landscapes) as our sampling units. We excluded wedge-shaped UTM quadrats, and quadrats with more than 10% lake area, to minimize variation in area among quadrats. Sampling effort varied considerably among quadrats. We therefore excluded quadrats with <20 or >600 hours of bird censusing effort (Cadman et al. 2007), and we used hours of sampling effort in the remaining 991 landscapes as a covariate in our models.

We used bird species distributions in southern Ontario (Canada) reported in the 2005 Ontario Breeding Bird Atlas (OBBA) (Fig. 1, Cadman *et al*., 2007). The OBBA reports the presence or absence of 202 breeding bird species in 10 km x 10 km landscapes (see Fig. 1). We excluded the data from the northern parts of the province where the OBBA quadrats were 100 km x 100 km, and sampling intensity was much lower. Volunteer ornithologists searched each OBBA landscape as thoroughly as possible for evidence of breeding birds over a five-year period (2000 – 2005). We eliminated species that occurred in <15% or >85% of the quadrats (i.e. quite rare or nearly ubiquitous), because the probability of occupancy of these species is nearly invariant among quadrats (Jiménez-Valverde *et al.*, 2008). Statistical analyses were performed with 128 bird species in 991 landscapes.

Species also were tallied up according to their preferred habitat, as characterized in Cadman et al. (2007). We used two categories: **forest** (n=46) and **non-forest** (n=82) species. The forest category includes "interior-edge" species that facultatively use forest land cover (n=22 species), and "forest-interior" species, which totally depend on forest interior to nest and/or to feed (n=24 species). The non-forest group of birds include "edge" species commonly found close to forest edges, rather than in the forest interior (n=13 species); "open-habitat" species found in grasslands, disturbed woodlands, scrub or hills / mountains (n=34 species); "urban" birds that are adapted to live in cities, nesting in buildings, backyards, light posts, etc. (n=7 species); and "wetland" specialist species found close to lakes or ponds, shorelines, marshes or close to river stream (n= 28 species).

Species' range margins

Many bird species present in our data reach the southern edge of their range within our study area (southern-edge species, n=25, Fig. 1), but they are commonly found farther north. Other species' ranges (northern-edge species, n=24) reach their northern limit in the study area (Fig. 1) but are commonly found farther south. Species with ranges extending over the entire study area were grouped as "mid-range" species (n=79 species). BirdLife range maps (www.birdlife.org) were used in order to classify these three groups of species.

To a degree, southern-edge species in southern Ontario are mainly associated with the coniferous forests of the Laurentian Shield, while northern-edge species are species characteristic of the mixed-wood forests bordering the Great Lakes (Fig. 1). However, the distributions of these species are not strictly limited to the biomes where they are most common, and there is no distinct boundary between the two (Fig. 1).

Natural Land Cover

We assessed the amount of natural- and human-dominated land cover for each OBBA square using the methodology described in De Camargo & Currie (2015). Remotely-sensed land cover data were obtained from the Ontario Provincial-Scale Land Cover data set produced by the Ontario Ministry of Natural Resources (2002). Five classes were considered human-dominated: recent cutovers, mine tailings, quarries and bedrock outcrops, settlement and developed land, and cropland. We considered the remaining land covers to be "natural", including forest (9 classes including older regenerated forest after clear-cuts and forest fires), and wetlands (7 classes). We included the small amounts of coniferous plantation that occur in southern Ontario in natural cover because plantations share more avian species with natural forests than they do with human-dominated land cover. Four other classes in the land cover classification did not occur in the study area. Total area is held constant by the fixed quadrat size.

Statistical Analysis

In order to test our predictions, first we relate individual species' probability of occurrence (p_{occ}) in each OBBA landscapes as a function the amount of remaining forest cover. We considered a species as being absent from a quadrat only if that quadrat fell within 20 km of an occupied quadrat. Otherwise, the quadrat was excluded from analysis for that species, since the quadrat may be unoccupied because it is out of the species' range, rather than due to land cover. Thus, our analyses relate presence/absence to land cover in occupied quadrats and neighbouring unoccupied quadrats.

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

$$\mathrm{p}_{occ} = \frac{e^{\alpha_i+\beta_1 A+\ \beta_2 A^2+\beta_3 log_{10}Effort}}{1+e^{\alpha_i+\beta_1 A+\ \beta_2 A^2+\beta_3 log_{10}Effort}}$$

(1)

We used the quadratic term in the logistic model because it better describes the shape of the relationship between species' probability of occurrence and area for about half of the species in comparison to models that included only the linear term (ΔAIC<-2, *Appendix 1*).

Bird species' sensitivity to low amount of natural land cover

The main goal of this study is to test whether the sensitivity of bird populations to the amount of forest land cover differs between southern-edge species and northern-edge species. We therefore compared the predicted species' probability of occurrence $\hat{p}_{occ}$

in low densities of natural land cover, versus $\hat{\rho}_{occ}$ in fully forested landscapes. To do this, we first fitted $\hat{\rho}_{occ}$ as a function of forest cover amount using eq. (1) for all 128 species in our data. Then, we calculated each species' sensitivity (Ω_i) to a given amount of land cover *i* below 100% as the ratio of predicted probability of occurrence $\hat{\rho}_{occ}$ within landscapes with reduced forest cover (e.g. 15% forest cover) relative to the probability of occurrence with 100% natural cover:

$$\Omega_i = \log_{10}\left(\frac{\hat{\rho}_{occ}(A_i{=}5\%,10\%\ldots95\%\ cover)}{\hat{\rho}_{occ}(A_{100}{=}100\%\ cover,)}\right)$$

(2)

where $\hat{\rho}_{occ}(A_i = 5\%, 10\% \ldots 95\%)$ is the predicted probability of occurrence of a species for a range of natural cover from 5%, to 95%, and $\hat{\rho}_{occ}(A_{100} = 100\%)$ is the $\hat{\rho}_{occ}$ at 100% forest cover. For this calculation, we held sampling effort constant at its median value. Values of Ω_i<0 indicate that the species has a lower probability of occurrence when the natural cover is low. Values of Ω_i>0 mean that $\hat{\rho}_{occ}$ is greater with reduced natural cover than with 100% natural cover.

Do southern- and northern-edge species respond differently to low forest cover?

To answer this question, we used one-way ANOVA to test whether the $\bar{\Omega}_{15\%}$ (i.e. mean ratio of $\hat{\rho}_{occ}$ at 15% to 100% forest cover) calculated for each group of species (southern-edge, northern-edge and mid-range species) differ from each other and from zero. Fifteen percent forest cover has been suggested as an extinction threshold for many species (Andrén, 1994; Fahrig, 2003; Rybicki & Hanski, 2013).

It is likely that $\bar{\Omega}_{15\%}$ differs between forest and non-forest species: forest species should be more adversely affected by low forest cover than open-habitat species. We hypothesize that this difference may depend as well upon what part of species' ranges are considered: northern-edge, mid-range, or southern edge.

RESULTS

The majority of bird species had a higher probability of occupancy (p_{occ}) in landscapes with <100% forest cover than in fully forested landscapes (Fig. 2). For example, with 40% forest cover in the landscape, 49 bird species showed lower p_{occ} than in continuous forested areas (Fig 2a); however, p_{occ} was reduced by ≥75% for only seven species. In contrast, 79 bird species had higher p_{occ} in comparison to full-forested landscapes (Fig. 2a). With less forest cover, increasing numbers of species have much lower p_{occ}.

Northern-edge, mid-range and southern-edge populations showed different responses to the amount of forest cover in landscapes of southern Ontario (Fig. 3). Northern-edge species tended, on average, to have increased probability of occurrence in landscapes with reduced forest cover (Fig. 3). Southern-edge species have a lower probability of occurrence in landscapes when natural land cover is low. For mid-range species, the mean ratio of the predicted probability of occupancy at 15% to 100% forest cover ($\bar{\Omega}_{i15\%}$) differs from southern- and northern-edge species, but it is close to zero (t=1.96, df=119, p=0.06): in other words, in southern Ontario, the species that are at their northern limits have higher probability of occurrence in landscapes with reduced forest cover, while the species that are at their southern limits have lower probability of occurrence when natural cover is lower (Fig. 3).

Not surprisingly, bird species' sensitivity to low natural land cover ($\bar{\Omega}_{15\%}$, mean ratio of $\hat{p}_{occ}$ at 15% to 100% forest cover) depends upon the type of habitat that the species utilize (forest and non-forest); more surprising, it also depends on their position in relation to the geographical range within the study area (Table 1). As one would expect, mid-range forest birds are less likely to occur, and mid-range open-habitat birds more likely to occur, in landscapes with reduced forest cover (Fig. 4). In contrast, southern-edge species were more likely to occur in landscapes with reduced forest ($\hat{\rho}_{occ} < 0$), regardless of whether they were forest or open-habitat species (Fig. 4). Similarly, northern-edge species were less likely to occur in landscapes with reduced forest cover ($\hat{\rho}_{occ} > 0$), irrespective of habitat guild. The frequencies of forest- and non-forest species do not differ among the three geographic species groups (X^2=2.45, df=4, p=0.65).

DISCUSSION

Climate change literature often argues that habitat loss and fragmentation threaten to pose a barrier to species tracking warmer temperatures (Opdam & Wascher, 2004; Manning *et al.*, 2009; van de Pol *et al.*, 2010; Mantyka-Pringle *et al.*, 2012; Oliver *et al.*, 2015; Selwood *et al.*, 2015). Mechanistically, as species' ranges expand northward (e.g. Hill et al., 2002; Parmesan & Yohe, 2003; Coristine & Kerr, 2015), or in other directions (Currie & Venne, 2016), the lack of landscape features used by the species as habitat could, in principle, prevent species from moving to new, climatically suitable areas (Hill *et al.*, 2001; Travis, 2003; Opdam & Wascher, 2004; Robillard *et al.*, 2015). At the global scale, the effects of habitat loss and fragmentation seem to be greatest in areas with high temperatures (Mantyka-Pringle *et al.*, 2012).

As in many other parts of the world (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Parmesan & Yohe, 2003; Brommer, 2004; Chen *et al.*, 2011; Coristine & Kerr, 2015), eastern North America has experienced both increased temperatures and species' range shifts. Zuckerberg, et al. (2009) found that southern range boundaries of northerly birds in New York State moved northwards between 1980-1985 and 2000-2005. The authors did not find the same pattern for northern range boundaries of species with more southerly ranges (Zuckerberg *et al.*, 2009). Coristine & Kerr (2015), using 34 species of birds across North America, report the opposite: smaller northward shifts of northern range limits than of southern limits. However, the average range shifts in the study of Coristine & Kerr (2015) is, in fact, not significantly different from zero.

Our findings do not support the concern that moderately reduced natural land cover (here, proportion of forest cover) poses a barrier to species' occupancy, and presumably to the movement of species tracking warmer temperatures. Most northern-edge bird species present in southern Ontario, which are likely to be experiencing warmer temperatures in the study area (Varrin et al., 2007), relate positively with reduced forest cover (Fig. 3). Some open-habitat bird species, commonly found farther south appear to be benefiting from forest cover removal and northward warming temperatures. Our analysis showed, for example, that Eastern Bluebird (*Sialia sialis*), a grassland species at its northern range edge, has p_{occ} >80% higher in landscapes with 15% forest cover than in fully forested landscape. Its abundance has increased dramatically in southern Ontario since the 1970's (Cadman et al. 2007, (Varrin *et al.*, 2007). Perhaps surprisingly, six forest-specialist, northern-edge species also showed positive p_{occ} with reduced land cover amount (Fig. 4, *Appendix 1*). For instance, the Blue-gray Gnatcatcher (*Polioptila caerulea*), an interior-edge species, showed p_{occ} >75% higher in 15% forested landscapes. The range of this species has shifted northward since the 1940's, which was attributed to warming climate (Hitch & Leberg, 2007) and to increased [sic] forest cover (Cadman et al. 2007, (Varrin *et al.*, 2007). Another example is the Eastern Screech-Owl

(*Megascops asio*), which also showed an increase in p_{occ} by >75% in reduced forest cover, relative to 100% cover. This species, apparently cannot survive in completely forest-depleted landscapes, but it has been found in parklands, farmlands and suburban landscapes (Gehlbach, F. R., 1995).

These forest species illustrate that reduced natural habitat at the northern-margin of the range does not necessarily decrease species' probability of occupancy. Rather, moderate amounts of forest cover reduction may favour species' occurrence irrespective of whether the species are forest- or open-habitat specialists. That could be due to reduced interspecific competition brought by some level of environmental disturbance, as empirical studies have shown the importance of competition in regulating community structure along disturbance gradient (Campbell & Grime, 1992; Turkington *et al.*, 1993; Violle *et al.*, 2010). For example, habitat fragmentation could facilitate the access of nest predators or parasites into forest patches, and ultimately interfere in the reproductive success of the most abundant forest birds (Robinson *et al.*, 1995). Some nectarivores birds that are normally numerically dominant in south-eastern Australia had their flower visitation patterns disrupted by Noisy Miners (*Manorina melanocephala*, an aggressive species of honeyeater) in disturbed-fragments when the nectivores were more abundant than the Noisy Miners (Bennett *et al.*, 2014).

In summary, empirically, many bird species have higher p_{occ} in landscapes with reduced land cover amount at the northern range edges. Warmer temperatures may make the northern edges of some bird species' ranges more climatically suitable. Whatever the negative effects of human modification of the land cover may be, something allows greater persistence even of many forest species in landscapes with some human presence. As a matter of pure speculation, it may be reduced competitive exclusion through reduction of the abundance of the competitive dominants in undisturbed forest. More specifically, consider forest patches within landscapes that have been partly clear. These patches will be firstly colonized by competitively-inferior species (e.g. coming from southern parts of the study area), which then will have time to reproduce and send out colonists to other newly-disturbed patches before competitively superior species arrive and exclude them. Low-frequency disturbances fail to clear patches fast enough to support the competitively-inferior species, while overly-frequent disturbances wipe out the competitively superior species faster than they can colonize. Thus, this can be a logically valid mechanism able to produce stable coexistence, and peaks in diversity at intermediate disturbance levels (Desrochers *et al.*, 2011; De Camargo & Currie, 2015)

Different responses of southern- and northern-edge populations towards environmental changes might reflect differences in the factors that determine those boundaries. For example, it has long been suggested that abiotic stressors are more important in limiting species' ranges at the harsh poleward edge, whereas biotic interactions should be more important at the climatically benign tropical edge (MacArthur 1972; Kaufman et al., 1995). Some literature has suggested that species' equatorward boundaries are stable, despite climate change (Hampe & Petit, 2005). Coristine & Kerr (2015) studying temporal responses of 34 passerine bird' ranges to temperature in North America found that equatorward range boundaries are closer to their upper realized thermal niche limits than poleward range populations, which could indicate that equatorward populations are strongly affected by abiotic factors, in this case temperature. Therefore, it could be that the southern-edge range bird species presence in southern Ontario are mostly affected by temperature, and their ranges are facing retraction. However, their lower probability of occupancy as a function of land cover could indicate that an interaction between climate and habitat loss is shaping the pattern observed.

On the other hand, species living at the warmer margin of their ranges (here, northerly species living at the southern parts of the range in the study area) could face higher risk of local extirpation due to the double whammy of poleward warming temperatures (Hewitt, 2000; Hampe & Petit, 2005; Coristine & Kerr, 2015) and reduced habitat amount. Species such as Cape May Warbler (*Dendroica tigrina*), Black-backed Woodpecker (*Picoides arcticus*), and Swainson's Thrush (*Catharus ustulatus*), all forest-interior species, showed extremely low p_{occ} in landscapes with reduced natural land cover (*Appendix 1*). Some species that can be found in open-forests or grass patches such as Tennessee Warbler (*Vermivora peregrine*) or Philadelphia Vireo (*Vireo philadelphicus*) also had lower p_{occ} with less human-dominated, mainly open, land cover. Although it is impossible to determine precisely whether habitat availability or climate are the proximal mechanisms lowering the species probability of occurrence of the species at the southern-edge of their range, an interaction between the two stressors is plausible (Oliver & Morecroft, 2014; Mantyka-Pringle *et al.*, 2015). Extinction risk is expected to increase due to range compression if species' climatic niches shift (in geographic space) but species' populations cannot. Moreover, climate-driven extinction is expected to happen in North America where warming causes local thermal conditions to exceed tolerable limits, which is anticipated along equatorward range margins of northerly species (Langham *et al.*, 2015).

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

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DATA CESSABILITY STATEMENT

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

BIOSKETCH

Rafael X. De Camargo is interested in analysing the underlying factors and processes driving species distributions (e.g. richness, occurrences, abundances) within meso-scale landscapes and across large regions. Author’s webpage: www.rafaeldecamargo.com

David J. Currie is interested in the predictable properties of the distribution of life on earth (when he is thinking as a scientist) and the beautiful intricacies of nature (when he is not)

TABLES

Chapter 3

Table 1. The ratio ($\bar{\Omega}_{15\%}$) of the probability of occupancy ($\hat{\rho}_{occ}$) at 15% forest cover to $\hat{\rho}_{occ}$ at 100% forest cover, as a function of each species' geographic group (mid-range species, southern-edge species, and northern-edge species), and habitat guild (forest and non-forest). Coefficient of determination of the overall model is R2=0.57.

Variables	Sum of Squares	d.f.	F	p
Geographic group	133.0	3	71.5	<0.0001
Habitat guild	12.3	2	13.2	<0.0001
Interaction	6.8	6	7.4	<0.0001
Residuals	113.5	122		

FIGURES

Chapter 3

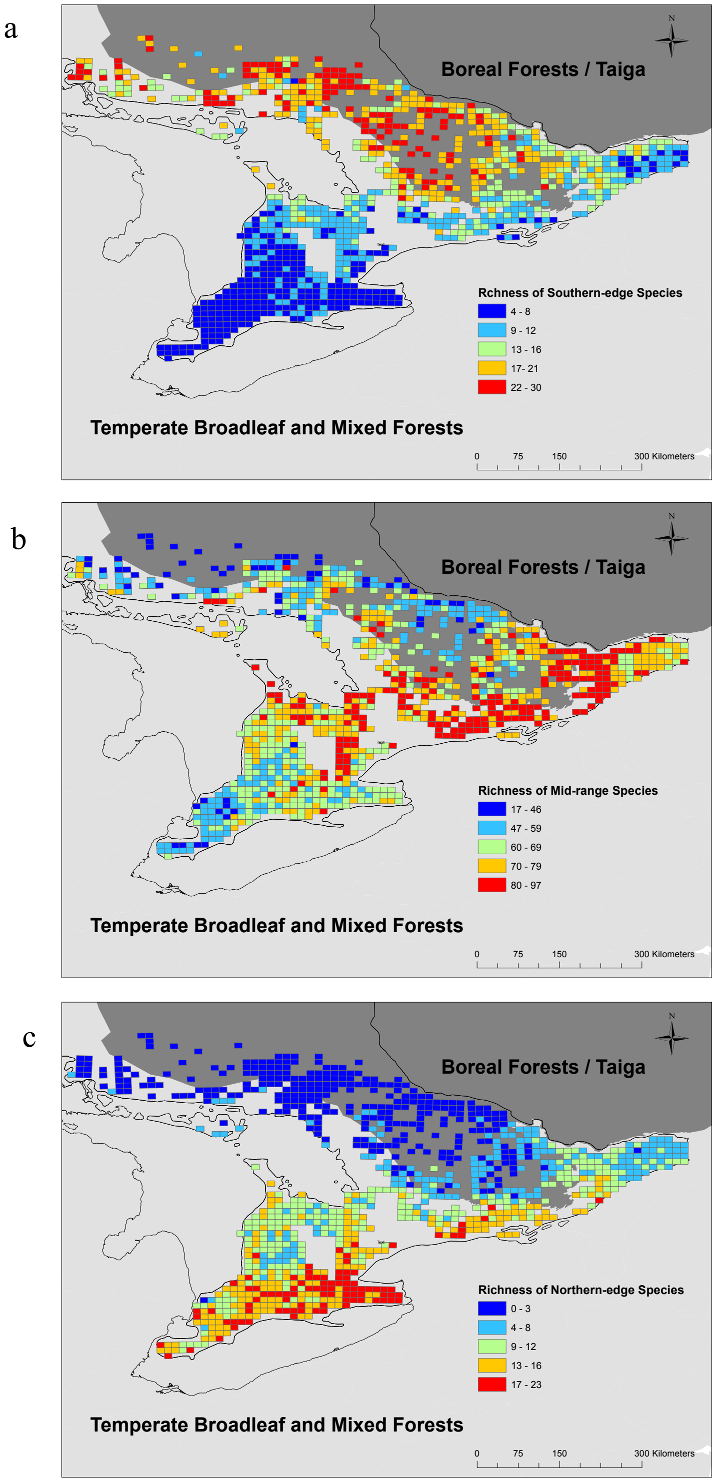

Figure 1. Numbers of species per 100 km^2 quadrat within each of three categories: a) species whose southern range edge occurs in the study area, b) mid-range species, whose range limits fall outside the study area, and c) species whose northern range limit occurs in the study area. Dark-grey background represents the conifer-dominated Canadian Shield, and the light-grey represents the Temperate Broadleaf and Mixed forests of the study area. The projection is Lambert conformal conic.

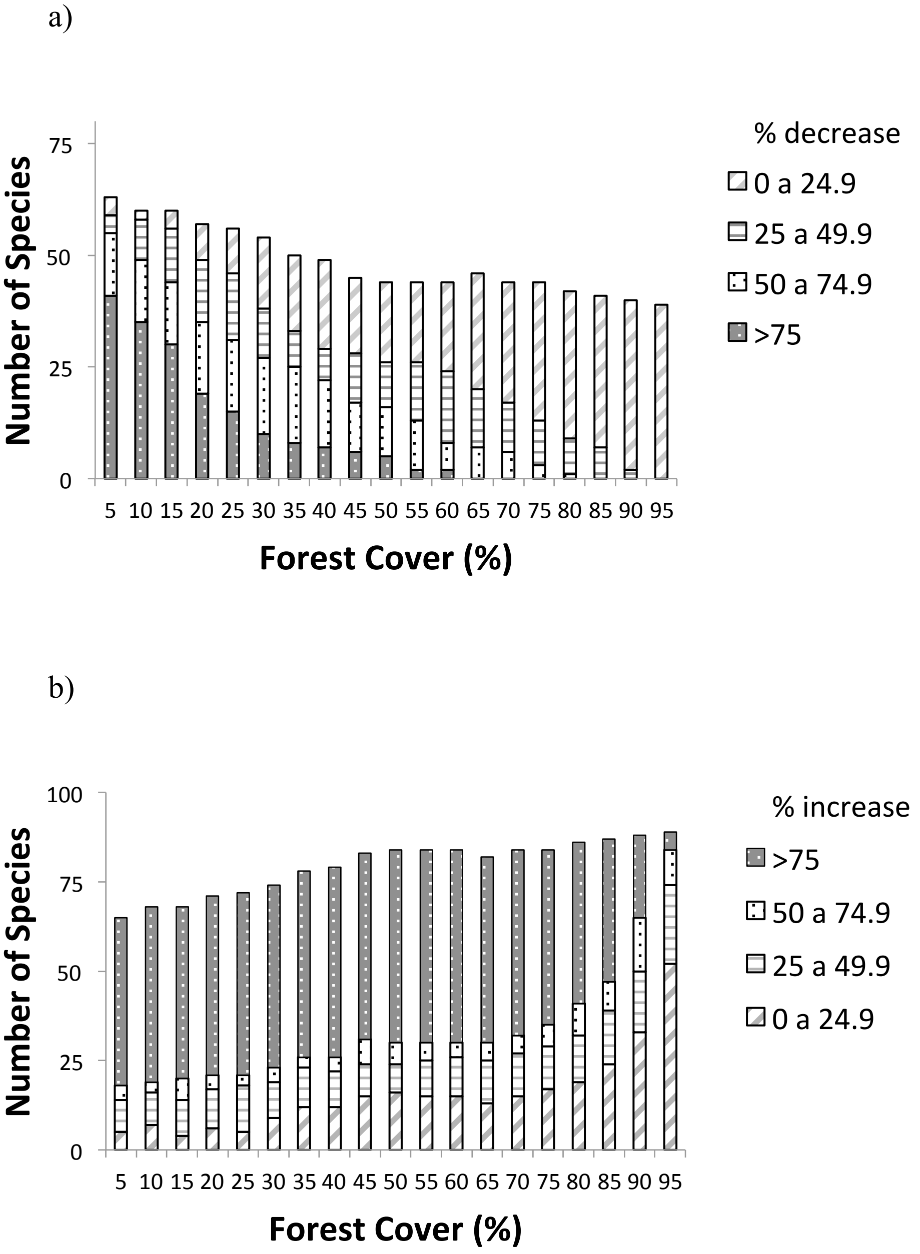

Figure 2. Number of bird species showing a) decrease, and b) increase predicted probability of occurrence ($\hat{\rho}_{occ}$) across a gradient of natural land cover from fully human-dominated landscapes (0% forest cover) to fully forested landscapes. Patterns on the bars represent by how much the $\hat{\rho}_{occ}$ increases or decreases (n=128 species).

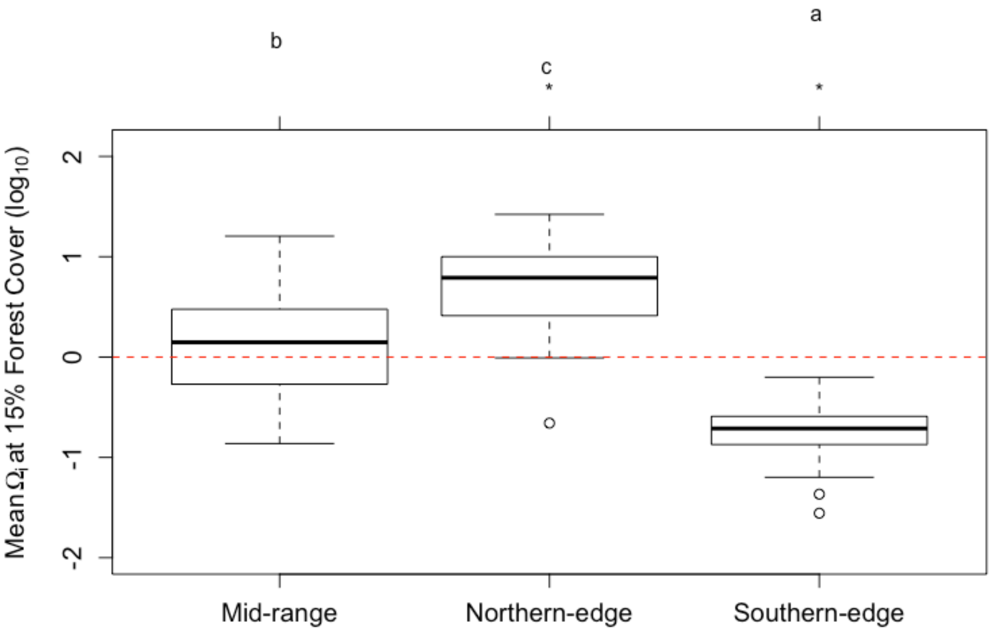

Figure 3. Mean predicted species' probability of occurrence at 15% forest cover amount ($\bar{\Omega}_{i\ 15\%}$), relative to the probability of occurrence at 100% forest cover, within landscapes of southern Ontario (n=991 landscapes, 128 species. Mid-range-, Northern- and Southern-edge species refer to the species' occupancy of within their range limits in southern Ontario (see methods). Values above the dashed-red line indicate that p_{occ} is higher at 15% forest cover than at 100% forest cover, whereas values below the red line indicate lower p_{occ} at 15% forest cover. Different letters represent significant statistical differences between means, and asterisk symbols represent that means differ from zero.

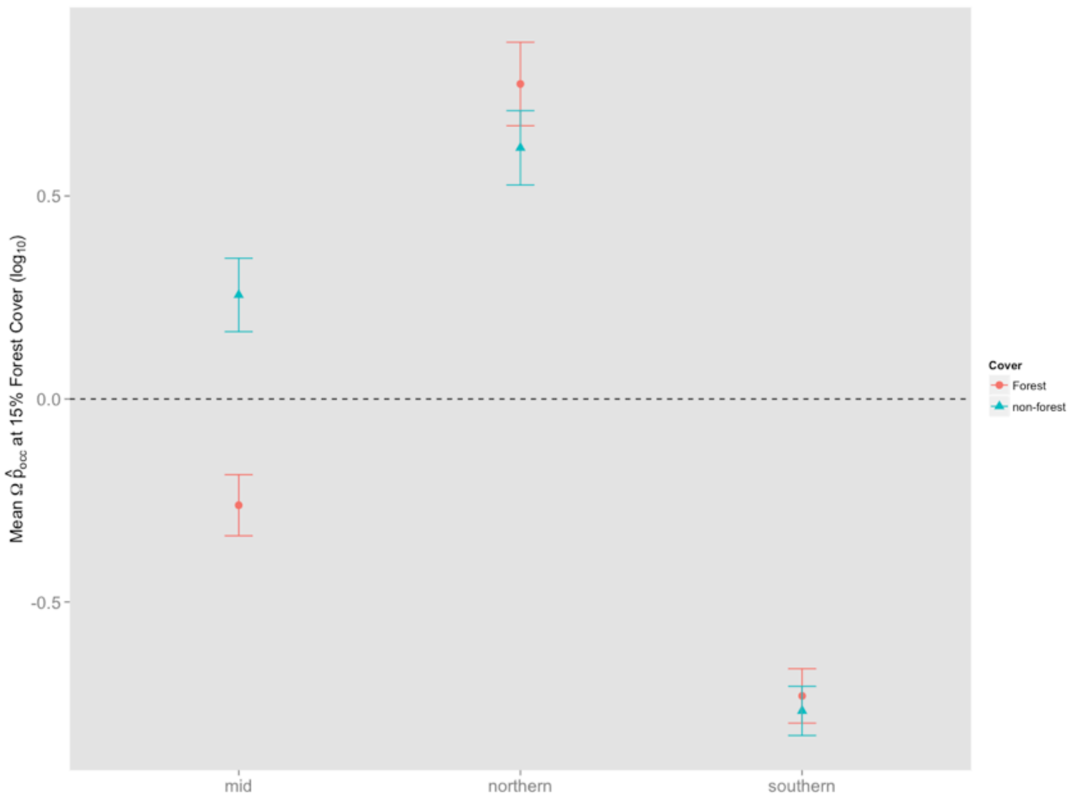

Figure 4. Interaction effect of edge-species groups (Mid-range-, Southern- and Northern-edge species) and habitat type (forest and non-forest birds) on the $\bar{\Omega}_{i15\%}$ (i.e. mean ratio of $\hat{\rho}_{occ}$ at 15% to 100% forest cover).

APPENDICES

Appendix 1: statistical outcome from logistic models and species characteristics

Table S1-1. Statistical outcome from logistic models and species characteristics

Species Code	English Name	Scientific Name	Range	Ecozone	COSEWICK	For_type	Omega_15
ABDU	American Black Duck	Anas rubripes	mid	Biome Generalists	Not_at_risk	non-forest	-0.36477101
ALFL	Alder Flycatcher	Empidonax alnorum	mid	Biome Generalists	Not_at_risk	non-forest	-0.146760404
AMBI	American Bittern	Botaurus lentiginosus	mid	Biome Generalists	Not_at_risk	non-forest	-0.321811322
AMKE	American Kestrel	Falco sparverius	mid	Biome Generalists	Not_at_risk	non-forest	0.458151816
AMWO	American Woodcock	Scolopax minor	mid	Biome Generalists	Not_at_risk	Forest	0.083496779
BANS	Bank Swallow	Riparia riparia	mid	Mixed-wood plains	Not_at_risk	non-forest	0.806449828
BAOR	Baltimore Oriole	Icterus galbula	mid	Biome Generalists	Not_at_risk	non-forest	0.479833384
BARS	Barn Swallow	Hirundo rustica	mid	Biome Generalists	Threatened	non-forest	0.368386987
BAWW	Black-and-white Warbler	Mniotilta varia	mid	Biome Generalists	Not_at_risk	Forest	-0.250938401
BBCU	Black-billed Cuckoo	Coccyzus erythropthalmus	mid	Biome Generalists	Not_at_risk	Forest	0.218507005
BBWO	Black-backed Woodpecker	Picoides arcticus	southern	Boreal	Not_at_risk	Forest	-1.366476786
BDOW	Barred Owl	Strix varia	mid	Biome Generalists	Not_at_risk	Forest	-0.791472433
BGGN	Blue-gray Gnatcatcher	Polioptila caerulea	northern	Mixed-wood plains	Not_at_risk	Forest	1.42224985
BHCO	Brown-headed Cowbird	Molothrus ater	mid	Biome Generalists	Not_at_risk	non-forest	0.479015462
BLBW	Blackburnian Warbler	Dendroica fusca	mid	Biome Generalists	Not_at_risk	Forest	-0.838008326
BOBO	Bobolink	Dolichonyx	mid	Biome	Not_at	non-	0.565490718

		oryzivorus		Generalists	_risk	forest	
BRCR	Brown Creeper	Certhia americana	mid	Biome Generalists	Not_at_risk	Forest	-0.278434685
BRTH	Brown Thrasher	Toxostoma rufum	mid	Biome Generalists	Not_at_risk	non-forest	0.495173545
BTBW	Black-throated Blue Warbler	Dendroica caerulescens	mid	Biome Generalists	Not_at_risk	Forest	-0.749909015
BTNW	Black-throated Green Warbler	Dendroica virens	mid	Biome Generalists	Not_at_risk	Forest	-0.424339135
BWHA	Broad-winged Hawk	Buteo platypterus	mid	Biome Generalists	Not_at_risk	non-forest	-0.622718918
BWTE	Blue-winged Teal	Anas discors	mid	Mixed-wood plains	Not_at_risk	non-forest	0.613562474
BWWA	Blue-winged Warbler	Vermivora pinus	northern	Mixed-wood plains	Not_at_risk	non-forest	1.11770798
CAGO	Canada Goose	Branta canadensis	mid	Biome Generalists	Not_at_risk	non-forest	0.228805945
CARW	Carolina Wren	Thryothorus ludovicianus	northern	Mixed-wood plains	Not_at_risk	non-forest	1.132855456
CAWA	Canada Warbler	Wilsonia canadensis	mid	Biome Generalists	Threatened	Forest	-0.608113371
CCSP	Clay-colored Sparrow	Spizella pallida	mid	Biome Generalists	Not_at_risk	non-forest	0.388387899
CHSW	Chimney Swift	Chaetura pelagica	mid	Biome Generalists	Threatened	non-forest	0.149484189
CLSW	Cliff Swallow	Petrochelidon pyrrhonota	mid	Mixed-wood plains	Not_at_risk	non-forest	0.592652366
CMWA	Cape May Warbler	Dendroica tigrina	southern	Boreal	Not_at_risk	Forest	-0.883818868
COHA	Cooper's Hawk	Accipiter cooperii	mid	Mixed-wood plains	Not_at_risk	non-forest	0.475181037
COLO	Common Loon	Gavia immer	mid	Biome Generalists	Not_at_risk	non-forest	-0.670889772
COME	Common Merganser	Mergus merganser	southern	Biome Generalists	Not_at_risk	non-forest	-0.711799346
COMO	Common	Gallinula	nort	Mixed-	Not_at	non-	0.827031649

	Moorhen	chloropus	hern	wood plains	_risk	forest	
CONI	Common Nighthawk	Chordeiles minor	mid	Biome Generalists	Threatened	non-forest	-0.141551095
CORA	Common Raven	Corvus corax	southern	Biome Generalists	Not_at_risk	non-forest	-0.554519434
COSN	Wilson's Snipe	Gallinago delicata	mid	Biome Generalists	Not_at_risk	non-forest	0.209821928
CSWA	Chestnut-sided Warbler	Dendroica pensylvanica	mid	Biome Generalists	Not_at_risk	non-forest	-0.163879395
DEJU	Dark-eyed Junco	Junco hyemalis	southern	Boreal	Not_at_risk	Forest	-0.851459415
EABL	Eastern Bluebird	Sialia sialis	northern	Biome Generalists	Not_at_risk	non-forest	0.595884959
EAME	Eastern Meadowlark	Sturnella magna	mid	Biome Generalists	Threatened	non-forest	0.726436661
EASO	Eastern Screech-Owl	Megascops asio	northern	Mixed-wood plains	Not_at_risk	Forest	0.979521032
EAWP	Eastern Wood-Pewee	Contopus virens	mid	Biome Generalists	Not_at_risk	Forest	0.106159183
EUST	European Starling	Sturnus vulgaris	mid	Biome Generalists	Not_at_risk	non-forest	0.547246639
EVGR	Evening Grosbeak	Hesperiphona vespertina	southern	Boreal	Not_at_risk	Forest	-0.871871076
FISP	Field Sparrow	Spizella pusilla	northern	Mixed-wood plains	Not_at_risk	non-forest	0.495388899
GBHE	Great Blue Heron	Ardea herodias	mid	Biome Generalists	Not_at_risk	non-forest	-0.011224997
GCKI	Golden-crowned Kinglet	Regulus satrapa	southern	Biome Generalists	Not_at_risk	Forest	-0.732674493
GHOW	Great Horned Owl	Bubo virginianus	mid	Mixed-wood plains	Not_at_risk	non-forest	0.574415468
GRAJ	Gray Jay	Perisoreus canadensis	southern	Boreal	Not_at_risk	Forest	-0.856200757
GRCA	Gray Catbird	Dumetella carolinensis	mid	Biome Generalists	Not_at_risk	Forest	0.332196709
GRHE	Green Heron	Butorides virescens	northern	Mixed-wood plains	Not_at_risk	non-forest	1.004578698

GRSP	Grasshopper Sparrow	Ammodramus savannarum	northern	Mixed-wood plains	Not_at_risk	non-forest	1.053210756
GWTE	Green-winged Teal	Anas crecca	mid	Biome Generalists	Not_at_risk	non-forest	0.095302363
GWWA	Golden-winged Warbler	Vermivora chrysoptera	mid	Biome Generalists	Threatened	non-forest	-0.421015251
HERG	Herring Gull	Larus argentatus	southern	Boreal	Not_at_risk	non-forest	-0.783452232
HETH	Hermit Thrush	Catharus guttatus	mid	Biome Generalists	Not_at_risk	Forest	-0.644775296
HOFI	House Finch	Carpodacus mexicanus	northern	Mixed-wood plains	Not_at_risk	non-forest	0.996563337
HOLA	Horned Lark	Eremophila alpestris	mid	Mixed-wood plains	Not_at_risk	non-forest	1.205466628
HOME	Hooded Merganser	Lophodytes cucullatus	southern	Biome Generalists	Not_at_risk	non-forest	-0.603544096
HOSP	House Sparrow	Passer domesticus	mid	Mixed-wood plains	Not_at_risk	non-forest	1.029648486
HOWR	House Wren	Troglodytes aedon	mid	Biome Generalists	Not_at_risk	non-forest	0.554934443
INBU	Indigo Bunting	Passerina cyanea	mid	Biome Generalists	Not_at_risk	non-forest	0.166070887
KILL	Killdeer	Charadrius vociferus	mid	Biome Generalists	Not_at_risk	non-forest	0.396881026
LISP	Lincoln's Sparrow	Melospiza lincolnii	southern	Boreal	Not_at_risk	non-forest	-0.59093385
MALL	Mallard	Anas platyrhynchos	mid	Biome Generalists	Not_at_risk	non-forest	0.142751428
MAWA	Magnolia Warbler	Dendroica magnolia	mid	Biome Generalists	Not_at_risk	Forest	-0.643256522
MAWR	Marsh Wren	Cistothorus palustris	mid	Mixed-wood plains	Not_at_risk	non-forest	0.35918149
MERL	Merlin	Falco columbarius	southern	Biome Generalists	Not_at_risk	non-forest	-0.653199942
MODO	Mourning Dove	Zenaida macroura	mid	Biome General	Not_at_risk	non-fore	0.354108043

				ists		st	
MOWA	Mourning Warbler	Oporornis philadelphia	mid	Biome Generalists	Not_at_risk	non-forest	-0.158996979
NAWA	Nashville Warbler	Vermivora ruficapilla	mid	Biome Generalists	Not_at_risk	Forest	-0.317126939
NOCA	Northern Cardinal	Cardinalis cardinalis	northern	Mixed-wood plains	Not_at_risk	Forest	1.179220107
NOGO	Northern Goshawk	Accipiter gentilis	mid	Biome Generalists	Not_at_risk	Forest	-0.368874354
NOHA	Northern Harrier	Circus cyaneus	mid	Biome Generalists	Not_at_risk	non-forest	0.545288817
NOMO	Northern Mockingbird	Mimus polyglottos	northern	Mixed-wood plains	Not_at_risk	non-forest	0.525550264
NOPA	Northern Parula	Parula americana	mid	Boreal	Not_at_risk	Forest	-0.792502693
NOWA	Northern Waterthrush	Seiurus noveboracensis	mid	Biome Generalists	Not_at_risk	Forest	-0.154992435
NRWS	Northern Rough-winged Swallow	Stelgidopteryx serripennis	northern	Mixed-wood plains	Not_at_risk	non-forest	0.572543962
NSWO	Northern Saw-whet Owl	Aegolius acadicus	mid	Biome Generalists	Not_at_risk	Forest	-0.703590961
OROR	Orchard Oriole	Icterus spurius	northern	Mixed-wood plains	Not_at_risk	Forest	0.895459284
OSFL	Olive-sided Flycatcher	Contopus cooperi	mid	Boreal	Threatened	non-forest	-0.862043305
OSPR	Osprey	Pandion haliaetus	mid	Biome Generalists	Not_at_risk	non-forest	-0.237025093
PBGR	Pied-billed Grebe	Podilymbus podiceps	mid	Biome Generalists	Not_at_risk	non-forest	-0.029844041
PHVI	Philadelphia Vireo	Vireo philadelphicus	southern	Boreal	Not_at_risk	non-forest	-0.68411499
PISI	Pine Siskin	Carduelis pinus	southern	Biome Generalists	Not_at_risk	non-forest	-0.68079935
PIWA	Pine Warbler	Dendroica pinus	mid	Biome Generalists	Not_at_risk	Forest	-0.262388216
PIWO	Pileated Woodpecker	Dryocopus pileatus	mid	Biome General	Not_at_risk	Forest	-0.141346386

				ists			
PUFI	Purple Finch	Carpodacus purpureus	southern	Biome Generalists	Not_at_risk	Forest	-0.490629321
PUMA	Purple Martin	Progne subis	mid	Mixed-wood plains	Not_at_risk	non-forest	0.695036005
RBNU	Red-breasted Nuthatch	Sitta canadensis	southern	Biome Generalists	Not_at_risk	Forest	-0.306243805
RBWO	Red-bellied Woodpecker	Melanerpes carolinus	northern	Mixed-wood plains	Not_at_risk	Forest	0.773167187
RCKI	Ruby-crowned Kinglet	Regulus calendula	southern	Boreal	Not_at_risk	non-forest	-0.901450995
RHWO	Red-headed Woodpecker	Melanerpes erythrocephalus	northern	Mixed-wood plains	Threatened	non-forest	0.216565012
RIPH	Ring-necked Pheasant	Phasianus colchicus	northern	Mixed-wood plains	Not_at_risk	non-forest	0.329368737
RNDU	Ring-necked Duck	Aythya collaris	southern	Boreal	Not_at_risk	non-forest	-0.66061461
RODO	Rock Pigeon	Columba livia	mid	Biome Generalists	Not_at_risk	non-forest	0.773075121
RSHA	Red-shouldered Hawk	Buteo lineatus	northern	Biome Generalists	Not_at_risk	non-forest	-0.658508625
RTHA	Red-tailed Hawk	Buteo jamaicensis	mid	Biome Generalists	Not_at_risk	non-forest	0.166083086
RUGR	Ruffed Grouse	Bonasa umbellus	mid	Biome Generalists	Not_at_risk	Forest	-0.100533054
SACR	Sandhill Crane	Grus canadensis	southern	Biome Generalists	Not_at_risk	non-forest	-0.408998799
SAVS	Savannah Sparrow	Passerculus sandwichensis	mid	Biome Generalists	Not_at_risk	non-forest	0.504837949
SCTA	Scarlet Tanager	Piranga olivacea	northern	Biome Generalists	Not_at_risk	Forest	-0.008382818
SEWR	Sedge Wren	Cistothorus platensis	mid	Biome Generalists	Not_at_risk	non-forest	0.148519065
SORA	Sora	Porzana carolina	mid	Biome Generalists	Not_at_risk	non-forest	0.566286158
SPSA	Spotted	Tringa	mid	Biome	Not_at	non-	0.162973867

	Sandpiper	macularia		Generalists	_risk	forest	
SSHA	Sharp-shinned Hawk	Accipiter striatus	mid	Biome Generalists	Not_at_risk	Forest	0.121583627
SWTH	Swainson's Thrush	Catharus ustulatus	southern	Boreal	Not_at_risk	Forest	-1.021672044
TEWA	Tennessee Warbler	Vermivora peregrina	southern	Boreal	Not_at_risk	non-forest	-1.556189646
TUVU	Turkey Vulture	Cathartes aura	northern	Biome Generalists	Not_at_risk	non-forest	0.083973818
UPSA	Upland Sandpiper	Bartramia longicauda	mid	Mixed-wood plains	Not_at_risk	non-forest	1.177678556
VESP	Vesper Sparrow	Pooecetes gramineus	mid	Biome Generalists	Not_at_risk	non-forest	0.527955916
VIRA	Virginia Rail	Rallus limicola	mid	Biome Generalists	Not_at_risk	non-forest	0.20810756
WAVI	Warbling Vireo	Vireo gilvus	mid	Biome Generalists	Not_at_risk	Forest	0.436463138
WBNU	White-breasted Nuthatch	Sitta carolinensis	mid	Biome Generalists	Not_at_risk	Forest	0.168897658
WIFL	Willow Flycatcher	Empidonax traillii	northern	Mixed-wood plains	Not_at_risk	non-forest	0.902970159
WITU	Wild Turkey	Meleagris gallopavo	northern	Mixed-wood plains	Not_at_risk	non-forest	0.807659968
WIWR	Winter Wren	Troglodytes troglodytes	southern	Biome Generalists	Not_at_risk	Forest	-0.356639956
WODU	Wood Duck	Aix sponsa	mid	Biome Generalists	Not_at_risk	non-forest	0.054170435
WOTH	Wood Thrush	Catharus mustelinus	mid	Biome Generalists	Not_at_risk	Forest	0.147002804
WPWI	Whip-poor-will	Caprimulgus vociferus	mid	Biome Generalists	Threatened	non-forest	-0.515737863
WTSP	White-throated Sparrow	Zonotrichia albicollis	mid	Biome Generalists	Not_at_risk	Forest	-0.190883554
WWCR	White-winged Crossbill	Loxia leucoptera	southern	Boreal	Not_at_risk	Forest	-0.837766416
YBCU	Yellow-billed Cuckoo	Coccyzus americanus	northern	Mixed-wood	Not_at_risk	non-fore	0.513286217

				plains		st	
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris	southern	Boreal	Not_at_risk	non-forest	-1.198470143
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius	southern	Biome Generalists	Not_at_risk	Forest	-0.201065047
YRWA	Yellow-rumped Warbler	Dendroica coronata	mid	Biome Generalists	Not_at_risk	Forest	-0.419187227
YTVI	Yellow-throated Vireo	Vireo flavifrons	northern	Biome Generalists	Not_at_risk	Forest	0.190766707

CHAPTER 4

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RUNNING TITLE

Biodiversity assessment from land cover

TITLE

Would conserving natural land cover in landscapes conserve biodiversity?

AUTHORS

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ABSTRACT

Aim: It is generally accepted that protecting natural land cover would protect biodiversity. This would only be true as a general statement if the relationship between richness and natural land cover were monotonic positive and scale- and method-independent. Assertions about habitat loss causing species losses often come from broad-scale assessment of richness (e.g., from range maps) and natural habitat conversion. Yet, the evidence about species loss following habitat loss or fragmentation typically comes from fine-scale experiments. Here, we test whether broad-extent relationships between avian species richness and natural land cover are independent of: 1) whether species distribution data come from systematic censuses (atlases) versus range maps, and 2) the grain size of the analysis.

Location: southern Ontario, CA, and New York State, US.

Time period: 2000-2005.

Major taxa studied: Birds.

Methods: We regressed census-based and range map-based avian species richness against the proportion of natural land cover and temperature. Censused richness at the landscape level was obtained from Breeding Bird Atlases of Ontario and New York State. Range-map richness derived from BirdLife International range maps. Comparisons were made across different spatial grains: 25-km^2, 100-km^2, and 900-km^2.

Results: Over regional extents, range-map-based richness relates strongly to temperature, irrespective of spatial grain. Censused species richness relates to temperature less strongly. Range-map richness is a *negative* function of the proportion of natural land cover, while realized richness is a peaked function. The two measures of richness are not monotonically related to each other.

Main Conclusions: The data do not indicate that conserving natural land cover has conserved species diversity in southern Ontario or in New York State, since greater natural cover does not imply higher richness. We argue that *habitat loss* has become a panchreston. It may be misguiding conservation biology strategies by focusing on a threat that is too general to be usefully predictive.

INTRODUCTION

Wilcove *et al.* (1998) wrote: “habitat loss is the single greatest threat to biodiversity...”. This hypothesis seems to have been accepted as a truism. Since 1990s habitat loss has been cited as “the major threat” (Wilcove et al. 1998, Pekin and Pijanowski 2012), “ the main cause” (Baillie et al. 2004, Krauss et al. 2010), or “the principal driver" of biodiversity loss (Sala et al. 2000, Tilman et al. 2001, Pereira et al. 2010), to mention just a few examples.

A corollary of the hypothesis that habitat loss is the main cause of species loss is that conserving natural land cover (first approximation of habitat) will conserve biodiversity. If that is true, a critical prediction can then be tested: in landscapes in which human activities have removed part of the natural habitat, areas with more natural land cover should have higher species richness. At least three types of data can be brought to bear on this prediction. The first type is experimentally manipulated habitat patches of varying areas (usually at fairly small scales). Patch-level studies (1-50ha) consistently find that larger patches of uninterrupted habitat have more species than smaller patches (e.g., Dooley & Bowers, 1998; Prugh, 2009; Guldemond & Van Aarde, 2010; Martin & Fahrig, 2012). However, conservation planning does not generally focus on individual patches of habitat; rather, planning more often involves landscapes (areas on the order of 10–1,000 km^2) with mixtures of land covers (Dale et al. 2000), consequently patch-scale is not the focus in this study. A second category of data involves systematic field observations of species presence/absence in replicated landscapes (typically, 10^1-10^3 km^2). Examples include regional or national breeding bird atlases, which may be called realised richness since it represents observed local assemblages of species. Finally, there are also stacked species range maps, typically over broad extents (e.g., continental). Since, broad-scale range maps (e.g., IUCN, BirdLife International) are typically resolved at fairly coarse grains, e.g. ~10^4 km^2 (Hurlbert and Jetz 2007), this represents the potential richness that is regionally available to occupy a landscape.

Biodiversity loss and its causes are clearly grain size dependent. There are many examples of extirpations of individual species, or even entire assemblages, associated with a variety of anthropogenic causes (Collinge 2000, Husté and Boulinier 2007, D'Amen and Bombi 2009, Arroyo-Rodríguez and Dias 2010, Cousins and Vanhoenacker 2011). In general, these extinctions are local. At local scales, there is no clear consensus on the environmental determinants and mechanisms giving rise to pattern in richness, or to patterns of species extinctions (Ricklefs 2004, Field et al. 2009, Newbold 2012, Newbold et al. 2014); however, in a recent study, land-use and land-use intensity have been proposed as potential drivers of local assembly patterns worldwide (Newbold et al. 2015). Similarly, at the landscape level, questions like "how much habitat is enough?" (Fahrig 2001) is still controversial (Francesco Ficetola and Denoël 2009, Estavillo et al. 2013), suggesting that, to a certain extent, land cover and suitable habitats should be important to species maintenance. On the other hand, at meso- or larger scales, species extirpations/extinctions have been relatively rare (Stork 2009). Abiotic variables may better explain the occurrence of individual species (Algar et al. 2008). Contemporary climate (e.g., temperature and precipitation) (Currie 1991, Francis and Currie 2003, Hawkins et al. 2003) and historical/evolutionary drivers (Wiens et al. 2010, Romdal et al. 2013) are the main competing hypotheses proposed to explain variation in species richness at broad scales.

The literature suggests that the relationship between richness and natural land cover should be scale-independent. At fine scales, species-area relationship modelling (e.g., richness as a power function of forest cover) has consistently shown a large negative effect of forest loss on biodiversity (Tilman et al. 1994, Findlay and Houlahan 1997, Drapeau et al. 2000, Schmiegelow and Mönkkönen 2002, Smith et al. 2011). In a given locality, it must be true that complete elimination of natural land cover leads to species' extirpation. However, researchers have long claimed that deforestation leads to loss of biodiversity worldwide (Lovejoy, 1980, Wilson, 1988, Pimm & Raven, 2000; Brooks *et al.*, 2002; Pimm *et al.*, 2006, 2014; Hubbell *et al.*, 2008). Early species-area estimates from tropical forest deforestation in 1980s predicted that Earth could lose up to 20% of its species by the year of 2000 (Lovejoy, 1980, Wilson, 1988). Later calculations from logging and deforestation predicted losses of between 37 and 50% of tree species of the Brazilian Amazon (Hubbell et al. 2008). Pimm & Raven (2000) predicted 18% extinction by 2100 in tropical hotspots due to due to forest loss. All of these predictions used coarse-grain species' ranges modelled as a function of the amount of forest cover. In a recent paper, Betts *et al.* (2017), using (coarse-grained) IUCN range maps predicted that 121–219 species will become threatened under current rates of forest loss over the next 30 years in Borneo, the central Amazon, and the Congo Basin.

In this study, we tested whether the relationship between avian species richness and natural land cover is dependent upon the data type: fine-grained distribution data, versus coarser-grain range map data, sampled in grid cells of varying size. The literature assumes that the relationship between avian species richness and natural land cover is the same using fine-grained (censused) species' distributions and coarser-grained (potential) species' ranges. Alternatively, since continental-scale studies of richness from range maps have generally observed strong richness-climate relationship, potential richness in our study may be more strongly related to temperature than to land cover. In contrast, one might expect that a stronger effect of land cover would be detected on censused richness. To test whether these relationships depend on grain size (cell sizes) at which species are recorded, we also tested the consistency of the richness-land cover relationship across 25-km^2, 100-km^2

and 900-km^2. Finally, to test the consistency of our results, we compare fitted models from separate datasets covering southern Ontario and New York State.

METHODS

Study region and species richness

The study geographical region includes southern Ontario, Canada (200,000 km^2), and New York State, USA (125,400 km^2) (Fig. 1). To calculate censused, landscape-level avian species richness, we used species distribution data from the Ontario Breeding Bird Atlas (OBBA, Cadman, 2007) and the New York State Breeding Bird Atlas (NYBBA, McGowan & Corwin, 2008). Both atlases were based on systematic surveys conducted between 2000 and 2005.

The NYBBA sampled birds on a 5x5km grid; the OBBA used a cell size of 10x10km. Both atlases used experienced birders to identify the breeding bird species occurring within each quadrat. Since the sampling was designed to sample all habitats in a grid cell, and hopefully to find all species breeding there, we treat species not observed in a cell as being truly absent (Trzcinski et al. 1999). Richness in a quadrat represents the total number of species presences observed in that quadrat.

Sampling effort varies between the two atlases. For the NYBBA, atlassers were assigned to survey one or more NYBBA quadrats and were expected to spend at least 8h in each block, visiting each habitat present, and recording at least 76 species. For the ABBO surveys, each volunteer was assigned to search a specific 100-km^{2}quadrat as completely as possible for evidence of all species breeding therein. Volunteers were instructed to search in particular for regionally rare species. Any species that was observed in a given quadrat in 2000-2005 was considered present. We excluded ABBO quadrats with <20 hours and > 600 hours of bird censusing effort (median effort ≅ 45 hours. Since the OBBA quadrats were four times larger than the NYBBA quadrats, the effort per unit area was similar in the two atlases.

In order to compare censused richness between atlases, we resampled the NYBBA at 10x10 km quadrat size (same cell-size as ABBO). We calculated censused richness by counting the number of unique species' presences from the original survey quadrats within each new 100-km^2 grid cells in New York State.

Potential bird species richness was extracted from species' range maps in the BirdLife International World Bird Database (available online at http://www. birdlife.org/datazone). We overlaid species' ranges on the 25-km^2 (NYBBA) and 100-km^2 (OBBA) quadrats. We also resampled New York using 10x10 km, and both Ontario and New York with 30x30km grid cells (900-km^2). Richness in a quadrat represents the total number of species' ranges that overlap that quadrat.

Richness predictors

In principle, species richness should be positively correlated to the proportion of natural land cover. We used a global 1-km consensus land cover data set (Tuanmu and Jetz 2014) to extract an estimate of the percent of natural area present within sampling sites (Fig. 1). The dataset is composed of 12 land-cover classes, observed at a spatial resolution of 30 arc-seconds (~1-km^2 pixels at the equator). The land-cover classes are: 1. Evergreen / Deciduous Needleleaf trees, 2. Evergreen broadleaf trees, 3. Deciduous broadleaf trees, 4. Mixedwood/other trees, 5. Shrubs, 6. Herbaceous vegetation, 7. Cultivated and Managed Vegetation, 8. Regularly flooded vegetation, 9. Urban/Built-up, 10. Snow/Ice, 11. Barren, and 12. Open Water. The proportion of pixels in each land cover class was determined within each quadrat (0-100%). To obtain the proportion of natural land cover in each of our sampling units, we summed the percentages of classes 1-6 and 8. We excluded grid cells containing more than 10% water. The total number of grid cells are: 4,822 for NY (5x5km), 985 and 1,075 for ON and NY, respectively, at 10x10km scale, and 251 covering ON and NY (30x30 km).

Temperature has been long known as a main correlate, perhaps the driver, of species richness patterns at broad-scales (Currie 1991, Algar et al. 2008). Hence, we used Mean Annual Temperature (MAT) from the WorldClim database (Fig. 2, Fick & Hijmans, 2017), as a predictor of avian richness for each grid cell at different spatial scale.

Statistical Analysis

We used Ordinary Least Squares (OLS) regression models to relate censused and potential bird species richness to the environmental predictors: MAT and proportion of natural land cover. We fitted censused richness as a quadratic function of temperature and of the proportion of natural land cover, as these relationships are non-linear. We also fitted multiple regression models to determine the variance explained by the predictor variables together. Spatial data, including satellite images and climate raster files were treated in ArcGIS, and all stats were performed in R (R Core Team, 2017).

Spatial autocorrelation can affect models coefficients in spatial analyses (Diniz-Filho et al. 2003). Hence, we also corrected the richness models for spatial autocorrelation by fitting simultaneous autoregressive error models (SARerr) proposed by Kissling & Carl (2007) in R (function “errorsarlm”, R Development Core Team, 2008).

RESULTS

The response of avian species richness to natural land cover depends on the type of data from which richness is generated, contradicting the assumption that species loss from habitat loss is scale- and method-independent. Richness obtained from species' range maps (the underlying data in which are relatively coarse grained) clearly reflects the climatic gradients in the region (Fig. 2) rather than land cover (Fig. 1). Like climate, the spatial variation of range-map richness is strongly autocorrelated in space, across cell sizes from 25 m^2 - 900 m^2 (Fig. 3a-c). Multiple regressions showed that range-map richness relates by and large to temperature, and it is *negatively* related to the proportion of natural land cover (Table 1), contradicting the expected positive richness-land cover relationship. Moreover, most of the small amount of variance in potential richness explained by natural land cover (Table 1) reflects collinearity between land cover and climate: forested areas in New York and Ontario are usually cold places (Fig. S1-1, Appendix S1). The observed patterns are very similar across 25-km^2, 100-km^2, and 900km^2 cell sizes (Fig. 3a-c, Table 1).

On the other hand, the distribution of richness obtained from fine-grained atlases is less spatially structured (Fig. 4), and it does reflect, to a certain degree, the spatial variation in the proportion of natural land cover in the study area (cf. Fig.1). Temperature still explains more variance in the models than the proportion of natural land cover (Table 2), but the censused richness-temperature relationships are peaked (Fig. 5a,c,e). Natural land cover increases the r-squared of the models between by 4-13% (Table 2). Yet, high richness landscapes are interspersed throughout the study area, and not associated with the areas having a high proportion of natural land cover (e.g. the Adirondaks of north-eastern NY, the Catskills of south-eastern NY, and northern Ontario). The pattern is consistent across 25-km^2, 100-km^2, and 900km^2 cell sizes (Fig. 4a-c, Table 2). Moreover, the relationships between censused richness and land cover remained peaked even when the datasets were subset in order to encompass only the coldest or warmest regions of the study area (Fig. S1-2, Appendix S1).

Censused richness is only weakly related to potential richness over this study area (Fig. 6), and the relationship is not monotonic, which is surprising since potential richness supposedly corresponds to the species pool available in the region (Cornell and Harrison 2014). An effect of land cover on censused richness is most apparent in multiple regression models, after controlling for potential richness (Table 3). Yet, the partial relationship is peaked, with maximum censused richness reached roughly between 52-65% natural land cover, depending on the data type and grain size (Fig. 5b,d,f). These results are only consistent with the proposition that protecting natural cover protects richness at very low natural cover.

Spatial autoregressive models do not change the qualitative patterns described above. Overall these models performed better than the OLS models based on AIC comparisons (Tables 1, 2 vs. Tables S1-1,3 – Appendix S1). However, spatial autocorrelation analysis increased very little variance explained in potential richness models by ≤ 1% (comparison of r-squares from Table 1 vs. Table S1-1, Appendix S1), and the coefficients differ little. For censused richness, the additional variance explained added by autoregressive error models was also very small, but it seems to be more relevant at the cell size 30x30km (comparison of r-square from Table 2 vs. Table S1-3, Appendix S1).

DISCUSSION

There is a substantial body of the conservation literature that relates species' distributions to land cover features (i.e., forest cover, fragmentation, land-use intensity, etc) at national or global scales in order to draw conclusions on the effect of habitat loss to biodiversity. The overall message from this type of research is that habitat loss is a major cause of species loss. Consider Betts *et al.* (2017), who tested the effects of deforestation on IUCN-red listed species. The authors found that deforestation greatly increases the likelihood of a species to be threatened worldwide, and predicted that up to roughly 220 species of vertebrates will fall within threatened categories in the next 30 years due to forest conversion in tropical regions. Similarly, Tilman *et al.* (2017) reviewed the future threats to biodiversity and argued that between 40-80% of all threatened mammal and bird species are imperilled due to broad-scale habitat loss (i.e., agriculture, logging and development, their Figure 1a). Both studies used IUCN/Bird Life International coarse-grain range maps to arrive at their conclusions. When examined closely, richness generated from range maps relates negatively to the proportional of natural land cover (i.e., mostly forest cover), probably because it is mainly driven by temperature (Fig. 3, Table 1). Land cover varies dramatically over relatively fine spatial scales (Fig. 1), but species' ranges do not become peppered with areas of absence. Given that ranges circumscribe occupied and unoccupied areas, there is little reason to expect them to respond to land cover changes. Rather, we suspect that the correlations observed by Betts et al (2017) and by Tilman et al. (2017) between range-map richness of *red-listed* species and natural land cover primarily reflect the fact that recent habitat loss within a species' range is a criterion used by IUCN to define red-listed species (IUCN Standards and Petitions Subcommittee, 2017). The same issue can be observed in other assessments of threats to biodiversity that nearly always include human-induced destruction of natural habitats (Wilcove et al. 1998, Czech et al. 2000, Venter et al. 2006, Tilman et al. 2017), making the causal link between habitat loss and biodiversity loss somehow circular

In contrast, the pattern we found in range-map-based richness is consistent with other studies showing that, at coarse-grain and broad-extent, richness is strongly related ($r^2 \cong 0.7$-0.8) to current climatic variables (Hillebrand 2004, Field et al. 2009, Buckley et al. 2012). While the mechanisms underlying such patterns are contentious (Mittelbach et al. 2007, Wiens et al. 2010, Romdal et al. 2013, Boucher-Lalonde et al. 2015), richness of most species groups increases monotonically with mean annual temperature (MAT) and/or precipitation (Field et al. 2009). Although the richness-climate relationship may vary somewhat among taxonomic groups (Wolters et al. 2006), and among regions (Francis and Currie 2003, Jiménez and Ricklefs 2014), climate always explain large amount of the variance and is congruent across space and time (Boucher-Lalonde et al. 2015).

If the conversion of natural areas to human-dominated landscapes makes those areas completely unavailable to species, then there should be a positive spatial relationship between species richness and the number of remnants of natural areas irrespectively of spatial grain (e.g., He & Hubbell 2011). Species-area relationships (SARs), therefore, have frequently been used to forecast species losses (e.g. number of species extinct or threatened) from removal of natural (usually forested) cover (Lovejoy, 1980, Wilson, 1988, Pimm *et al.*, 2006, 2014; Hubbell *et al.*, 2008; Stork, 2009). At coarse spatial grains and large extents, those forecasts have greatly exceeded observed species losses (Stork 2009, Pereira et al. 2010, 2012, He and Hubbell 2011). The discrepancy is sometimes attributed to "extinction debt":

extinctions that are predicted to occur, but that have not had time to do so. The difficulty is that "extinction debt" assumes that habitat loss invariably causes species extinction, given data to the contrary. Nonetheless, species-areas relationships are still commonly applied in conservation studies to predict loss of species as a function of habitat modification (Pimm et al. 2006, 2014, Stork 2009, Pereira et al. 2010, Haddad et al. 2017).

While it is generally accepted that richness is determined by climate at coarser grains, environmental disturbances and stochastic processes may play a role in determining number of species at smaller grains (Ricklefs 2004). Newbold et al. (2015) suggest that land use and land-use intensity may have major consequences for global biodiversity at local scales. They find that within high-disturbed sites (i.e., urban, pasture, croplands) richness can be reduced by >70%. It is not surprising that diversity is low in highly disturbed landscapes (Bender et al. 1998, Norris et al. 2010, Guldemond and Van Aarde 2010, Kajzer et al. 2012, Fahrig 2013). However, at the landscape scale, moderate habitat conversion appears *not* to lead to species loss. For example, bird species richness peaks at intermediate amounts of natural land cover in southern Ontario, Canada (Desrochers et al. 2011), and at intermediate availability of trees in landscapes of Florence, Italy (Chiari et al. 2010). In our analysis, censused (Fig. 5b,d,f) species richness does not increase monotonically as a function of the proportion of natural habitat at any sampled grain size. Rather, censused richness-land cover relationships are peaked, leading to the conclusion that land cover is important to maintain biodiversity at very low natural cover, at its best. Our results are in striking contrast to a study by Betts *et al.*, (2017), which argues that the loss of biodiversity should be highest when natural cover is lost in fully forested areas.

What, then, should cause the peaked relationship between avian richness and natural land cover? Using the same dataset as ours for southern Ontario, Desrochers *et al.*, (2011) proposed that the peaked relationship results from the sum of two SAR curves: the number of forest birds increases with the amount of forest cover, while the richness of open-habitat birds species increases with human-dominated areas. Thus, habitat heterogeneity may increase richness within landscapes (Desrochers *et al.*, 2011). De Camargo & Currie (2015) further detailed the relationship by proposing a modified SAR models to predict avian species occurring in human-dominated landscapes in southern Ontario. Their model proposes there are some parts of the human-dominated land covers that are "available" for bird species to be present, while some other parts of the landscape are simply "lost", and no species can thrive there. Because of the environmental similarities between Ontario and New York State, in term of biomes and climatic conditions, it is reasonable to assume that the same sort of mechanisms should be shaping the peaked richness-land cover relationships in New York State.

Habitat loss *per se* may not be the biggest threat to biodiversity. Instead, other factors may play a major role in explaining diversity decline, or act synergically with habitat loss to imperil species (Brook et al. 2008). For instance, hunting practices have been linked to pre-historic (Malhi et al. 2016) and modern (Corlett 2007) species extinctions. Yet hunting is poorly represented in assessments of threats to biodiversity (Joppa et al. 2016). Pesticides have been related to species losses in agricultural landscapes (Tilman et al. 2001, Gibbs et al. 2009, Coristine and Kerr 2011). Also, land-use intensity has emerged as a potential main driver of species decline worldwide (Tylianakis et al. 2006, Hendrickx et al. 2007, Pekin and Pijanowski 2012, Newbold et al. 2015, Kehoe et al. 2016). The southeastern parts of southern Ontario, and western NY State, are heavily agricultural. Long Island has high human population density. It is in these areas that censused richness is lowest. Habitat destruction could be the first environmental disturbance happening at a locality, followed by other human-induced environmental stressors, but it may not be the primary cause of species loss since the other factors may act independently to eliminate species.

In conclusion, our study suggests that conserving natural land cover *per se* would not necessarily conserve species diversity. Remaining natural land cover in landscape is a poor, inconsistent predictor of species richness. Censused richness only seems to be negatively affected at low levels natural land cover. Clearly, better environmental predictors of diversity changes are necessary, instead of aiming for "evidence complacency" (Sutherland and Wordley 2017) by creating a panchreston around habitat loss.

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TABLES

Chapter 4

Table 1. Statistical outcome of OLS regression between potential richness as a function of temperature (MAT, top line at each grain size) and the proportion of natural land cover (LC, middle line at each grain), or both (bottom line in each grain) in grid cells of southern Ontario and New York State. Terms in parentheses are not statistically significant (p>0.05).

Grain Size	**Location**	**Standardized coefficients**		r^2	AICc
		MAT	**LC**		
5x5km	NY (n=4,822)	4.58		0.55	31475
			-0.19	0.21	34177
		4.41	-0.02	0.55	31461
10x10km	NY (n=1,075)	4.48		0.52	6978
			-0.21	0.25	7463
		4.16	-0.03	0.53	6971
	ON (n=985)	7.72		0.77	6512
			-0.33	0.65	6932
		6.14	-0.08	0.78	6460
30x30km	NY (n=165)	8.18		0.69	1192
			-0.36	0.35	1314
		8.01	(-0.01)	0.69	1194
	ON (n=138)	7.62		0.77	912
			-0.36	0.65	973
		6.22	-0.08	0.78	908

Table 2. OLS regressions of censused richness as a function of temperature (MAT) and the proportion of natural land cover (LC) in grid cells in southern Ontario and New York State. Conventions as in Table 1.

Grain Size	**Location**	**Standardized coefficients**				**r^2**	**AICc**
		MAT	**MAT^2**	**LC**	**LC^2**		
5x5km	NY (n=4,822)	2.02				0.04	40048
		28.04	-1.82			0.22	39060
				-0.10		0.02	40142
				1.40	-0.01	0.16	39388
		1.78		-0.02		0.04	40045
		28.08	-1.82	(0.00)		0.22	39062
		21.52	-1.38	0.85	-0.01	0.26	38830
10x10km	NY (n=1,075)	1.40				0.02	8484
		27.52	-1.85			0.26	8189
				-0.06		0.01	8501
				1.52	-0.01	0.20	8265
		1.37		(-0.01)		0.02	8486
		28.11	-1.87	(0.03)		0.26	8188
		20.84	-1.38	0.89	-0.01	0.30	8124
	ON (n=985)	1.82				0.03	8327
		34.88	-2.86			0.30	8009
				-0.05		0.01	8346
				1.63	-0.01	0.31	7993
		3.38		0.08		0.03	8321
		37.28	-2.89	0.11		0.31	7992
		24.00	-1.65	2.82	-0.11	0.43	7802
30x30km	NY (n=165)	-2.92				0.07	1406
		25.21	-1.82			0.24	1375
				0.18		0.07	1406
				1.54	-0.01	0.27	1365
		(-1.83)		(0.10)		0.08	1406
		26.60	-1.83	(0.10)		0.25	1375
		12.55	-10.92	1.10	-0.00	0.32	1359
	ON (n=138)	9.12				0.28	1263
		57.20	-4.58			0.55	1199
				-0.33		0.14	1288
				2.10	-0.02	0.32	1257
		13.84		0.28		0.30	1260
		57.65	-4.50	(0.08)		0.55	1200
		49.80	-3.73	0.92	-0.00	0.57	1198

Table 3. Multiple regressions between censused richness and land cover (LC), accounting for potential richness (Pot).

Grain Size	**Location**	**Standardized coefficients**				**r^2**
		Pot	**Pot^2**	**LC**	**LC^2**	
5x5km	NY (n=4,822)	0.08				0.006
		7.10	-7.05			0.10
				-0.14		0.02
				2.02	-2.20	0.16
		(0.03)		-0.10		0.02
		6.82	-6.77	0.70		0.10
		4.74	-4.65	1.82	-1.90	0.21
10x10km	NY (n=1,075)	0.03				0.00
		6.84	-6.82			0.11
				-0.10		0.01
				2.55	-2.68	0.20
		(-0.03)		-0.12		0.01
		6.67	-6.67	-0.04		0.11
		4.20	-4.15	2.27	-2.34	0.24
	ON (n=985)	0.20				0.04
		9.76	-9.56			0.14
				-0.01		0.01
				3.20	-3.34	0.31
		0.36		0.19		0.06
		9.75	-9.55	(0.00)		0.14
		(1.50)	(-1.03)	3.70	-3.48	0.40
30x30km	NY (n=165)	-0.40				0.15
		3.80	-4.20			0.18
				0.26		0.07
				2.27	-2.05	0.27
		-0.36		(0.04)		0.14
		4.48	-4.80	(0.12)		0.19
		(2.43)	(-2.66)	1.83	-1.72	0.33
	ON (n=138)	0.43				0.19
		4.40	-3.57			0.20
				-0.37		0.14
				2.34	-2.75	0.31
		0.38		(0.06)		0.19
		5.55	-5.28	(-0.20)		0.21
		(-1.30)	(1.76)	2.92	-2.95	0.38

FIGURES

Chapter 4

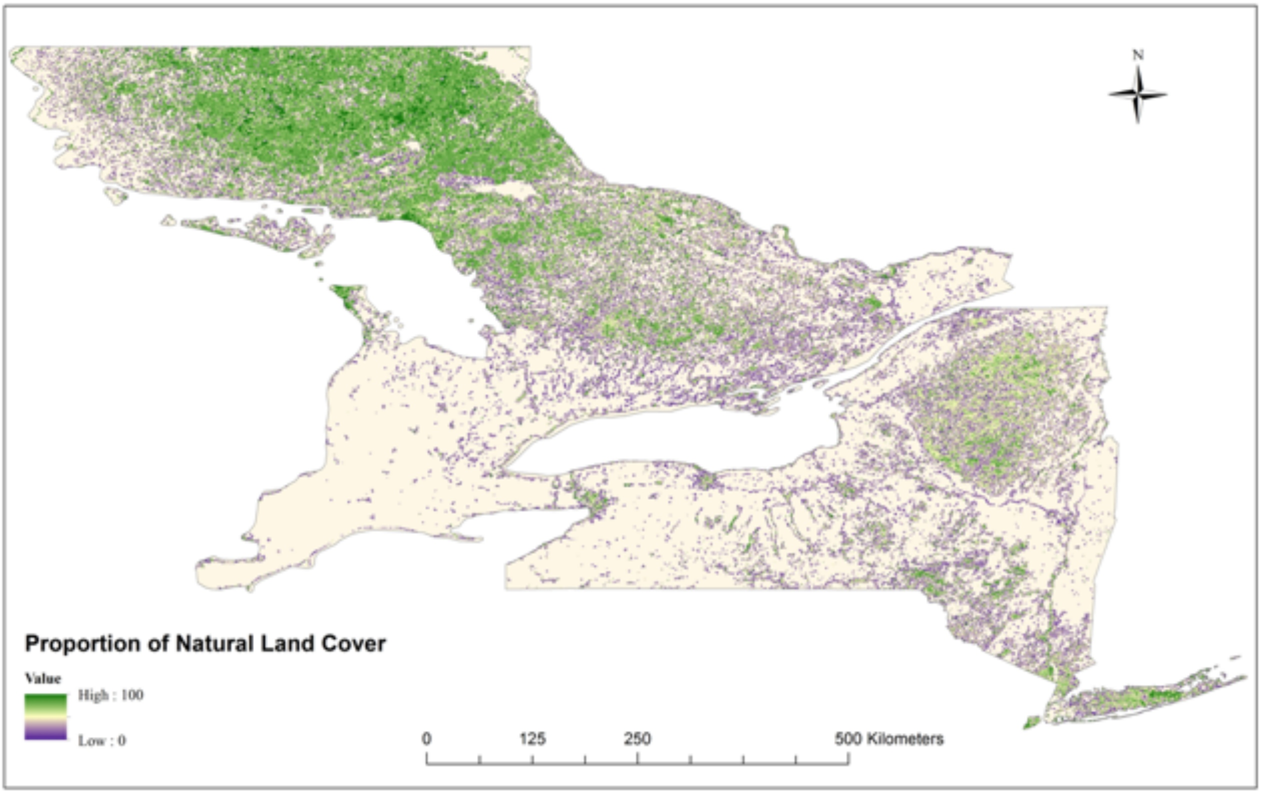

Figure 1. The proportion of natural land cover covering the study area according to the global 1-km consensus land cover data set (Tuanmu and Jetz 2014). The projection is WGS84 datum.

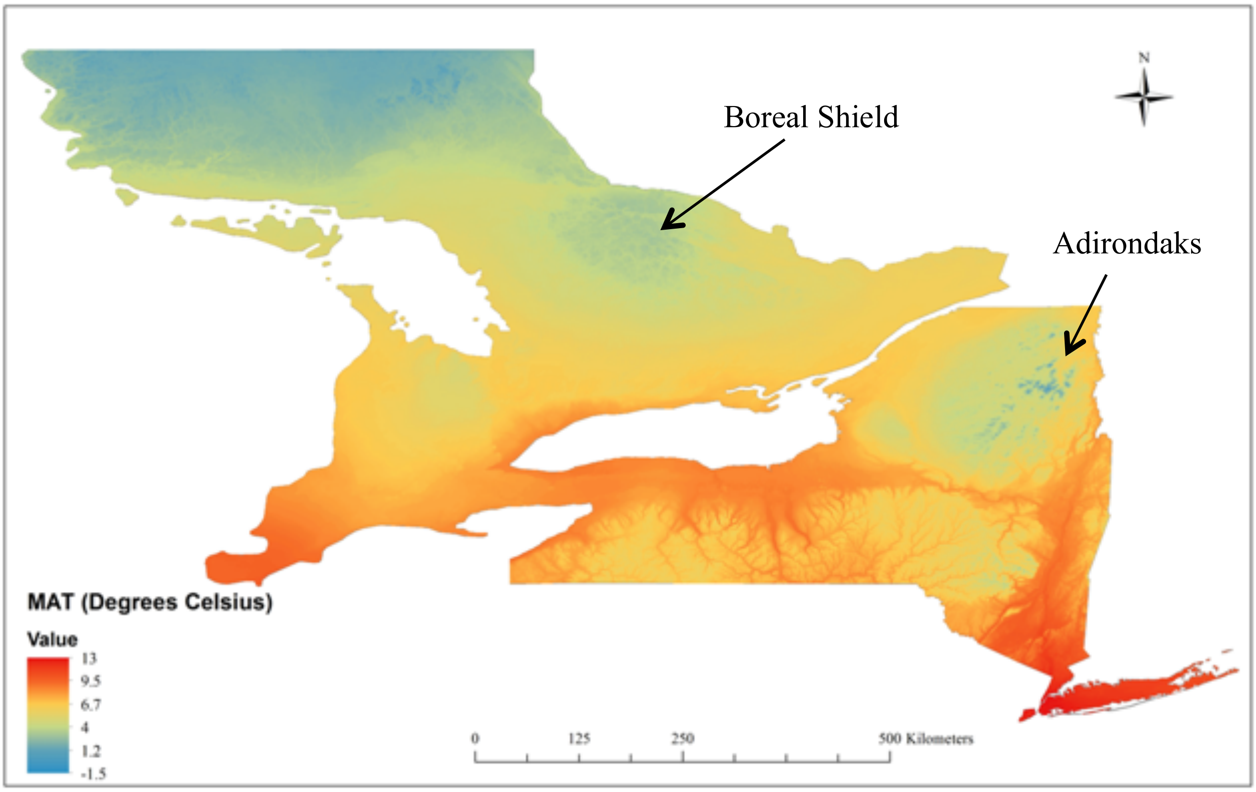

Figure 2. Mean Annual Temperature (MAT) covering the study area according to WorldClim (Fick and Hijmans, 2017). The projection is WGS84 datum.

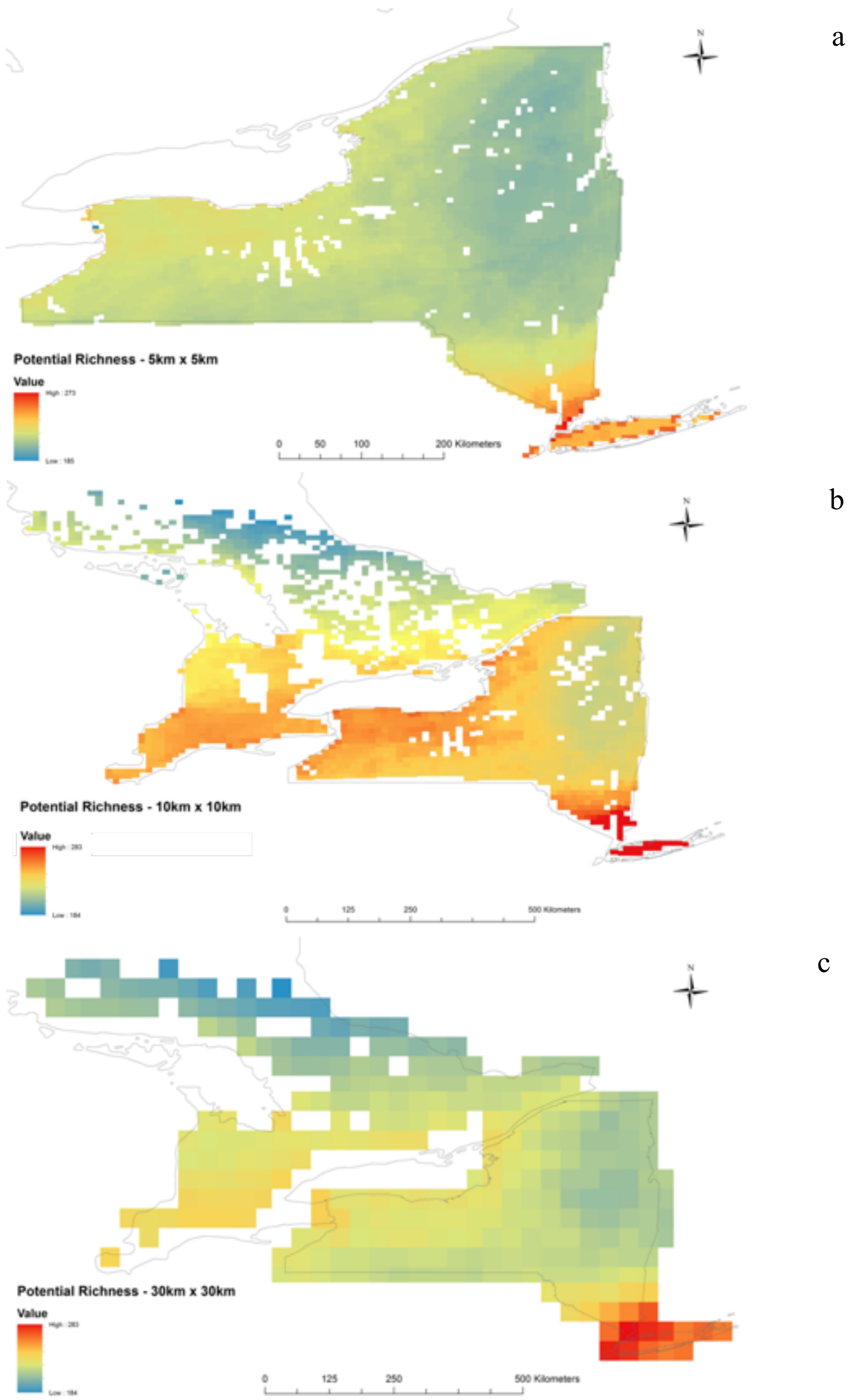

Figure 3. Distribution of potential avian species richness in a) 4,822 cells of 25-km2 in NY, b) 2,060 cells of 100-km2 in ON nad NY, and c) 303 cells of 900-km2 in ON and NY.

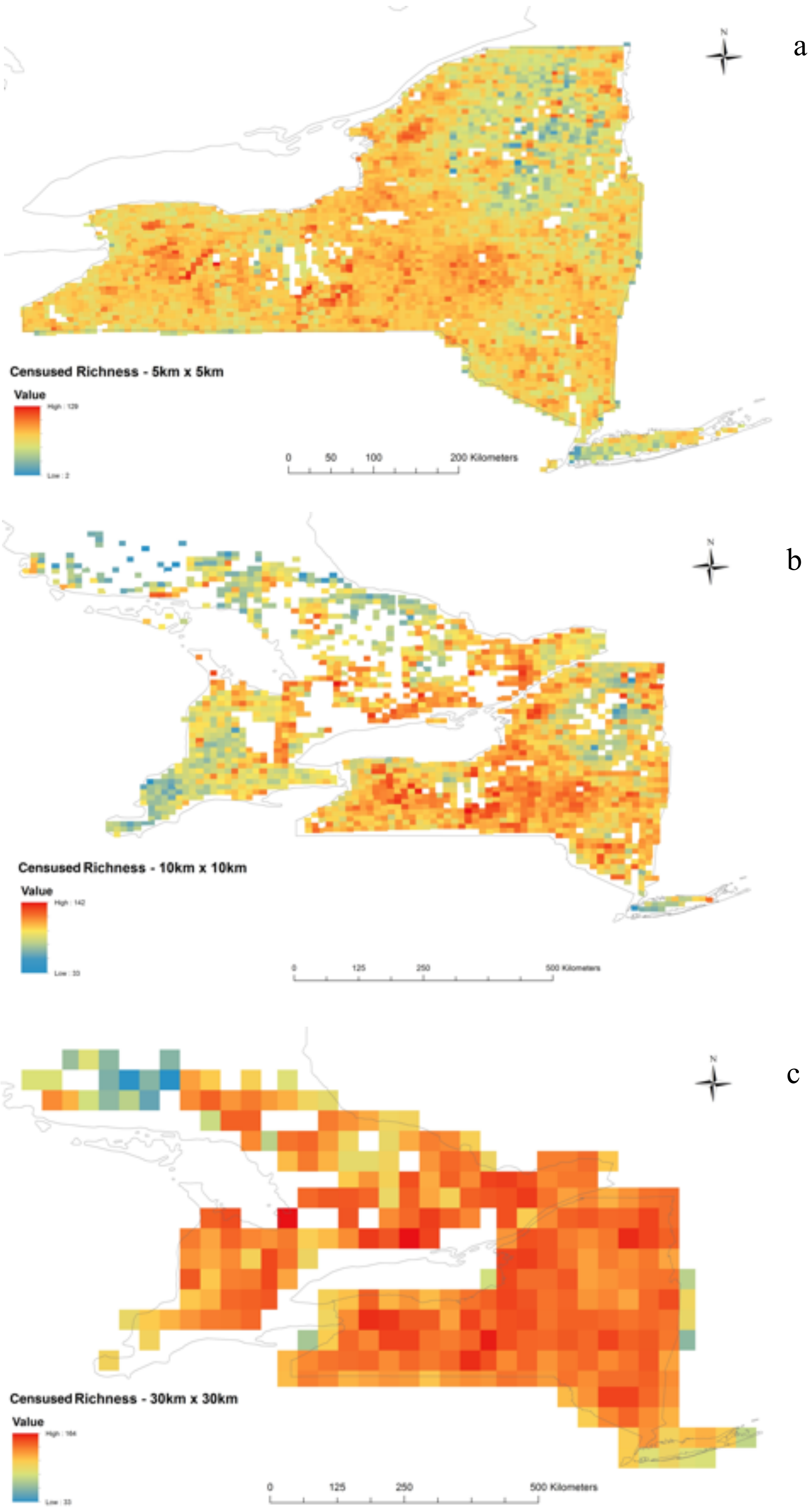

Figure 4. Distribution of censused avian species richness in a) 4,822 cells of 25-km2 in NY, b) 2,060 cells of 100-km2 in ON nad NY, and c) 303 cells of 900-km2 in ON and NY.

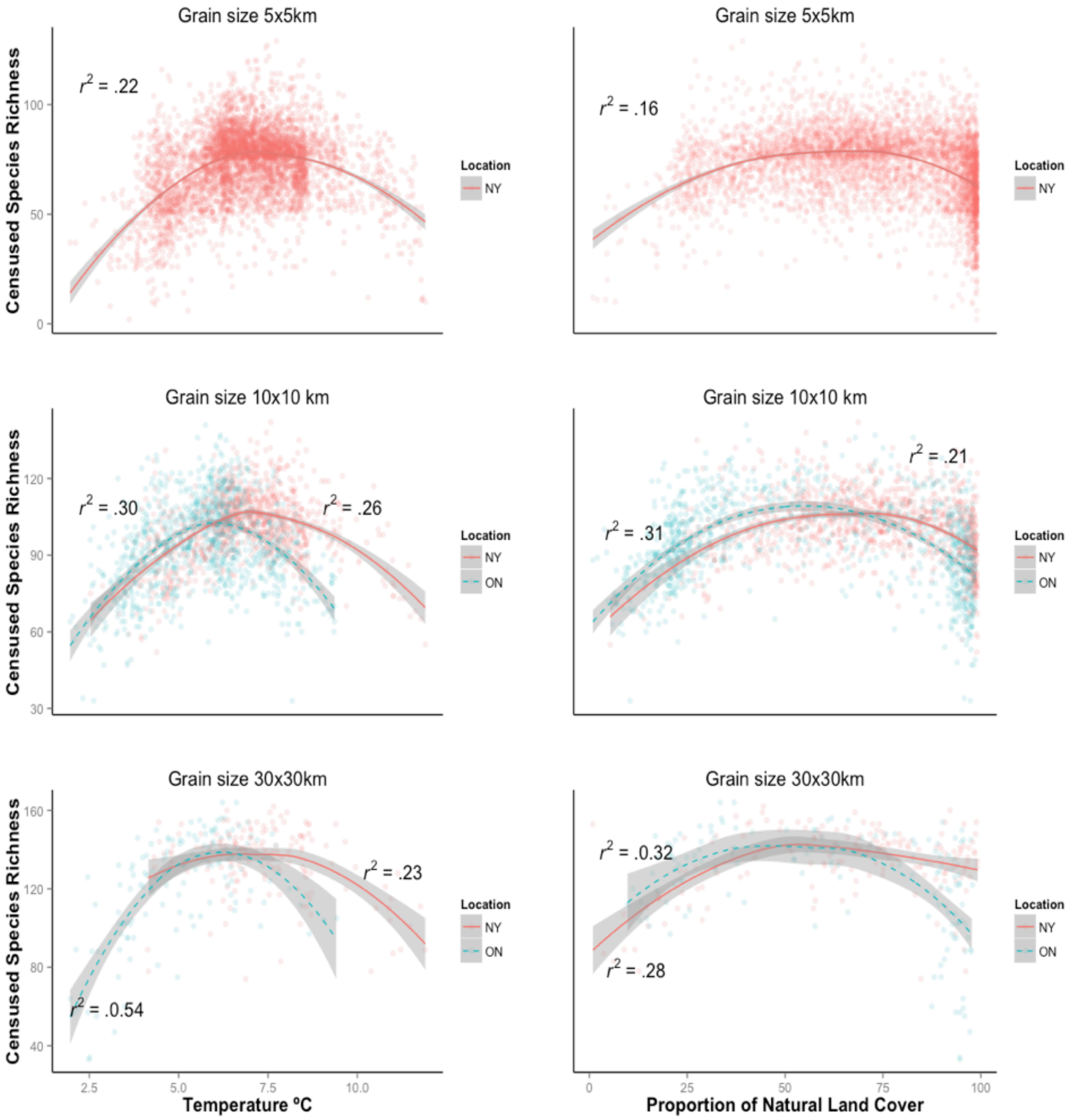

Figure 5. Censused species richness generated from atlases as a function of temperature (a,c,e) and the proportion of natural land cover (b,d,f) in grid cells covering southern Ontario and New York State at different spatial grain sizes. R2 represents the goodness of fit of OLS regression models. Richness peaks roughly at 53% (NY, 5x5km), 65% (NY, 10x10km), 55% (ON, 10x10km), 64% (NY, 30x30km), and 52% (ON, 30x30km) of natural land cover.

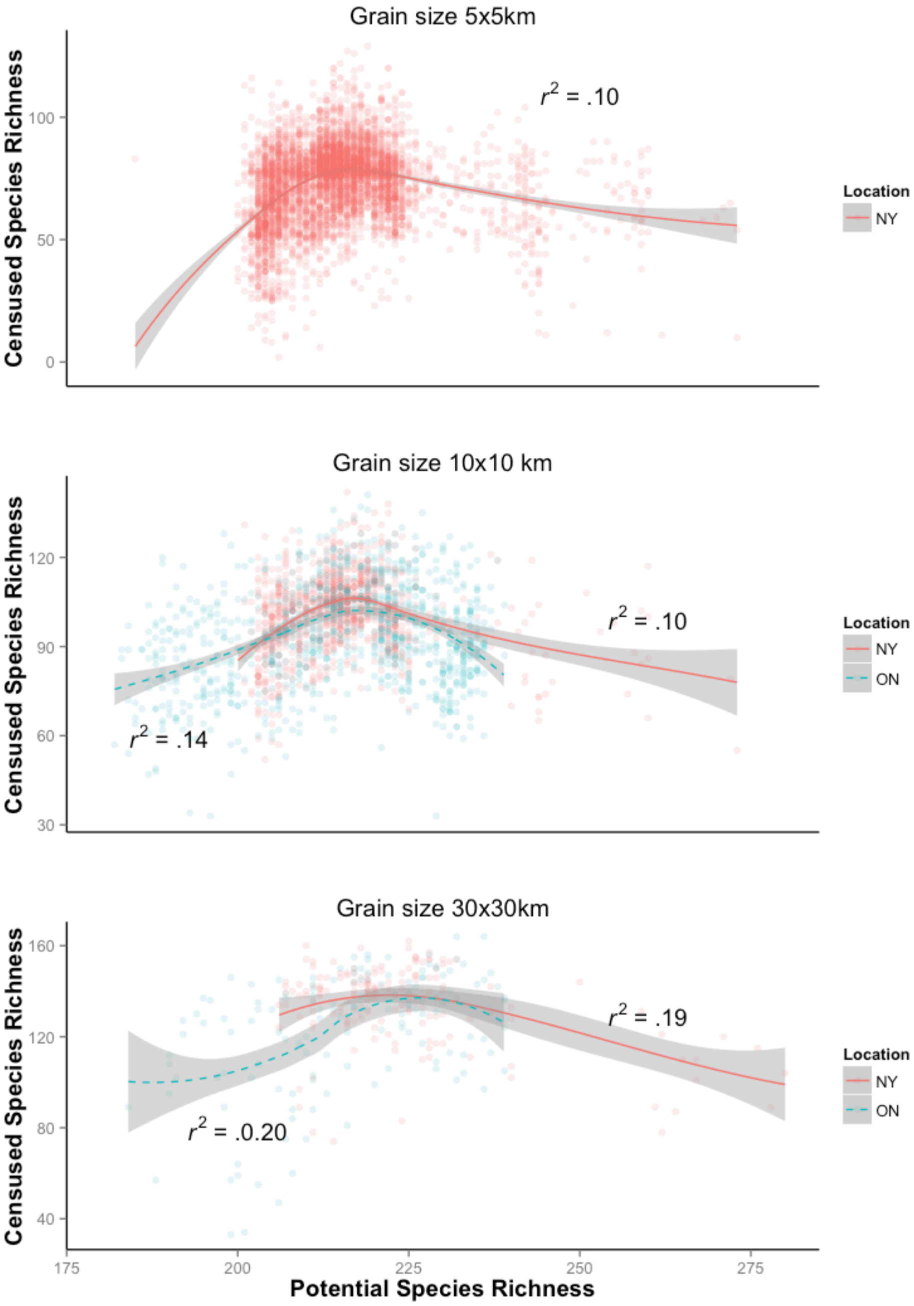

Figure 6. Censused richness as a function of potential richness at different spatial grain sizes. a) n=4,822 in NY (5x5km), b) 985 and 1,075 for ON and NY, respectively, at 10x10km scale, and 251 covering ON and NY (30x30 km).

APPENDIX

Appendix S1. Complementary statistical analysis.

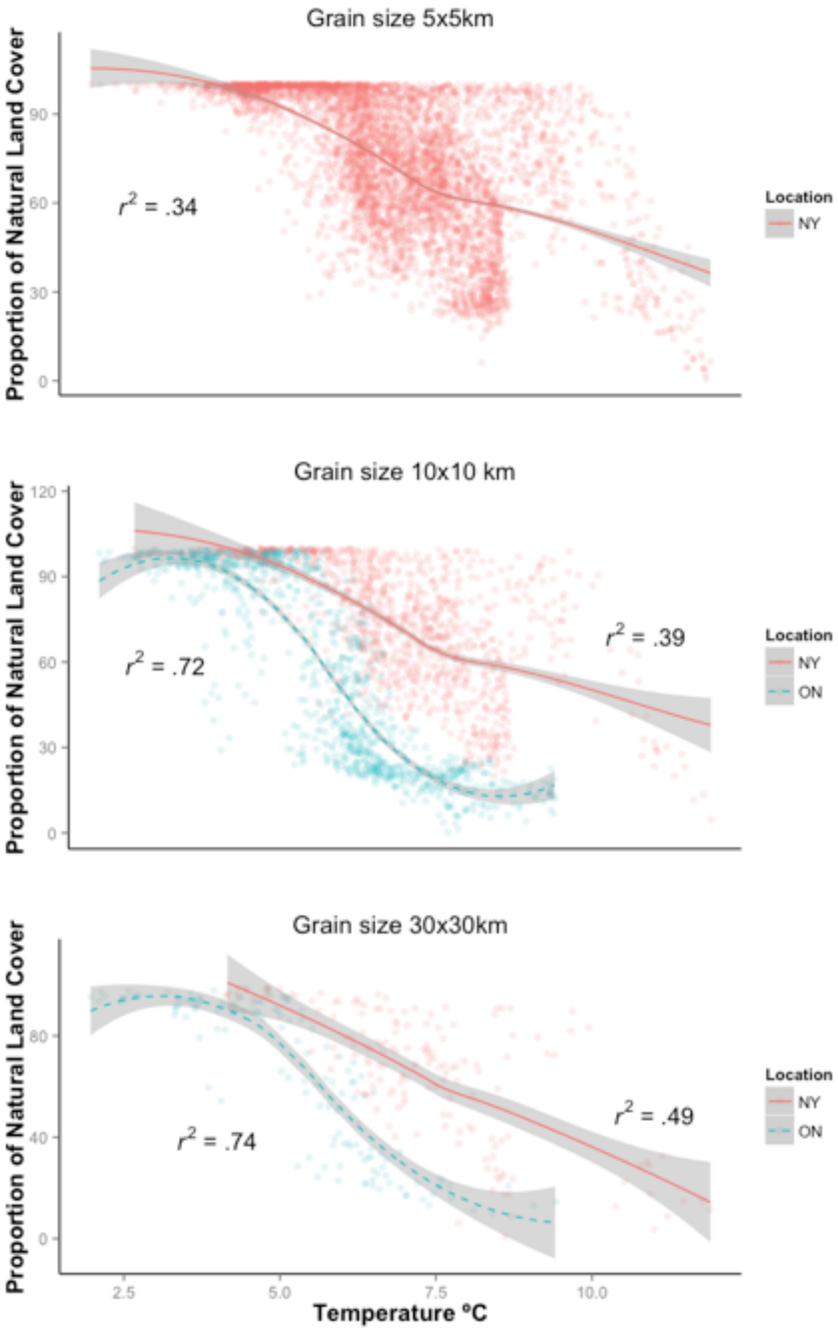

Fig. S1-1. Linear regressions between the proportion of natural land cover and temperature at different spatial grain sizes.

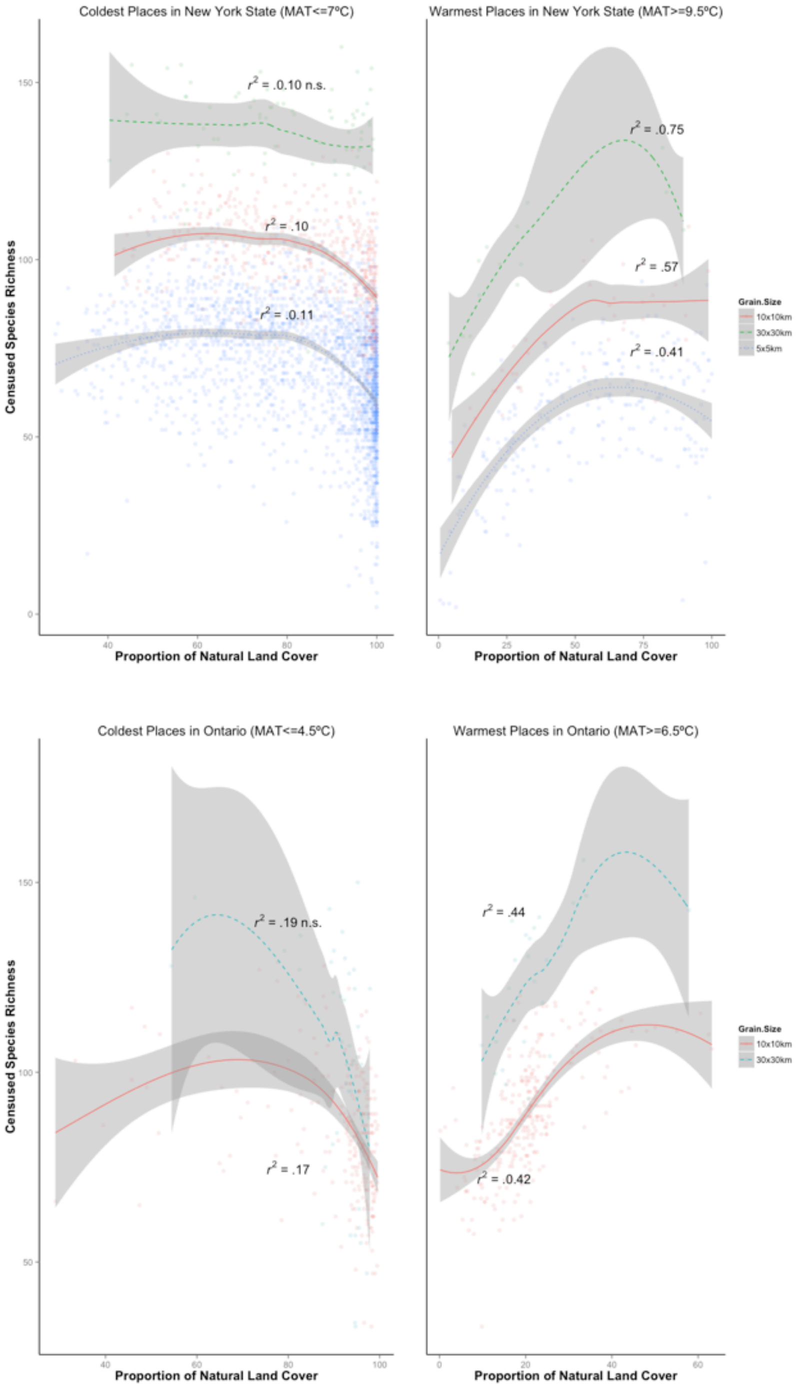

Fig. S1-2. Censused richness-natural land cover relationships for the warmest and coldest places in southern Ontario and New York State. a) Coldest places in New York State (5x5km – n=1,097, 10x10km – n=244, 30x30km – n=28 cells); b) Warmest places in New York (5x5km – n=240, 10x10km – n=40, 30x30km – n=15 cells); c) Coldest places in Ontario (10x10km – n=243, 30x30km – n=46 cells); d) Warmest places in Ontario (10x10km – n=291, 30x30km – n=26 cells).

Table S1-1. Statistical outcome of **spatial autocorrelation** models between **potential richness** as a function of temperature (MAT) and the proportion of natural land cover (LC) in grid cells of southern Ontario and New York State. * - term statistically not significant.

Grain Size	Location	Coefficients		Nagelkerke r^2	AICc
		MAT	LC		
5x5km	NY (n=4,822)	4.58		0.56	31357
			-0.19	0.23	34103
		4.41	-0.02	0.56	31343
10x10km	NY (n=1,075)	4.48		0.53	6963
			-0.21	0.26	7443
		4.16	-0.03	0.53	6955
	ON (n=985)	7.72		0.77	6489
			-0.33	0.66	6913
		6.14	-0.09	0.79	6438
30x30km	NY (n=165)	8.18		0.74	1168
			-0.37	0.45	1291
		0.82	(0.01)	0.74	1169
	ON (n=138)	7.62		0.82	878
			-0.36	0.71	948
		6.22	-0.08	0.83	880

Table S1-2. Statistical outcome **spatial autocorrelation** models between **realised richness** as a function of temperature (MAT) and the proportion of natural land cover (LC) in grid cells of southern Ontario and New York State. * - term statistically not significant.

Grain Size	Location	Coefficients				r^2	AICc
		MAT	MAT^2	LC	LC^2		
5x5km	NY (n=4,822)	2.02				0.04	40029
		28.04	-1.82			0.22	39040
				-0.10		0.02	40119
				1.40	-0.01	0.17	39369
		1.78		-0.02		0.04	40026
		28.03	-1.82	(0.00)		0.23	38998
		21.50	-1.38	0.85	-0.01	0.26	38791
10x10km	NY (n=1,075)	1.40				0.06	8446
		27.52	-1.85			0.27	8170
				-0.06		0.03	8479
				1.52	-0.01	0.22	8245
		1.37		(-0.01)		0.04	8465
		28.10	-1.87	(0.03)		0.27	8168
		20.85	-1.38	0.89	-0.01	0.32	8103
	ON (n=985)	1.82				0.05	8302
		34.90	-2.85			0.31	7987
				-0.05		0.03	8325
				1.63	-0.01	0.32	7972
		3.40		0.10		0.06	8299
		37.30	-2.90	0.10		0.33	7972
		2.40	-1.65	1.44	-0.01	0.45	7782
30x30km	NY (n=165)	-0.29				0.20	1382
		25.20	-1.82			0.35	1351
				0.18		0.21	1381
				1.54	-0.01	0.40	1339
		(-0.17)		(0.10)		0.21	1382
		26.60	-1.83	(0.10)		0.36	1349
		12.55	-0.92	1.10	-0.01	0.43	1335
	ON (n=138)	9.10				0.67	1157
		57.20	-4.58			0.64	1169
				-0.33		0.48	1220
				2.10	-0.02	0.47	1225
		13.85		0.28		0.61	1180
		57.65	-4.50	(0.09)		0.65	1170
		49.80	-3.73	0.92	-0.01	0.66	1168

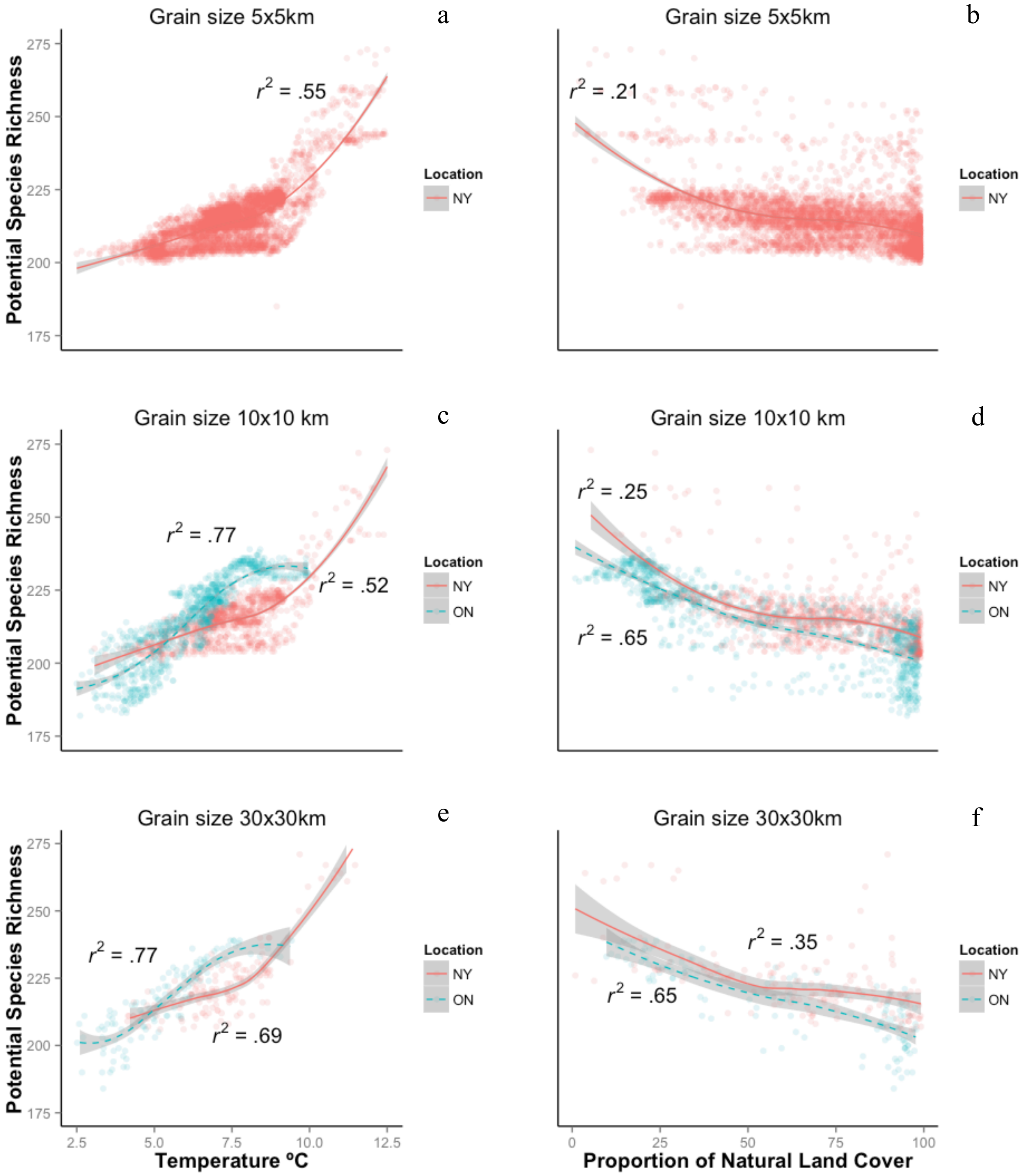

Figure S1-2. Potential species richness generated from range maps as a function of temperature (a,c,e) and the proportion of natural land cover (b,d,f) in grid cells covering southern Ontario and New York State at different spatial grain sizes. R2 represents the goodness of fit of second degree polynomial OLS regression models.

CONCLUSIONS

I set out in this thesis to test the overwhelmingly stated hypothesis that both habitat loss and habitat fragmentation lead to biodiversity loss. Using a macroecological approach I tested predictions of some hypotheses by analysing the relationships between avian species' ecological responses to amounts or configuration (i.e., fragmentation) of land covers types in landscapes varying in sizes of southern Ontario and New York State.

The overall conclusion of this thesis is that the proportion of natural land cover (from 0-100%) is a relatively poor predictor of total avian species richness at the level of landscapes. In the analysed landscapes, the richness-land cover relationships have a consistent peaked pattern across spatial grain sizes (25-900km^2) and geographical regions (Ontario and New York State), meaning that quite a lot of land cover can (roughly up to 50%) be converted into human-dominated covers before total richness starts to show any signal of species loss. That contradicts the expected monotonic relationship calculated with species-areas models (e.g., Pimm et al. 1995, 2014): more natural land cover does not mean more species; reduced natural land cover does not imply reduced species left within landscapes. Natural areas are transformed into new environments capable of supporting a still relatively high number of species (Desrochers et al., 2011) before becoming completely unavailable for species (De Camargo & Currie, 2015). Moreover, overall the richness-land cover models explain roughly 10-40% of the variance in avian richness. This is very little if we compare these numbers to the variance in richness explained by climatic variables at coarser grains (e.g., Currie et al. 2004). However, the low variance explained that were found in our models is consistent with other studies showing that environmental variables tend to explain less than forty percent of the variance in species richness at regional scales (Field et al., 2009; Belmaker & Jetz, 2011). Thus, it remains uncertain whether there are one, or a few, important predictors of total species richness at the landscape levels.

Nonetheless, the outcome of this thesis has some implications for biodiversity management, especially considering that land use decisions that affect species diversity are made at landscape/regional scales (Dale et al., 2000; Miller et al., 2009). First, Chapter 1's modelling approach demonstrated that it is possible to predict total richness fairly well ($r^2 \cong 0.60$) by relating guilds of species to coarsely defined preferable land covers they utilize in landscapes. Therefore, this could be easily applied to plan the desired amount of natural areas intertwined with human-dominated ones at a city or provincial scale, for example, without knowing much of the specific habitat requirements of each species, which is always a hard task.

Second, habitat fragmentation (as opposed to habitat loss) does not seem to affect avian species richness in landscapes of southern Ontario, but it might be somewhat detrimental for very few individual species. Both richness and individual bird species respond primarily and strongly to land cover amount. That is not surprising, since Fahrig (2017)'s literature review has shown that in most fragmentation studies the effect of habitat fragmentation is positive on species' ecological responses after accounting for habitat amount. Therefore, the findings of Chapter 2 empirically demonstrate that managing habitat fragmentation conservation strategies at the landscape level, at least for bird species in eastern North America.

Third, an interaction effect between climate change and habitat loss could severely affect northern bird species living at the southern-edge of their ranges, rather than southern species living at the northern-edge of their ranges (Chapter 3). Presumably that is because, as climate warms, the ranges of southerly species expand into new climatically suitable areas, and partially disturbed landscapes are more readily occupied than undisturbed landscapes. However, northern species will be negatively affected at their southern-edge limits by both warmer temperatures, and disturbed landscapes become unsuitable for species' persistence. Consequently, land planners and policy makers should direct their efforts to protect natural land covers in regions where the sums of the two environmental stressors, habitat loss and climate change, might be acting synergically.

However, it is important to note that this thesis has some important limitations, which are mainly (but not limited to) related to the system/ geographical regions, taxonomic group, and data utilised in the thesis. First, the studies were focused on bird species living in temperate biomes of eastern North America. Therefore, it is difficult to make generalizations about whether the correlations observed in this system would be similar in other biomes and with other taxa. Second, even though atlas data attempt to measure the actual occurrences of species on the ground, they have their methodological flaws. Atlas data have problems with temporal resolution and representativeness as a result of sampling error or incompleteness (Hurlbert & Jetz, 2007; Hortal, 2008). Species may not be recorded in places where they actually occur creating false absences. That can, ultimately, affect the number of species compiled in each landscape. However, correcting for sampling effort can minimize this problem (Chapter 1), and richness measurements obtained from atlases have been shown useful for studying ecological processes at the landscape level (Hortal, 2008; Robertson et al., 2010; Sadoti et al., 2013)

In closing, this thesis has opened new research questions that I would like to explore in my future career as a researcher. For instance, I would like to test whether the patterns I found in the richness-land cover relationships can be held at continental or global scales, or whether species traits or phylogenetic signals can affect these species-land cover relationships across spatial and temporal scales. I believe that these research topics can be extremely important if one wants to predict what it is likely to be the species' ecological responses to environmental conditions facing rapidly and substantial changes.

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