Habitat loss and avian range dynamics through space and time

Rachelle Desrochers

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
University of Ottawa
in partial fulfillment of the requirements for the
PhD degree in the

Ottawa-Carleton Institute of Biology

Thèse soumise à la
Faculté des étude supérieures et postdoctorales
Université d'Ottawa
en vue de l'obtention du doctorat

L'institut de biologie d'Ottawa-Carleton

ACKNOWLEDGEMENTS

It took six Tanzanian men to get me to the top of Mount Kilimanjaro. It has taken many more people than that to get me to this point. I would like to begin by thanking my thesis supervisors, Dr. Jeremy Kerr and Dr. David Currie: Jeremy, for his constant faith in me and David, for always encouraging me to reach a little farther.

I am grateful to my committee members, Dr. Antoine Morin and Dr. Lenore Fahrig. Antoine has been a committee member, my TA supervisor and departmental chair while I was president of the graduate student association. I have been the lucky recipient of his guidance and experience not only on matters regarding this thesis but also pedagogy and other aspects of academia. His door has always been open for me and for that I am very thankful. I am grateful to Lenore for her focused attention every time I sought her advice and the value she places on clarity of thought and language.

I want to thank my labmates, past and present, official and unofficial, for always answering in the affirmative the two most important questions for any grad student: Can I run some ideas by you? and Do you want to go get tea/coffee/beer? In particular, I want to thank:

- Dr. Manisha Kulkarni Woodstock for being a great female role model in science, opening up Africa to me and sharing Molly with me.

- Dr. Adam Algar for challenging what I think and how I think more than anyone I have ever known. I am a better thinker, scientist and person for knowing you.

-Heather Kharouba and Erin Koen, whose friendship made the University of Ottawa a home for me. I have searched in vain for words to express how much your love and support has meant to me. I could not have finished this without it.

-Katie Gibbs, Martha Mullaly, Shinjini Pal and Véronique Boucher-Lalonde for having some of the most interesting brains I have ever had the pleasure of picking on a regular basis.

-Katie Hierlihy for, literally, climbing the mountain with me.

-Eric Young for being the most entertaining field work partner ever.

and

-Marilyn MacMillan for teaching me the few bird calls that I recognize and being tremendously supportive from the beginning of this journey.

As much as I have teased them, I have taken immense joy in getting to know some really great undergraduate students. I would like to highlight some of the poor souls who have had to put up with me the most: Ryan Burke, Luba Reshitnyk, François Thériault, Isabelle Létourneau, Miriam Neufeld, Deirdre Leowinata, Andy Thompson, Jeremy Newman and Monique Marguerie. Working with you may not have sped up the completion of this thesis but it certainly made it a lot more fun.

Doreen Smith and Gita Kanags in the biology office and Lorraine Houle in the grad office have always remembered my name, greeted me with a smile and made my time here easier in a dozen ways that I know about and a hundred that I'm sure I don't.

None of this would have been possible without the love and support of my family. I want to thank my mom, Wanda Faris, for teaching us to question the status quo and to have and express our opinions (though I suspect she sometimes wishes that I had slightly fewer opinions ☺); my dad, Jean Desrochers, for turning math problems into car games and for sharing with us the joy of figuring things out; and finally my sister, Annie Desrochers, for being the other half of "us", being organized enough to also organize her scatterbrained sister, being able to make me laugh no matter what, and for marrying the best geek ever.

Finally, a few people made, perhaps, the most important contribution to helping me finish this thesis by keeping me fed: most notably my mama but also my stepmom Ginette Larocque, my aunt Claire Desrochers, and my dear friends Michèle Gannon and Will Woodstock. My brain would not have functioned as well without you.

ABSTRACT

The species–area relationship (SAR) has been applied to predict species richness declines as area is converted to human-dominated land covers.In many areas of the world, however, many species persist in human-dominated areas, including threatened species. Because SARs are decelerating nonlinear, small extents of natural habitat can be converted to human use with little expected loss of associated species, but with the addition of more species that are associated with human land uses. Decelerating SARs suggest that, as area is converted to human-dominated forms, more species will be added to the rare habitat than are lost from the common one. This should lead to a peaked relationship between richness and natural area. I found that the effect of natural area on avian richness across Ontario was consistent with the sum of SARs for natural habitat species and human-dominated habitat species, suggesting that almost half the natural area can be converted to human-dominated forms before richness declines. However, I found that this spatial relationship did not remain consistent through time: bird richness increased when natural cover was removed (up to 4%), irrespective of its original extent.

The inclusion of metapopulation processes in predictive models of species presence improves predictions of diversity change through time dramatically. Variability in site occupancy was common among bird species evaluated in this study, likely resulting from local extinction-colonization dynamics. Likelihood of species presence declined when few neighbouring sites were previously occupied by the species. Site occupancy was also less likely when little suitable habitat was present. Consistent with expectations that larger habitats are easier targets for colonists, habitat area was more important for more isolated sites. Accounting for the effect of metapopulation dynamics

on site occupancy predicted change in richness better than land cover change and increased the strength of the regional richness–natural area relationship to levels observed for continental richness–environment relationships suggesting that these metapopulation processes "scale up" to modify regional species richness patterns making them more difficult to predict. It is the existence of absences in otherwise suitable habitat within species' ranges that appears to weaken regional richness–environment relationships.

RÉSUMÉ

La relation espèce-aire (REA) est utilisée afin de prédire la réduction en richesse spécifique lorsque des habitats naturels sont convertis en habitats dominés par l'humain. Par contre, dans une grande partie du monde, un grand nombre d'espèces, incluant des espèces en péril, occupent des régions dominées par l'humain. La forme non-linéaire et décélérante de la REA suggère que, au fur et à mesure que les paysages sont convertis en formes dominées par l'humain, les espèces associées à la forme rare seront ajoutées en plus grand nombre que seront perdues celles associées à la forme commune. Ceci devrait mener à une relation unimodale entre richesse et couvert naturel. J'ai trouvé que l'effet de l'aire des habitats naturels sur la richesse aviaire en Ontario était conséquent avec la somme des REA pour les espèces associées aux habitats naturels et pour celles associées aux habitats dominés par l'humain. Ceci suggère que presque la moitié de l'aire de couvertures naturelles peut être convertie avant que la richesse diminue. Par contre, j'ai trouvé que la relation spatiale n'est pas demeurée constante avec le temps : la richesse aviaire a augmentée avec la perte d'habitats naturels (jusqu'à 4%) peu importe l'aire initiale de couvertures naturelles.

L'inclusion de processus associés aux dynamiques de métapopulations dans des modèles prédictifs de présence d'espèce a dramatiquement amélioré les prédictions de changements temporels en richesse spécifique. Une occupation de sites variable était commune pour les espèces d'oiseaux considérés ici, probablement dû aux dynamiques d'extinction et de colonisation. L'occupation d'un site était moins probable si peu de sites avoisinants étaient occupés auparavant par des individus de la même espèce. De plus, l'occupation d'un site était moins probable si le site contenait une aire plus petite

d’habitat approprié pour l’espèce. En outre, l'effet de l’aire d’habitat appropriée pour l’espèce était plus important pour les sites isolés, ce qui est conséquent avec l’idée que les grands habitats représentent des cibles plus atteignables pour les immigrants. En prenant compte l’effet des dynamiques de métapopulations sur l’occupation de sites, la prédiction de changements en richesse fut amélioré par rapport à la prédiction basée sur le changement de couvert. De plus, ceci a amélioré la force de la relation entre richesse et aire de couvert naturel, la rendant aussi forte que celles des relations richesse – environnement observées à l’échelle continentale. Ceci suggère que ces processus de métapopulations se manifestent à des échelles supérieures pour modifier les patrons de richesse spécifique régionale, les rendant plus difficile à prédire. Ce sont les absences dans des habitats pourtant appropriés à l’intérieur même de l'aire de répartition des espèces qui semble affaiblir les relations richesse –environnement.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FOREWORD

The central focus of this thesis is on the processes that determine avian distributions and the richness of avian species in space and time, particularly habitat loss. This work is motivated by a profound interest in how human activities impact biodiversity in general and bird diversity in particular. I must however begin with a confession: I am not a birder. I can identify but a handful of birds by sight and even fewer by sound. Despite this, I have a deep fondness for the symphony of bird calls to which I have long awoken on lazy Saturday mornings, though I can only identify the low moan of the Mourning Dove and the electronic whistle of the Red-winged Blackbird. (My fondness for these two ubiquitous birds is likely sufficiently damning evidence of my lack of credibility as a birder.) It is primarily the plurality and variety of these voices that has most intrigued me, whether they are calling to one another in my rural backyard or providing the peaceful soundtrack of a hike in Gatineau Park. In this work, I sought to gain a better understanding of how human activities, particularly conversion of natural areas to human-dominated forms, affect the number of voices that are heard. My attempt to answer this question led me to also question the extent to which the number of species found in a given area is shaped by deterministic factors (i.e. environment) and by more stochastic population-level factors affecting individual species. Though the work presented here cannot fully answer these questions, I hope that it may provide valuable pieces of the puzzle.

INTRODUCTION

Human land use activities have altered much of the Earth's surface through forest clearing, urban development and the practice (followed by the intensification) of agriculture. These activities have led to declines in biodiversity in general, as well as more specifically in birds, by degrading or removing habitat and overexploiting native species (Foley *et al*., 2005; Stutchbury, 2007). Most endangered bird species in Canada are threatened at least in part by habitat loss, resulting chiefly from agricultural conversion and urbanization (Venter *et al*., 2006). Consequently, management of human uses of the land plays a key role in the management and protection of biodiversity (Dale *et al*., 2000).

Land management should consider impacts on species that inhabit human-dominated areas in addition to those that inhabit natural areas. Given the pervasiveness of the human footprint worldwide (Sanderson *et al*., 2002), it is important to manage natural areas to protect (or minimize human impacts on) the species inhabiting these areas. We are often most concerned with the protection of natural areas, particularly forests, which have tended to be the victims of human encroachment in the past (Ramankutty & Foley, 1999; Ellis *et al*., 2010).In some parts of the world, however, the number of species occupying human-dominated areas is comparable to numbers occupying natural areas (Daily, 2001). Because some landscapes have been modified for millennia, many species have adapted to these altered landscapes. In Europe, these bird species are often in decline, likely due to agricultural intensification, while forest and woodland species have remained stable (Gregory *et al*., 2005). In Canada, where the clearing of forests for conversion to agriculture occurred much more recently (Ramankutty & Foley, 1999; Ellis *et al*., 2010), species that prefer open habitats (including grasslands and fields) are often relegated to areas that have at least some level of human impact, mostly agricultural areas, because natural open habitats are quite rare below the tree line (Kerr & Cihlar, 2003).

Macroecological approaches to global change research are proving increasingly useful in addressing broad-scale problems quickly and thoroughly (Kerr *et al*., 2007). The macroecological approach involves taking a step back to examine the properties of ecological systems as a whole, usually focusing on the abundance and distributions of large numbers of species over landscape to continental scales (Gaston & Blackburn, 2000; Kerr *et al*., 2007). This approach has been particularly valuable for identifying general patterns and processes. Experimental studies can do this too, of course, but results from one experimental contribution may not generalize. The broad scale focus of macroecology makes it well-suited for addressing the broad scales over which human impacts occur (Kerr *et al*., 2007) as well as considering the broader context that affects local species populations and communities. This is particularly true for a taxon as highly mobile as birds (Gaston & Blackburn, 2000).

Macroecology is founded on a statistical approach to test hypotheses, detect generalities and establish the importance of determinants of species' abundances, distributions and richness (Gaston & Blackburn, 2000; Kerr *et al*., 2007; Fisher *et al*., 2010). A consequence of the broad spatial focus that makes the macroecological approach so valuable is the difficulty of conducting manipulative field or laboratory experiments because it is often logistically and ethically impossible to do so over such large areas (Gaston & Blackburn, 2000; Kerr *et al*., 2007). Correlative studies are inferentially weaker. However, natural systems, particularly at broad scales, are more realistic systems in which to test macroecological hypotheses than those used for field or laboratory experiments (Gaston & Blackburn, 2000; Kerr *et al*., 2007). Consequently, the results from this type of study can be more insightful and relevant for conservation planning and land management than could be achieved through manipulative studies (Kerr *et al*., 2007).

The species – area relationship is a macroecological pattern that potentially provides an important tool with which conservation scientists and land managers can evaluate the possible impacts of land use decisions (such as forest clearing and urban growth) on species richness (Pimm *et al*., 1995). Regarded as one of the few laws in ecology, the species – area relationship refers to the consistent relationship observed between the number of species inhabiting an area and its size, where species richness is a positive and decelerating function of area (Rosenzweig, 1995; Ricklefs & Lovette, 1999; Schreiner, 2003). Species–area relationships have been used to forecast the magnitude of species losses from habitat destruction, usually the loss of forests (Pimm & Askins, 1995; Brooks & Balmford, 1996; Pimm & Raven, 2000; DeFries *et al*., 2005; Sala *et al*., 2005). When natural land cover is converted, area is not lost; it is only transformed to human-dominated forms, some of which provide habitat for other desirable species (Pereira & Daily, 2006). Therefore the relationship between species richness and natural area can provide a tool with which to assess the impact of land cover conversion on both species that prefer natural land covers as habitats but also those that use human-dominated land covers as habitat.

In the first chapter of this thesis, entitled *How, and how much, natural cover loss increases species richness,* I examined how the richness of Ontario breeding birds varied as a function of the amount of remaining natural land cover and assessed how this differed for species that prefer forested (and therefore natural) habitats and species that prefer open (and therefore generally human-dominated) habitats. The total area of each sampling unit was held constant, therefore conversion of land to human-dominated land covers necessarily occurred at the expense of natural land cover. In this case, species richness reflected the balance of open habitat species gained given the increase in open/human-dominated area and the loss of natural habitat species from the loss of natural area. Because the species – area relationship is positive and decelerating, one would expect small losses of natural area to carry small losses of natural habitat species but relatively large initial gains of open habitat species. Consequently, critical questions addressed in Chapter 1 are: “Can natural cover loss lead to increased species richness?”, “At what point does land conversion to human-dominated forms lead to decreasing richness?” and “How many natural land cover species are lost as natural land cover is converted to human dominated cover?”.

There remains much uncertainty as to the most important determinants of terrestrial species richness at regional scales. Climate can confidently be concluded to be the most important determinant of species richness at continental scales since the majority of studies on richness – environment relationships show that climate best predicts species richness at this scale and explains most of the variation in species richness (Field *et al*., 2009 and references therein). However, of the many hypotheses regarding the determinants of species richness, no one hypothesis has consistently found support at regional scales (Field *et al*., 2009). Moreover, environmental variables tend to explain less than forty percent of the variance in species richness at this scale (Mayer & Cameron, 2003; Koh *et al*., 2006; González-Taboada *et al*., 2007; Hortal *et al*., 2008; Lepczyk *et al*., 2008; Belmaker & Jetz, 2010). This has implications for biodiversity management because land use decisions that affect biodiversity are most often made at local to regional scales (Beatley, 2000; Dale *et al.*, 2000; Miller *et al.*, 2008).

In the second chapter of this thesis, entitled *The role of metapopulation dynamics in determining regional species richness patterns*, I sought to determine why richness is so much more difficult to predict at regional scales. Regional scale richness – environment studies tend to use field observations of species occurrences to derive measures of species richness (see Mayer & Cameron, 2003; Virkkala *et al.*, 2005; Koh *et al.*, 2006; González-Taboada *et al.*, 2007; Rompré *et al.*, 2007; Lepczyk *et al.*, 2008; Honkanen *et al.*, 2009). Unlike species range maps, field observations reflect local absences within species ranges. If these absences within species' ranges are due to unsuitable environmental conditions, then the relationship between species richness and environment should still be quite strong. However, if local absences within species' ranges occur at sites that are environmentally suitable, then the resulting richness – environment relationships will necessarily be weaker than those detected at continental scales where species richness is measured by superimposing individual species' ranges. Metapopulation theory suggests that there should be temporal variability in site occupancy (here one year, gone the next) due to demographic and environmental stochasticity. As a result, many suitable sites within a species' range may be unoccupied in any given census (Hanski, 1999). The resulting temporal variability in site occupancy caused by metapopulation dynamics would increase spatial variability in species richness. I tested the hypothesis that metapopulation-like processes of local colonization and extinction lead to unoccupied sites within individual species ranges and that this in turn leads to a weakened relationship between avian richness and the proportion of remaining natural land cover, the best environmental predictor of avian richness in Ontario (Chapter 1).

Arguably the best way of knowing how environmental conditions affect species distributions and richness is by manipulating aspects of the environment to assess species' response. Macroecology's main weakness is its reliance on correlative inference. Global change increasingly provides the quasi-experimental opportunities that the discipline has been lacking (Kerr *et al.*, 2007; Algar *et al.*, 2009; Fisher *et al.*, 2010). Climate change and human modification of landscapes ironically are providing opportunities to test hypotheses regarding the role that climate plays in shaping patterns of species richness and how species respond to land cover modification (Kerr *et al.*, 2007). Taking advantage of these opportunities depends upon the availability of long term datasets of species distributions, land cover and climate at commensurate spatial and temporal scales (Kerr *et al.*, 2007; Fisher *et al*., 2010). For this, initiatives like the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/), repeated regional Breeding Bird Atlases and the North American Breeding Bird Survey (BBS; http://www.pwrc.usgs.gov/BBS/) provide vital, freely available data on species occurrences, abundances and/or distributions through time.

In the final chapter of this thesis, entitled *Metapopulation dynamics, not environmental change, predict change in species richness*, I determined if species richness responded through time in the way predicted by the spatial relationship between richness and natural area (Chapter 1) and in the way predicted by metapopulation dynamics (Chapter 2). I detected a peaked spatial relationship between richness and natural area relationship in Chapter 1. From this, I expected that gains or losses of natural area that bring the amount of natural area closer to the peak of the richness-natural area relationship would increase species richness. I also tested if avian richness changed as predicted by the metapopulation models developed in the second chapter of this thesis. From metapopulation theory, I would expect that sites that have larger amounts of species-specific habitat area (as these are analogous to larger patches) and that are surrounded by sites occupied by conspecifics (as these are analogous to less isolated patches) are more likely to be occupied in any given census (Hanski, 1999). Some species may be absent from sites where there is a high likelihood of their occurrence. Over time species should appear at these sites. Similarly species may be present at sites where there is a low likelihood of their occurrence but over time, they should disappear from these sites. Therefore, species richness should increase in sites where many previously absent species were likely to occur and decrease in sites where many previously present species were unlikely to occur. Lastly, I assessed the relative contributions of land cover change and metapopulation dynamics in determining how avian richness has changed through time.

I have addressed the questions described above using the birds that breed in the southern portion of Ontario as a study system. Birds have long been objects of fascination for many biologists and amateur naturalists. This is reflected in the number of birding projects from Breeding Bird Atlases (where projects exist for most Canadian provinces, American states and European countries), the nearly 50 year old North American Breeding Bird Survey that relies on thousands of volunteers to sample thousands of routes across North America each year (Sauer *et al*., 2011), and eBird that now includes more than 1.5 million entries (eBird, 2011). Consequently the availability of information on avian occurrences, abundances and distributions is unparalleled in any other species group in terms of its spatial and temporal resolutions and extents.

Breeding Bird Atlases are among the most complete information on regional species distributions. In Ontario, two Breeding Bird Atlases (censused using consistent methodology from 1981 to 1985 and again from 2001 to 2005) have been created to map and monitor the distributions of the birds that breed in the province. In avian atlases, individual sampling units (known as atlas squares), that typically vary from 2km to 10km in size, are thoroughly sampled for evidence of all bird species breeding within them (Cadman *et al.*, 1987; Väisänen *et al.*, 1998; Martí & del Moral, 2003; Bibby, 2004; Cadman *et al*, 2007; Lemoine *et al.*, 2007). This increases the likelihood of detecting rare or cryptic species relative to line transects or point counts (Gregory *et al.,* 2004). The standards for breeding evidence are precisely defined and generally consistent across atlases (Bibby, 2004); however, the specific level of sampling effort and sampling method (random, regular or stratified) are often not predefined, particularly in earlier atlases (Cadman *et al.*, 1987; Väisänen *et al.*, 1998; Martí & del Moral, 2003). More recent atlases have combined the typical atlas sampling methodology with more quantitative estimates of abundance, usually point counts, in at least a subset of the atlas squares (Cadman *et al.*, 2007; Lemoine *et al.*, 2007). This will further increase the value of Breeding Bird Atlases as it will allow for the assessments of changes in species' relative abundances as well as their distributions.

I focused on the southern portion of Ontario (south of the latitude of Sudbury) because these were sampled intensively at the grain that I desired to study species distributions (Cadman *et al.*, 2007) and this is the area of Ontario where land cover is and has been converted to more permanent forms of human-dominated land cover (agriculture and developed land as opposed to logged forests that can regenerate; OMNR, 2002). Data collection for the two Ontario Breeding Bird Atlases took four years for each atlas and the assistance of more than 1,300 volunteers for the first atlas in 1985 and 3,000 for the second atlas in 2005 (Cadman *et al.*, 1987 & 2007). To collect data on species distributions over so broad a spatial and temporal scale would have been well beyond the capabilities of any one researcher. As such, I am indebted to the hard work and dedication of the thousands of avid and skilled birders that created this dataset.

CHAPTER 1: HOW, AND HOW MUCH, NATURAL COVER LOSS INCREASES SPECIES RICHNESS

Desrochers, R.E., Kerr, J.T. & Currie, D.J. (2011) Global Ecology and Biogeography, **20,** 857-867.

ABSTRACT

Aim: The species–area relationship has been applied in the conservation context to predict monotonic species richness declines as natural area is converted to human-dominated land covers. However, some conversion of natural cover could introduce new habitat types and allow new open habitat species to occur. Moreover, decelerating richness–area relationships suggest that, as natural area is converted to human-dominated covers, more species will be added to the rare (human-dominated) habitat than are lost from the common (natural) one. Area effects and increased habitat diversity could each lead to a peaked relationship between species richness and the relative amount of natural area. The purpose of this study is to quantify the effect of conversion of natural area to human-dominated land cover on avian species richness.

Location: Ontario, Canada

Methods: I evaluated the responses of total avian richness, forest bird richness and open habitat bird richness to remaining natural area within 993 quadrats, each 100 km^2. I quantified the amount of natural land cover and land cover heterogeneity using remote sensing data. I used Structural Equation Modelling (SEM) to disentangle the relationships among avian richness, natural area and land cover heterogeneity.

Results: Spatial variation in avian richness was a peaked function of remaining natural area, such that losses of up to 44% of the natural area increased avian richness. This partly reflects increased land cover variety; however, SEM suggests that much of the increase in richness is due to pure area effects. Richness of forest species declined by two species over this range of natural cover loss while open habitat bird richness increased by approximately 20 species. The effect of natural area on species richness is consistent with the sum of species–area curves for natural habitat species and human-dominated habitat species.

Main Conclusions: At least in northern temperate forests, almost half of the natural land cover can be converted to human-dominated forms before avian richness declines. Conversion of <50% of regional natural area to human-dominated land cover can benefit open-area species richness with relatively few losses of forest-obligate species. However, with > 50% natural area conversion, species begin to drop out of regional assemblages.

INTRODUCTION

Understanding how species richness responds to habitat change is vital to successful conservation and management of diversity as habitat loss has become the primary cause of species endangerment and occurs mainly as a result of agricultural conversion and urbanization (Czech *et al.*, 2000; Kerr & Cihlar, 2004; Venter *et al.*, 2006). To the extent that conversion of natural habitat to human-dominated forms renders that habitat completely unavailable to species, then there should be a positive spatial relationship between species richness and the amount of remaining unaltered habitat. Species–area relationships (SAR) based on island biogeography theory have been used to predict the magnitude of species losses from habitat destruction (Pimm & Askins, 1995; Brooks & Balmford, 1996; Pimm & Raven, 2000; DeFries *et al.*, 2005; Sala *et al.*, 2005). However, “habitat” is a slippery concept that is species- and context-specific. For operational purposes, land cover that has not been extensively altered by human activity is often taken as a first approximation of available habitat to large groups of species.

In classic island biogeography, richness should increase with area because of the parallel influences of patch area (larger patches support more individuals) and habitat heterogeneity (Rosenzweig, 1995; Ricklefs & Lovette, 1999). Studies deriving empirical SARs typically have done so from sets of islands or island-like patches that vary in size (Stiles & Schreiner, 2007; Guilhaumon *et al.*, 2008; Williams *et al.*, 2009; Honkanen *et al.*, 2010). In contrast, in the typical conservation situation, area remains unchanged. Natural land cover is converted to human-dominated forms rather than lost, and some human-dominated land covers provide habitat for other desirable species. In this case, conversion of small amounts of natural area to human-dominated land covers could increase land cover heterogeneity as continuous habitat is fragmented, which could lead to an increase in species richness. Eventually, conversion of more and more natural area to human-dominated forms should lead to fewer habitat types. The amount of remaining natural area and species richness therefore need not be related to each other simply or positively.

A peaked relationship between species richness and natural area could also arise from the sum of two species–area relationships, one for the natural “habitat” and one for human-dominated “habitat”. Species–area relationships are positive, decelerating relationships (e.g., the classic power law with $S = cA^z$, with $0 < z < 1$). Because of the shape of this relationship, if one habitat type is replaced by another (which is necessarily the case when total area is held constant), then the more common habitat should lose species less quickly than the rarer habitat gains species, resulting in a peaked relationship between species richness and natural area.

The first purpose of this study is to test whether richness relates to the amount of natural land cover according to a peaked function, in situations where grain size (total area) is held constant. If so, the critical question is: at what point does habitat conversion to human-dominated forms lead to decreasing richness? The second purpose of this study is to determine how natural cover loss can lead to increased species richness. Does the shape of the species richness–natural area curve reflect habitat diversity, area effects, or both? How many natural land cover species are lost as natural land cover is converted to human dominated cover?

METHODS

Study area and species richness

I assessed avian richness in Ontario, Canada from distributional data for individual bird species taken from the 2005 Ontario Breeding Bird Atlas (OBBA) (Cadman *et al.*, 2007). I tallied the number of breeding bird species present within 100 km^2 OBBA squares based on the Universal Transverse Mercator (UTM) grid system. I included data only from OBBA squares that had at least 10 hours of sampling effort, and I limited the study to the southern portion of Ontario (corresponding to atlas regions 1 to 33) as these were sampled intensively at the grain that I desired to study (Cadman *et al.*, 2007). I excluded squares containing more than 10% lake area (e.g. squares bordering the Great Lakes and Lake Nipissing) and wedge-shaped UTM quadrats to minimize pure area effects (Figure 1.1). The total sample size was 993 OBBA squares.

I held area constant at a spatial grain relevant for conservation and management by examining the richness–natural area relationship at a grain of 100 km^2. Conservation-related decisions are often made at grains on the order of 10–1000 km^2, and reflect planning, zoning, and other landscape or conservation management ordinances (Dale *et al*., 2000). Mean conservation area size in North America is approximately 250 km^2 (ERIN Consulting Ltd, 2000). This is also roughly the scale of local administrative units: median census division area in Canada (which generally represent municipalities) is 650 km^2, median county area in the USA is 1700 km^2 and median county size in the UK and Ireland is 560 km^2 (Hijmans *et al.*, 2009).

Natural land cover

Natural land cover and land cover heterogeneity were determined from the Ontario Provincial-Scale Land Cover data set produced by the Ontario Ministry of Natural Resources (OMNR; 2002) from Landsat Thematic Mapper (TM) scenes captured primarily in the 1990's (re-sampled by OMNR from 30m to 25 m resolution). Land cover is divided into 28 land cover classes including water and unclassified land cover, which were excluded from the analyses. Five classes were considered human-dominated: recent cutovers; mine tailings, quarries and bedrock outcrops; settlement and developed land, cropland, and pasture and abandoned field. Because habitat loss is often quantified as conversion of natural habitat to human-dominated habitat (Sala *et al.*, 2005), I measured the amount of remaining natural area as the proportion of each OBBA square covered by natural land covers including forests (9 classes including older forest clear-cuts and forest fires), wetlands (7 classes), and alvar (dry grassland found over limestone substrate with thin soils). I included the small amounts of coniferous plantation that occur in southern Ontario in natural cover because plantations are likely to 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.

Constructing a species–area relationship between avian richness and the amount of natural area in this manner is similar to constructing a Type IV species–area curve *sensu* Schreiner (2003). Type IV species–area curves are built using species richness data from distinct areas of varying size, usually islands rather than measurements of richness from contiguous or nested sampling units and are therefore not constrained to be nondecreasing (Schreiner, 2003). Similarly, species richness–natural area curve was constructed from distinct (non-nested) areas with varying amounts of natural land cover. It differs, however, in that species richness is not measured within biologically defined patches of natural land cover but rather within a regular grid that includes varying amounts of natural land cover. This was necessary to observe the impact of land conversion on total avian richness.

Habitat heterogeneity

To measure habitat heterogeneity within each 100 km^2 quadrat, I calculated three measures of heterogeneity: land cover variety, land cover diversity and vegetation heterogeneity. I defined land cover variety as the number of different natural and human-dominated land cover classes in a quadrat. I calculated land cover diversity using the Shannon index (Pielou, 1969). The results for land cover variety and land cover diversity were qualitatively similar (Table 1.1), therefore I will only present the results for the simpler measure, land cover variety.

I calculated the measure of vegetation heterogeneity based on the number of distinguishable vegetation clusters in the raw satellite data since generalized land cover classifications may not distinguish differences among habitats that are most relevant to birds. I created a mosaic of raw Landsat TM data for the study region from images captured primarily from 1999 to 2003. I performed a cluster analysis to identify pixels with similar spectral signatures. Statistically distinguishable spectral clusters reflect potentially relevant differences in landscapes, and this step is the first in the process of land cover classification (Lillesand *et al.*, 2004). Reflectance data from the red, near infrared, and short wave infrared bands were used and the number of clusters was capped at 150. These spectral channels have been related to photosynthetic capacity of leaf tissue, leaf structure, and vegetation vigour and moisture content (Kerr & Ostrovsky, 2003; Lillesand *et al.*, 2004). The resulting number of spectral clusters is not necessarily strongly collinear with the number of classified land cover types, since a single land cover class may include few or many statistically distinctive spectral clusters. In this case, land cover variety was very weakly related to vegetation heterogeneity ($r = -0.07$; $p = 0.02$, $n = 993$).

Climate and productivity

Species richness may also be affected by climate and/or productivity, particularly over broad scales (Hawkins *et al.*, 2003; Field *et al.*, 2009). While it seems intuitively true that habitat degradation/destruction exerts a negative effect on species richness (Kerr & Currie, 1995; Foley *et al.*, 2005; Lepczyk *et al.*, 2008), the relationship can be confounded by the tendency of human density and species richness to be positively correlated with temperature and productivity (Gaston & Evans, 2004; Luck, 2007; Lepczyk *et al.*, 2008). I therefore also controlled for climatic gradients.

Macroclimate varies little across the study region; local climatic conditions are primarily affected by slope and aspect. I therefore used incoming solar radiation as a descriptor of microclimate. Mean solar radiation for the summer solstice was estimated for each OBBA square from a digital elevation model (DEM) at 100 m resolution for Ontario (Centre for Topographic Information, 2000) using the Solar Analyst extension for ArcView 3.2 (ESRI, 2000).

Productivity was estimated by calculating the Normalized Difference Vegetation Index (NDVI) for each pixel in the mosaic of raw Landsat TM data. NDVI is a satellite-derived measure of the 'greenness' of land cover (Pettorelli *et al.*, 2005). NDVI correlates closely with absorbed photosynthetically active radiation and has become a common surrogate of net primary productivity (Kerr & Ostrovsky, 2003). NDVI was calculated using the equation:

$$NDVI = (NIR - RED) / (NIR + RED) \quad (1)$$

where RED and NIR are red radiation and near infrared radiation respectively (Pettorelli *et al.*, 2005) and the mean was taken for each OBBA square.

I resampled the land cover map, the NDVI map and the Landsat mosaic to a 100 m resolution to match the DEM data before computing all measures for the OBBA squares. All geographic data were processed using ArcInfo Grid 9.3 (ESRI, 2008) and Geomatica 10.2 (PCI Geomatics, 2009).

Statistical Analysis

The shape of the relationship between avian richness and the proportion of natural land cover was evaluated by comparing the fits of a quadratic function of natural area ($S = a + bA - dA^2$), versus the classic SAR power law ($S = cA^z$) using least squares regression, where S is species richness (in our case, avian richness), A is area (in our case the proportion of natural area) and a, b, c and z are empirical constants. Effort (the number of hours spent censusing a given OBBA square) varied spatially among OBBA squares; therefore $\log_{10}$(effort) and $[\log_{10}(\text{effort})]^2$ were included in all regression models as covariates. The relative importance of the amount of remaining natural land cover, land cover heterogeneity, climate and productivity was assessed as the additional variation explained above effort.

Since avian richness is spatially autocorrelated (Moran's I = 0.33 at the nearest distance class and declines with distance), I fitted conditional autoregressive (CAR) models using the spdep package (Bivand *et al.*, 2007) in R, version 2.7.2 (R Development Core Team, 2008). CAR models, like other autoregressive models, assume that the dependent variable depends not only on the explanatory (environmental) variables but also on its neighbouring values (Lichstein *et al*., 2002). To account for the spatial autocorrelation in the dependent variable, a matrix of spatial weights representing the influence of neighbouring values on avian richness was included in the model of the avian richness as a function of the explanatory variables. The influence of the neighbouring values took the following form: $w_{ij} = d_{ij}^{-\alpha}$, where w_{ij} is the influence of location i on location j and d_{ij} is the distance between them. I allowed α (representing the degree of decay in the influence of neighbouring values with distance) to vary from 1, 1.5 and 2 and retained the results of the model that resulted in the lowest level of spatial autocorrelation in the model residuals. See Szabo *et al.*, (2009) for more details regarding the methods used for fitting the conditional autoregressive models. All other statistical analyses were performed using S-Plus 8.0 (Insightful Corporation, 2007).

RESULTS

The spatial variation in avian richness was a peaked, rather than a monotonically increasing function of the proportion of remaining natural land cover (Figure 1.2a). The equation describing the relationship between avian richness and the proportion of natural land cover is:

$$S = 6.6 + 53.4 * \log_{10}E - 7.7 * (\log_{10}E)^2 + 120.8 * A - 107.8 * A^2 \qquad (2)$$

where S is avian richness, E is effort (observer hours) and A is the proportion of natural land cover for each OBBA square. Controlling for effort, the relationship between avian richness and remaining natural land cover reaches a maximum at 56% natural area ($R^2 = 0.480$, partial $R^2 = 0.219$, $p < 0.0001$, AIC = 7825.1; Table 1.1; Figure 1.2a). To determine if the “hump-shaped” fit was significantly better than the fit of the classic species–area relationship, a second regression was constrained to the expected form, $S = cA^z$, where S is species richness (avian richness in our case), c and z are empirically derived constants and A is area (proportion of natural land cover in this case) using nonlinear regression in R (R Development Core Team, 2008) on untransformed variables so that results could be compared to the quadratic (“hump-shaped”) model. Controlling for effort and using the power relationship yields $S = 47.2 * \log_{10}E - 4.7 * (\log_{10}E)^2 + 34.3*A^{0.17}$ (3). The coefficient estimates were statistically significant, but the model provides a poorer fit to the data (AIC = 8064.3) than the hump-shaped model (AIC = 7825.1) and residuals from this model were heteroscedastic and not normally distributed.

I hypothesized that richness is a peaked function of the amount of natural area because richness increases linearly with habitat heterogeneity, which in turn is a peaked function of natural area. As expected, the relationship between land cover variety (a surrogate for habitat heterogeneity) and natural area was peaked, with a maximum at 43% natural area ($R^2 = 0.359$, $p < 0.0001$; Figure 1.2b). Again as my hypothesis predicts, avian richness was linearly and positively related to land cover variety. Land cover variety explained a similar portion of the variation in richness above effort as did natural area (R^2 = 0. 457, partial r^2 = 0.190, $p < 0.0001$, AIC = 7858.3; Figure 1.2c). The proportion of natural land cover and land cover variety explained similar and overlapping portions of the variation in avian richness because they are strongly correlated. Inclusion of natural land cover amount and land cover variety in a multiple regression increased the variance explained by less than 5%. Both variables remain significant, therefore both probably have at least small independent effects on richness.

The effect of land cover variety is unlikely to be predominantly due to an effect of edge. Total edge (length of forest edge per quadrat), like land cover variety, could be expected to peak at intermediate amount of natural area and cause avian richness to increase. Avian richness did have a positive relationship with the total length of forest edge, but it explained a slightly smaller portion of the variation in avian richness than did land cover variety after controlling for effort (R^2 = 0.422, partial r^2 = 0.161, $p < 0.0001$, AIC = 7928.26), and it increased explained variation very little in a multiple regression.

The variety of natural land cover classes alone was not sufficient to explain the peaked relationship between avian richness and natural area. The number of natural land cover classes increased by only approximately one land cover class with losses of up to 50% of the natural land cover (Figure 1.2d). This is interesting as it suggests that human activity may diversify natural habitats to a degree. The additional land cover class would be sufficient to account for about four additional species (Table 1.1, Figure 1.2c), relative to 100% natural cover. The addition of one human-dominated land class (Figure 1.2b minus Figure 1.2d) accounts for four more species. However, richness increased by approximately 25 species over this range (Figure 1.2a). The remaining 17 species, I hypothesize, reflect effects of increased richness due to increased area in the rarer land cover classes.

I used structural equations modelling (SEM) to test to what extent the effect of natural land cover on avian richness is through its relationship with habitat heterogeneity (as measured by land cover variety), as opposed to an independent effect of natural area, as depicted in Figure 1.3a. I used maximum likelihood methods to generate standardized estimates of the direct, indirect and total effects of natural area and land cover variety on avian richness. Standardized estimates were used so the magnitude of the effects of natural area and land cover variety along the proposed pathways could be directly compared. The SEM was conducted using Amos 17.0 for SPSS (Arbuckle, 2007). If the effect of natural area is through land cover variety then I would expect a large indirect effect of natural area, a similarly large direct effect of land cover variety and a negligible direct effect of natural area on avian richness (Figure 1.3b). The direct effects of the amount of remaining natural land cover and land cover variety on avian richness were approximately equal (standardized estimate = 0.310 for natural land cover amount; 0.311 for land cover variety). One third of the total effect of the amount of natural land cover was indirect through land cover variety (standardized estimate = 0.155). The total effect of the amount of natural land cover (standardized estimate = 0.469) was considerably larger than that of land cover variety (standardized estimate = 0.311). Therefore, only part of the effect of the amount of natural area was through land cover variety. The amount of natural area per se appears to have had an additional effect on avian richness that is not wholly explained by its relationship with land cover variety.

I examined the response of groups of birds, specifically forest and open habitat birds, to natural area by regressing forest bird richness and open habitat bird richness against the proportion of the natural area while controlling for effort in the manner described above. Avian species groups were defined based on the habitat associations reported in the Birder's Handbook (Ehrlich *et al.*, 1988). Species that were described as only inhabiting forest (regardless of the type of forest or the affinity for interior or edge) were grouped as forest obligate species. Species that were described as possibly inhabiting open or urban habitat (including those that could potentially inhabit forested habitat) were grouped as open habitat species, while those that could only inhabit open or urban habitat were grouped as open obligate species. Losses of as much as 40% of the natural area led, on average, to a loss of approximately two forest obligate species (ascertained by examining Figure 1.4a from right to left; $R^2 = 0.478$, $p < 0.0001$) but an increase of approximately twenty species that can inhabit open or urban land covers (Figure 1.4b; $R^2 = 0.687$, $p < 0.0001$), approximately ten of which can only inhabit open or urban habitat (Figure 1.4c; $R^2 = 0.680$, $p < 0.0001$). I cannot rule out the possibility that bird communities may currently include more species than these landscapes will support over the long term, and that species losses following conversion of natural land covers may be delayed.

I found that species richness was not closely associated with climate and productivity, and these factors did not appear to confound the relationship between avian richness, natural area and land cover variety. Avian richness was only weakly related to mean solar radiation and mean NDVI, and not significantly related to vegetation heterogeneity (Table 1.1). Accounting for microclimate or productivity did not alter the relationship detected between richness and natural land cover amount. At broad-scales, climate (measured as temperature and/or precipitation) and productivity are often strong predictors of species richness (Hawkins *et al.*, 2003; Field *et al.*, 2009). Here I found a weak species–energy relationship, which is more common at finer scales where habitat descriptors tend to drive species richness (Kerr *et al.*, 2001). In particular, recent findings by Coops and colleagues have suggested that avian richness in Ontario depends strongly on the differences in land cover (Coops *et al.*, 2009).

Many have cautioned that failure to account for spatial autocorrelation can lead to incorrect model selection and consequently erroneous conclusions regarding the hypotheses being tested (Diniz-Filho *et al.*, 2003; Kühn, 2007). In our study, conclusions as to the shape and relative importance of the relationships using conditional autoregressive models were similar to those from the ordinary least squares regression. Most importantly, taking spatial autocorrelation into account had little effect on the sign or magnitude of the coefficients (Table 1.1). In particular, the shape of the relationship between avian richness and the amount of natural land cover remains peaked with a maximum at 55% natural area.

DISCUSSION

I found that as much as 44% of the natural land cover can be converted to human-dominated forms before avian richness begins to decline. In areas with high amounts of natural land cover, loss of natural land cover increased avian richness. More specifically, loss of up to 40% of the natural land cover led, on average, to a gain of approximately 20 open habitat bird species with a loss of approximately 2 forest species.

I had predicted that the conversion of natural land cover to human-dominated forms would lead to a peaked relationship between avian richness and natural area because conversion of small amounts of natural area to human-dominated land uses would increase land cover variety, a proxy for habitat heterogeneity, and thereby increase richness. Land cover variety did increase with losses of as much as half the natural area and explained an important portion of the variance in avian richness. However, SEM indicated that only a portion of the effect of natural area was through land cover variety and that area *per se* had a large, independent effect of its own.

Natural area's distinct effect may be explained by the same theory that would lead conservation biologists to expect a monotonic increase in species richness with increasing natural area, the species–area relationship. Natural land covers in Ontario generally consist of forests and wetlands because few natural open habitats remain (see Kerr & Cihlar, 2003 for a Canadian example). Thus, species that prefer open habitats are generally relegated to human-dominated land covers such as pastures, settled areas and, occasionally, crop-growing areas. Natural land cover is, to a first approximation, equivalent to forested areas because the extent of forests is vastly greater than that of wetlands in southern Ontario (Kerr & Cihlar, 2003). If we consider only the number of forest obligate species as a function of the remaining natural land cover, the relationship more closely resembles the monotonically increasing pattern that is expected (Figure 1.4a). Because human-dominated area is necessarily created at the expense of natural area, the proportion of human-dominated land cover, a proxy for open habitat, is one minus the proportion of natural land cover. Therefore, the decelerating species–area curves for these two broad “habitat” types cross, generating a peaked relationship between species richness and natural area (Figure 1.4a and c).

This process can be demonstrated mathematically. Suppose that there are habitat types 1 (natural) and 2 (human-dominated), with area A_1 and A_2, respectively. Species richness S is given by

$$S = c_1 A_1^{y} + c_2 A_2^{z} \qquad (4).$$

Suppose also that the habitat types can be inter-converted, and that total area equals 1. Then the change in species richness as a result of conversion of habitat 1 to habitat 2 is

$$dS/dA_1 = c_1 y A_1^{(y-1)} - c_2 z(1-A_1)^{(z-1)} \qquad (5).$$

To find the natural area $\hat{A}_1$ at which species richness is maximal, I set the derivative equal to 0 and rearrange, yielding:

$$(c_1 / c_2)\ (y/z) = (1- \hat{A}_1)^{(z-1)} / \hat{A}_1^{(y-1)} \qquad (6).$$

If I assume that the richness values of the two groups scale with area in approximately the same way (i.e., z ≈ y) because both groups are from the same taxon and the curves are generated from the same sampling scheme (MacArthur & Wilson, 1967; Rosenzweig, 1995). This gives

$$\hat{A}_1 = 1 / [1 + (c_1 / c_2)^{1/(z-1)}] \qquad (7).$$

If the size of the potential species pool (related to c) for one habitat type is greater than the other, then the peak richness will shift toward a greater amount of that habitat type. In our case, the maximum richness for both forest obligates and open habitat obligates is approximately 15. Thus, if $c_1 = c_2$, $\hat{A}_1$ peaks at 0.5, that is, 50% of each habitat type, which is very close to our empirical peak at 56% natural area (for a graphical representation, see Figure 1.5). Although this simple two-habitat model captures the general species richness–area pattern that was observed, it is possible that finer characterization of the area dependence of birds dwelling in various habitats might improve predictive ability.

I have assumed that species richness for each habitat type is at equilibrium with the area of a given habitat, implying that there is no lingering extinction debt from the loss of the natural habitat or colonization debt from creation of the human-dominated habitat. This assumption likely holds in our study area since conversion of natural area to human-dominated land covers occurred predominantly in the 19th century (Ellis *et al*., 2010), though some studies have found that centuries can be required to pay extinction debt (Kuussaari *et al.*, 2009). If loss of natural area created an extinction debt for forest bird richness that remains today, then we would expect forest bird richness to be stable in areas with large amounts of natural area and declining where there is little natural area. Change in forest bird richness over the past 20 years (using data from the first Ontario Breeding Bird Atlas; Cadman *et al.*, 1987) varies only weakly and negatively with the amount of remaining natural area (slope = -4.7, $r^2 = 0.045$, $p < 0.0001$). On the other hand, change in open habitat bird richness varies somewhat more strongly with the amount of natural area (slope = -2.9, $r^2 = 0.114$, $p < 0.0001$) suggesting that there may be some remaining colonization debt.

It is important to note that three forest bird species, Bay-breasted Warbler, Ruby-crowned Kinglet and Spruce Grouse rarely occurred in OBBA squares with less than 80% natural area (Figure 1.6). (Individual species are referred to by common name only. The common and scientific names for all species can be found in Appendix A.) Conversion of relatively small amounts of natural land cover, and particularly coniferous land cover, to human-dominated forms could greatly reduce the probability of encountering these three species. Even though conversion of as much as 40% of the natural land cover led to increased avian richness, conservation decisions should consider the potential impact of the loss of smaller amounts of natural area on the conservation of habitat specialists separately.

When using the SAR for predicting extinctions from habitat loss, one must consider that the relationship between species richness and natural area may be peaked rather than monotonically increasing because non-natural land covers provide habitat for many species (Pereira & Daily, 2006). Some of these are likely to be rare or endangered. For example, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2010) has listed seven open habitat species as endangered or threatened: Northern Bobwhite, Barn Owl, Loggerhead Shrike, Henslow's Sparrow, Common Nighthawk, Chimney Swift and Golden-winged Warbler, while only two open habitat species are introduced, Gray Partridge and Ring-necked Pheasant, both of which are declining through most of the study area (Cadman *et al*., 2007). The trend in Europe, where land use histories are dissimilar, is for farmland birds to decline with agricultural intensification while woodland bird populations remain stable (Gregory *et al*., 2005). In cases such as these, it would be valuable to sub-divide human-dominated habitat into intensity levels of agriculture. The peaked shape of the relationship between species richness and remaining natural area may have important implications for bird conservation, but, if birds are representative of other taxa, also more broadly for applications of SAR to biodiversity conservation and predictions of species losses from habitat destruction.

I suggest that these results provide a more general perspective on the relationship between expanding human domination of previously natural landscapes and species persistence. The most pronounced species-level response to initial land cover conversion comes in the form of colonization by open habitat species, but this is not accompanied by losses of species specializing on forest habitats (one exception being spruce grouse, Cadman *et al.*, 2007). Smaller losses of natural area can be regarded as beneficial by increasing available habitat for open habitat species and by increasing the habitat heterogeneity of even natural areas, but only if natural area loss remains below 50% in a given area. Progressive conversion of natural land covers can lead to increasing species richness overall, until that threshold is reached, at which point species losses are pronounced and occur rapidly. It is essential to note that the threshold at which extinctions are likely to accelerate was not predicted theoretically in this study and may vary among taxa. It would be very valuable to develop theoretical predictions for such "extinction cascade thresholds".

ACKNOWLEDGEMENTS

I am grateful to Karl Evans and three anonymous reviewers for very helpful comments (Desrochers *et al*., 2011). Thanks to the official sponsors of the Ontario Breeding Bird Atlas (Bird Studies Canada, Canadian Wildlife Service, Federation of Ontario Naturalists, Ontario Field Ornithologists, and Ontario Ministry of Natural Resources) for supplying Atlas data, and to the thousands of volunteer participants who gathered data for the Ontario Breeding Bird Atlases. In particular I would like to thank Mike Cadman, Denis Lepage and Peter Blancher for providing the Ontario Breeding Bird

Atlas data as well as considerable advice regarding analysis of the data. I am grateful to Rob Fraser and Ian Olthof at the Canada Center for Remote Sensing for assistance in the creation of the Ontario Landsat mosaic. Finally I would like to thank Adam Algar for assistance with the statistical analysis as well as helpful comments.

TABLES

Table 1.1: The shape and strength of the relationships between avian richness and predictors of richness for 993 Breeding Bird Atlas squares in the southern portion of Ontario, Canada. The relative importance (partial R^2) of the amount of natural area, habitat heterogeneity, microclimate and productivity was assessed as the additional variation explained above effort. The partial slopes, coefficients of determination (R^2) and relative importance (partial R^2) for conditional autoregressive models are presented in parentheses.

	Variable	**Partial slope**	**R^2**	**Partial R^2**	**p-value***
Effort Alone	Log_{10} Effort	†	0.26 (0.17)		<0.0001
Natural Area	Proportion of natural area	‡	0.48 (0.27)	0.22 (0.09)	<0.0001
Habitat Heterogeneity	Land cover variety	4.23 (3.42)	0.45 (0.25)	0.19 (0.08)	<0.0001
	Land cover diversity	10.13 (11.57)	0.46 (0.26)	0.20 (0.08)	<0.0001
	Vegetation heterogeneity	0.09 (0.46)	0.26 (0.20)	0.00 (0.03)	0.0602
Microclimate	Mean solar radiation	-0.06 (-0.06)	0.30 (0.19)	0.03 (0.02)	<0.0001
Productivity	Mean NDVI	43.12 (41.69)	0.27 (0.18)	0.01 (0.01)	0.0001

*All models have p-values <0.0001, the reported p-values are for each variable.
†Avian richness is a concave quadratic function of $\log_{10}$Effort described by $64.32x – 10.71x^2$
‡Avian richness is a concave quadratic function of the proportion of natural area described by $103.94x - 94.87x^2$

FIGURES

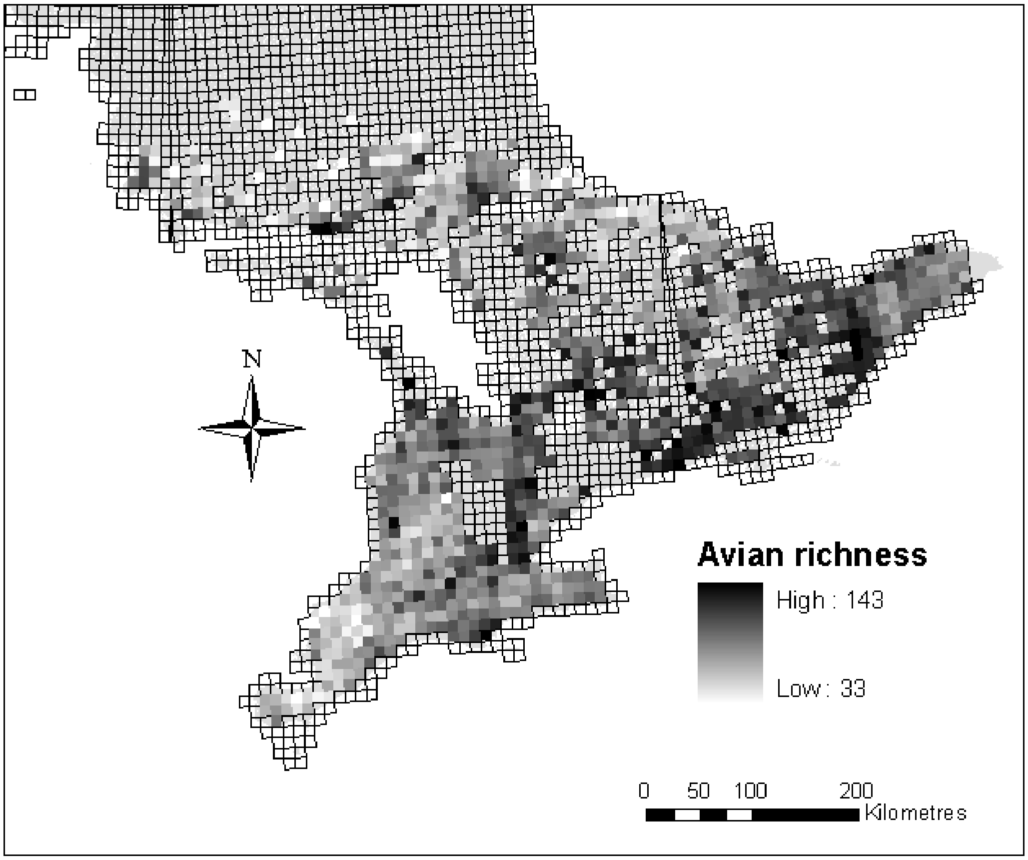


Figure 1.1: Avian richness in the southern portion of Ontario. Breeding Bird Atlas squares are outlined in dark grey. Richness appears only for squares with at least 10 hours of effort and less than 10% area covered by water. Excluded squares are shown in light gray. The projection is Lambert Conformal Conic.

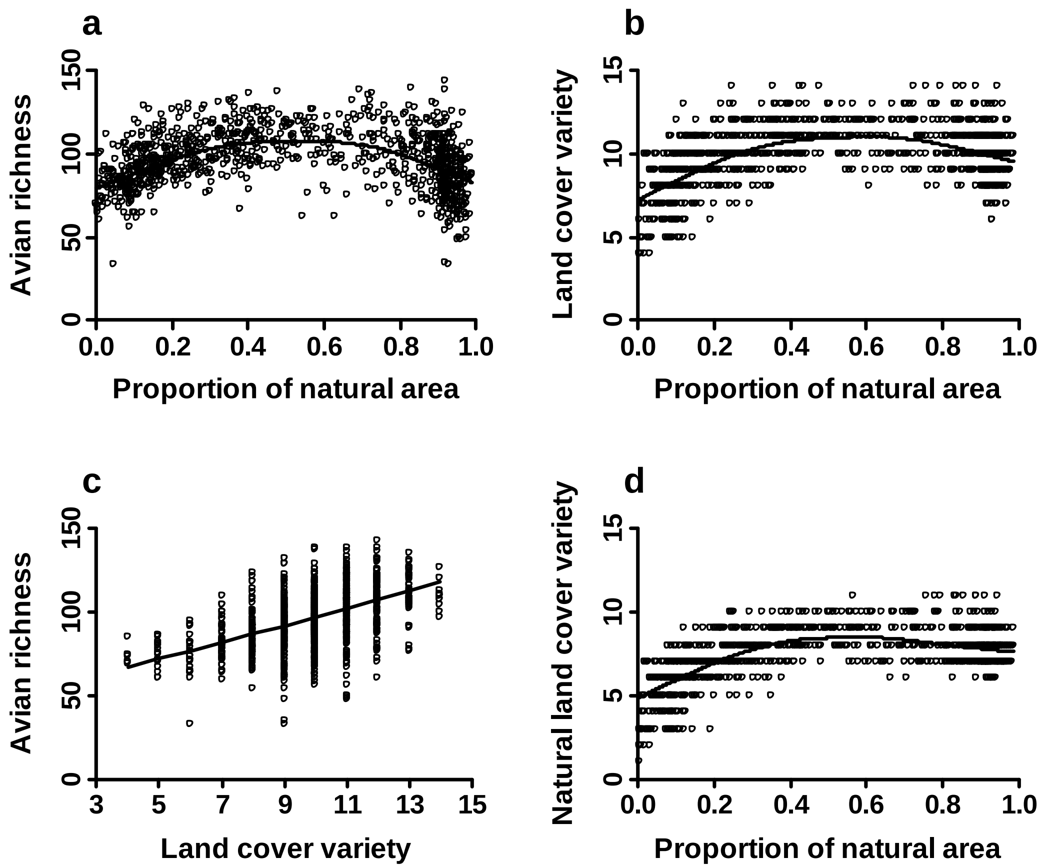
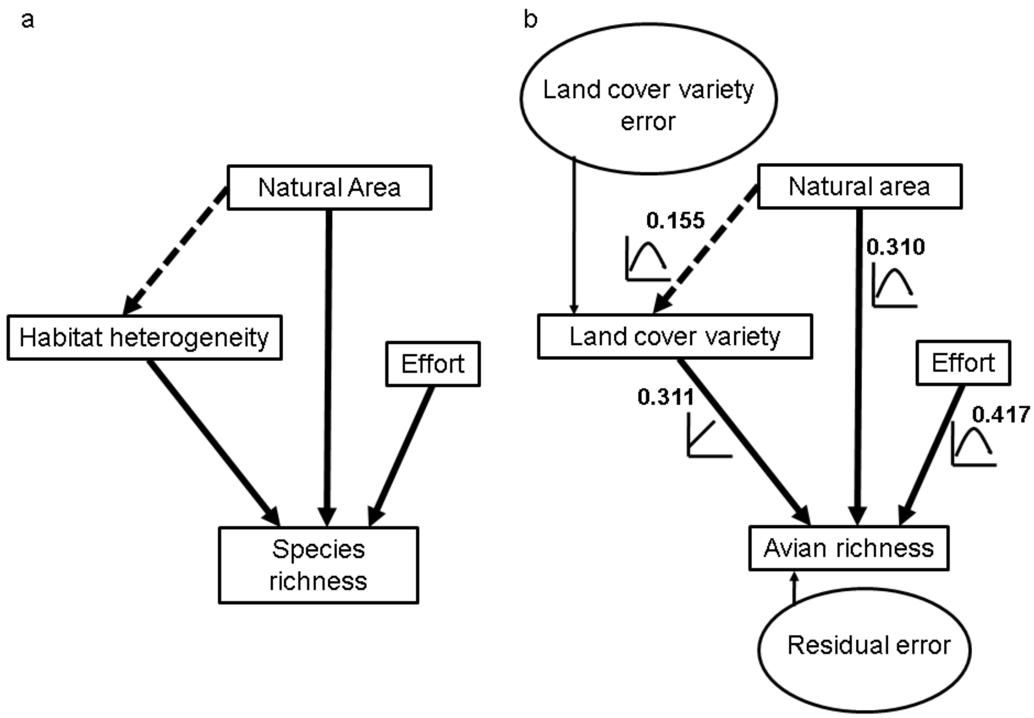


Figure 1.2: Avian richness as a function of a) the amount of natural area (measured as the proportion of natural land cover) fitted with a Loess smoothing line and c) habitat heterogeneity (measured as land cover variety) fitted with a linear least squares smoothing line. b) Land cover variety and d) the variety of natural land cover types as a function of the amount of natural area fitted with a Loess smoothing line for 993 Breeding Bird Atlas squares in the southern portion of Ontario.

Figure 1.3: a) The pathways tested using Structural Equations Modelling for the relationship between species richness and natural area. Direct effects are shown by solid arrows; indirect effects are shown by dashed arrows. I have also included atlassing effort (in hours) as it is known to affect the estimates of avian richness. b) The variation in avian richness explained by the Structural Equation Modelling is 49%. The measure of habitat heterogeneity shown is land cover variety. Since the best fit between avian richness and natural area is a quadratic function, I used the fit from the OLS regression including the amount of natural land cover and its squared term as a measure of the total effect of the amount of remaining natural land cover. Similarly, I used the fit from the OLS regression including log10-transformed effort and its squared term as a measure of the total effect of effort. The numbers represent the maximum likelihood standardized estimates of the direct and indirect effects of the amount of natural land cover, land cover heterogeneity and effort on avian richness. All effects are significant at $p<0.05$.



a
Natural Area
Habitat heterogeneity
Effort
Species richness
b
Land cover variety error
Natural area
0.155
0.310
Land cover variety
Effort
0.311
0.417
Avian richness
Residual error

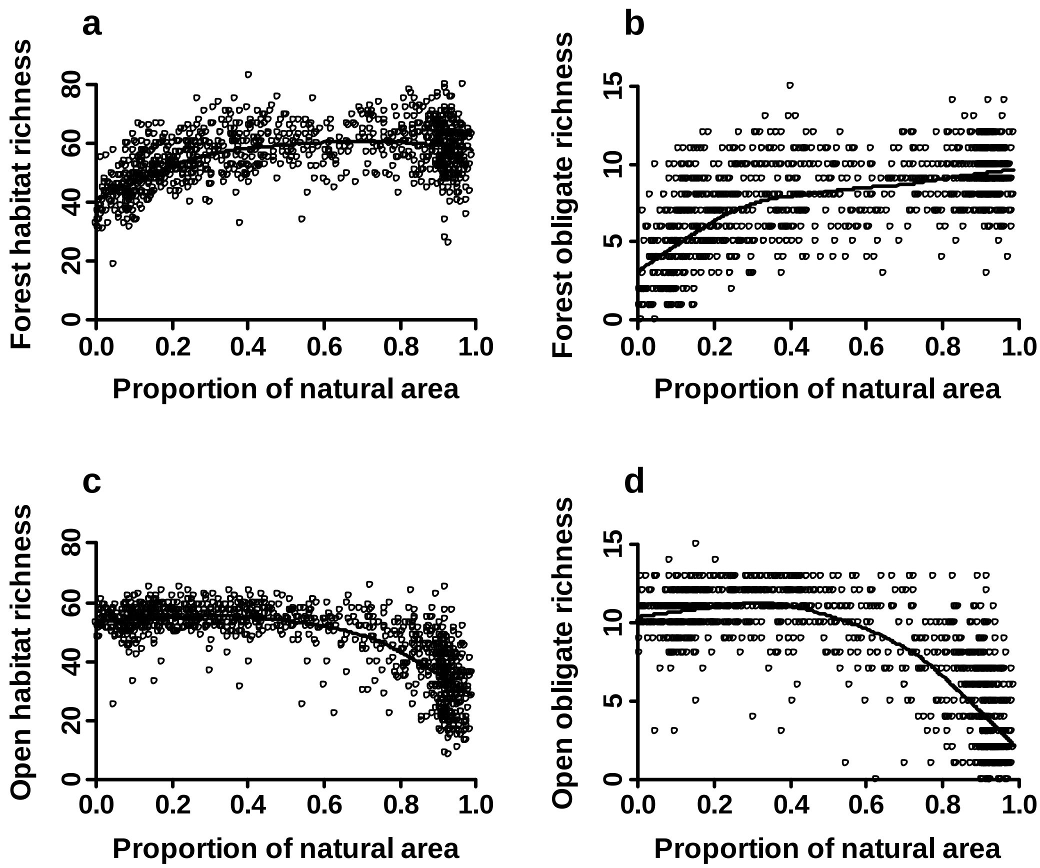


Figure 1.4: a) Richness of all bird species that can inhabit forested areas, b) richness of bird species that can only inhabit forested areas (forest obligate bird richness), c) richness of all bird species that can inhabit open and urban areas and d) richness of bird species that can only inhabit open or urban habitats (open obligate bird richness) as a function of natural land cover amount for 993 Breeding Bird Atlas squares in the southern portion of Ontario. Each is fitted with a Loess smoothing line.

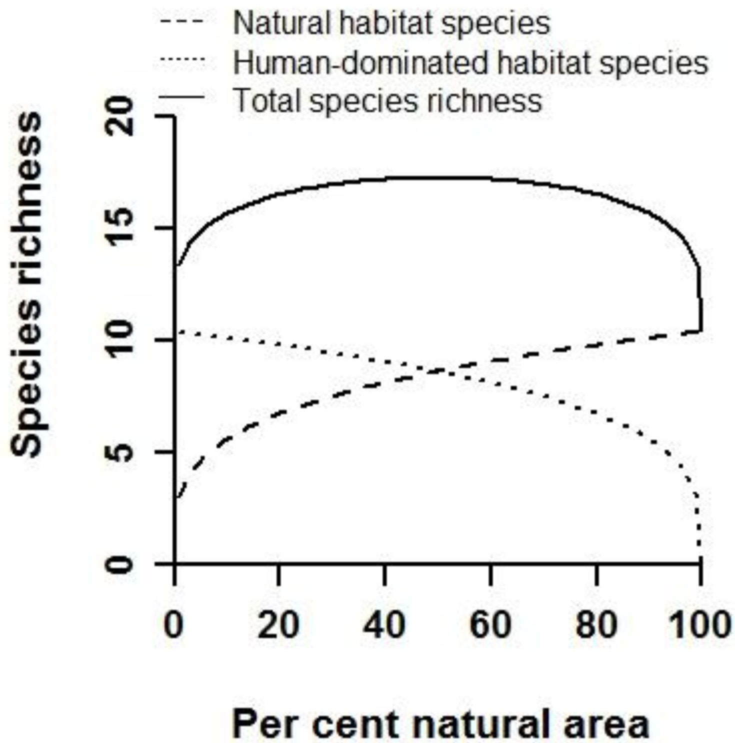
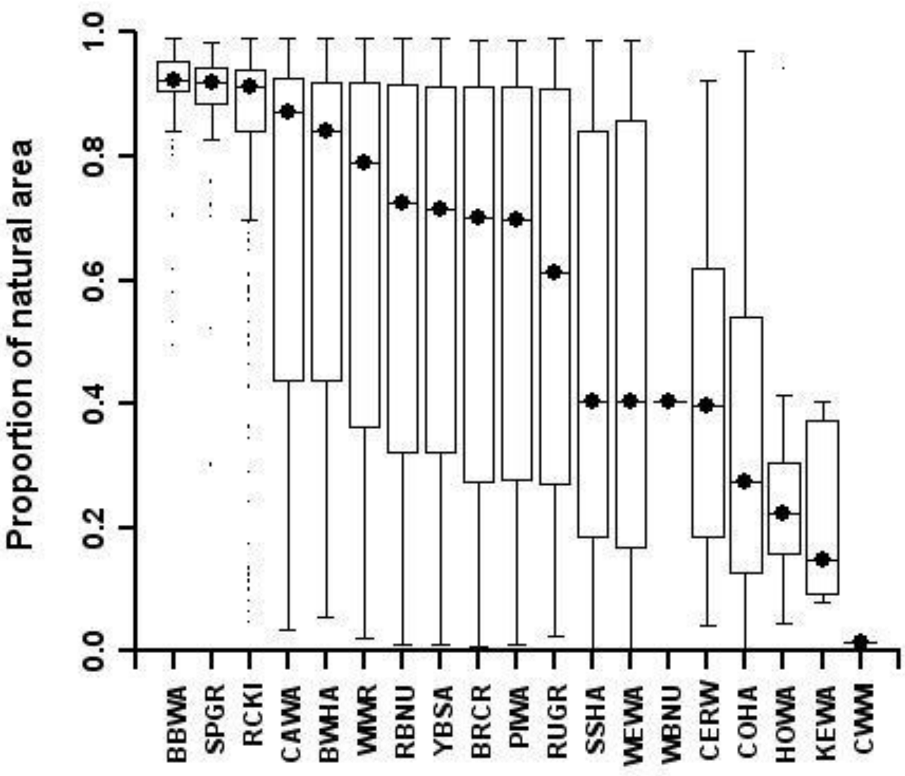


Figure 1.5: Theoretical species–area curves for two broad habitat types, natural habitat and human-dominated habitat (1-natural habitat), and the relationship between total richness and natural area. The species–area curves were generated using S = cAz. I assumed that c for the natural habitat (which is related to the size of the species pool for that habitat) was equal to c for the human-dominated habitat and set it to 3 (the mean of the intercepts for the curves, see Figure 1.4). I used the same scaling coefficient z for both habitat types and set it to 0.27. This is the value used by Preston (1962) and is in the mid-range of empirically derived z values (MacArthur & Wilson, 1967). See the text for complete mathematical details.

Figure 1.6: Distribution of values for the proportion of natural area per species in Ontario Breeding Bird Atlas squares where the nineteen forest obligate bird species were found. The large circles represent the median values while the top and bottom limits of the boxes represent the 1st and 3rd quartiles respectively. The whiskers extend to the nearest value that is not beyond a standard span, which is 1.5 times the inter-quartile range, from the quartiles. Outliers beyond this value are represented by small circles. Species are ranked by median in descending order. The definition of the four letter species code is as follows: BBWA is Bay-breasted Warbler, BRCR is Brown Creeper, BWHA is Broad-Winged Hawk, CAWA is Canada Warbler, CERW is Cerulean Warbler, COHA is Cooper's Hawk, CWWI is Chuck-will's-widow, HOWA is Hooded Warbler, KEWA is Kentucky Warbler, PIWA is Pine Warbler, RBNU is Ruby-breasted Nuthatch, RCKI is Ruby-crowned Kinglet, RUGR is Ruffed Grouse, SPGR is Spruce Grouse, SSHA is Sharp-shinned Hawk, WBNU is White-breasted Nuthatch, WEWA is Worm-eating Warbler, WIWR is Winter Wren, and YBSA is Yellow-bellied Sapsucker.


Proportion of natural area
1.0
0.8
0.6
0.4
0.2
0.0
BBWA
SPGR
RCKI
CAWA
BWHA
WWR
RBNU
YBSA
BRCR
PIWA
RUGR
SSHA
WEWA
WBNU
CERW
COHA
HOWA
KEWA
CWWI

CHAPTER 2: THE ROLE OF METAPOPULATION DYNAMICS IN DETERMINING REGIONAL SPECIES RICHNESS PATTERNS

ABSTRACT

Aim: To test six predictions derived from the hypothesis that metapopulation-like processes of local colonization and extinction, occurring on a regional scales, lead to unoccupied sites within individual species ranges and that this in turn leads to a weakened relationship between species richness and its environmental drivers.

Location: Ontario, Canada.

Methods: I tested the predictions, which relate the probability of local presence to habitat amount (analogous to patch size) and the proportion of neighbouring sites previously occupied by conspecifics (analogous to patch isolation), for a set of avian assemblages derived from the 1985 and 2005 Ontario Breeding Bird Atlases (OBBA). I used generalized linear models to determine the direction of their main effects and interactions, and deviances explained for each species. I then pooled the results for all species to establish if the central tendencies of the coefficients and deviances explained varied in the predicted directions. Lastly, I evaluated if accounting for metapopulation-like processes strengthens the relationship between regional species richness and environment.

Results: The results were consistent with all six derived predictions. Species were less likely to be locally present in 2005 if few of the neighbouring sites had been occupied in 1985. Species were less likely to be locally present if there was less available habitat. Additionally, the area of habitat was more important if the surrounding sites were not

previous occupied by conspecifics, which is consistent with the idea that, like larger patches, larger habitat areas represent larger targets for immigrants. Accounting for the probability of local occurrence due to the metapopulation-like processes strengthened the regional species richness–environment relationship. Environment explained only 36% of the variation in species richness using a snapshot of species richness from 2005 but explained 62% of variation after accounting for the impact of metapopulation-like processes on local species presence.

Main conclusions: This analysis suggests that processes typically associated with metapopulation dynamics that affect local distributions of individual species "scale up" to modify regional species richness patterns. Accounting for the effect of metapopulation dynamics on species' presence strengthened the regional richness–environment relationship to match that of continental richness–environment relationships. This suggests that regional richness patterns are more difficult to predict than continental ones because metapopulation processes have a substantial effect on local presence beyond the effect that environmental controls have on determining species' distributions. It is the reflection of the resulting local absences in the data used for regional studies that weakens observed richness–environment relationships.

INTRODUCTION

Describing and predicting the distributions of species and species richness in time and space is a central goal of ecology (Begon *et al*., 1996). Continental patterns of species richness are generally quite predictable from environmental characteristics. At this scale, measures of climate are consistently the best predictors of terrestrial species richness, explaining most of the geographic variation in richness (e.g., Currie, 1991; Francis & Currie, 2003; Hawkins *et al*., 2003; Field *et al.*, 2009).

Biodiversity management questions often focus at regional scales, where modelling patterns of richness is generally less successful. Regional scales, defined as those extending less than 1000 km (Field *et al*., 2009), encompass studies focusing at the level of states, provinces, or small individual countries. At regional scales, individual species' distributions are often more accurately described than those at continental scales. Yet, in contrast to broad-scale variation in richness, no hypothesis emerges as consistently the best explanation of regional patterns of species richness (Field *et al*, 2009). The variation in richness at regional scales explained by environmental characteristics is often less than 40% (Mayer & Cameron, 2003; Koh *et al*., 2006; González-Taboada *et al.*, 2007; Hortal *et al.*, 2008; Lepczyk *et al.*, 2008; Belmaker & Jetz, 2010; Desrochers *et al.*, 2011). This phenomenon does not appear to be due to reduced variation in the independent variables at regional scales (as would be expected for many measures of climate) because many of the examined environmental predictors are measures such as land cover heterogeneity, natural or forested area and population density that vary considerably at regional scales.

Why is species richness so much more difficult to predict at regional scales? Continental scale studies tend to measure species richness by superimposing individual species' ranges, whether all species are present at a particular location or not. Regional scale studies, on the other hand, use observations of species presences and absences (Mayer & Cameron, 2003; Virkkala *et al.*, 2005; Koh *et al*., 2006; González-Taboada *et al.*, 2007; Rompré *et al.*, 2007; Lepczyk *et al.*, 2008; Honkanen *et al.*, 2009; Desrochers *et al.*, 2011). These data sources are more likely to reflect the true patchiness (holes) within species distributions than range maps and therefore yield more accurate patterns of species richness (Hurlbert & Jetz, 2007). If absences within species' ranges reflect unsuitable environmental conditions, then it should be possible to accurately model individual species' presence/absence, and patterns of richness, as functions of the environment. However, if regional absences within species' ranges were due to something other than unsuitable environmental conditions (see below), then richness-environment relationships might be quite poor. This can be demonstrated with a simple simulation of species ranges randomly placed along a one-dimensional environmental gradient (for simulation details, please see Appendix B). The strength of the species richness–environment relationship systematically weakens (as evaluated by the mean coefficient of determination) as increasing numbers of random absences are allowed to occur within the species' ranges (Figure 2.1).

Many factors may contribute to the patchiness of individual species' distributions. A species' presence in a given location is at least partly limited by the same environmental characteristics that predict broad-scale distributions: temperature, precipitation and land cover (Brown *et al.*, 1996). There may be micro-scale variations in these factors. However, in addition, metapopulation theory suggests that there should be temporal variability in site occupancy (here one year, gone the next) due to demographic and environmental stochasticity. Consequently many suitable sites within a species' range may be unoccupied in any given census (Hanski, 1999). This temporal variability could in turn increase spatial variability in species richness. For example, successive Ontario breeding bird surveys conducted in 1980-1985 and 2000-2005 show that species richness can change quickly (Pearson r for species richness recorded in the surveys = 0.56) even in the absence of extensive environmental changes in surveyed areas (Ellis *et al.,* 2010). Gradients of species richness can be highly dynamic even when the factors that often influence them remain nearly constant.

One reason that species richness could be locally dynamic despite little environmental change is that metapopulation-like processes of local extinction and colonization cause richness to fluctuate. I hypothesize that weak regional relationships between variation in species richness and environmental characteristics are due, in considerable part, to metapopulation-like processes of local extinction and colonization that occur among landscapes (here, 100 km^2) within a region (here, roughly 150,000 km^2). These processes increase spatial and temporal patchiness in species' distributions. Sites that contain more habitat can support a higher number of individuals (Preston,

1962) and therefore local extinctions due to demographic or environmental stochasticity are less likely. After a local extinction, a site can be recolonized by immigrants from neighbouring sites. Unoccupied sites with a greater area of habitat present larger targets for immigrants and are therefore more likely to be recolonized. Similarly, local populations are more likely to persist at sites that are surrounded by sites occupied by conspecifics due to rescue effects from these surrounding populations. Here, habitat area is analogous to patch size in classic metapopulation theory (Hanski, 1999), and the occupancy of neighbouring sites by conspecifics is analogous to patch isolation.

Approach

I tested six predictions of the above hypothesis for a set of avian assemblages. For a given species, the probability of being present at a site should be positively related to previous presence at that site, species-specific habitat amount, and neighbourhood occupancy (the proportion of neighbouring sites occupied by conspecifics in the previous time period). Moreover, the latter two variables (neighbours and habitat) should account for additional explained variance after controlling for previous site occupation, because there would have been suitable but unoccupied sites at any previous census. The interaction between habitat amount and neighbourhood occupancy should be negative: the effect of habitat area is greater when there are fewer occupied neighbouring sites. (See Table 2.1A for a detailed description of the predictions.)

Testing these predictions required data on species presences and absences through both space and time at the relevant scale. Avian atlases are among the most complete information on regional species distributions. I compared the presence/absence of 151 bird species in 100 km^2 atlas squares across southern Ontario using the 1985 and 2005 Ontario Breeding Bird Atlases (OBBA). I sought to ascertain the effect of habitat amount and neighbourhood occupancy by conspecifics on the probability of local presence of each individual species. To do so, I first fitted statistical models to determine the direction of their effects and the deviances they explained for each species. I then summarized the effect sizes and directions for all species, and I compared these distributions to the predictions in Table 2.1. Lastly, I evaluated whether accounting for metapopulation-like processes strengthened the relationship between regional species richness and environment.

It is also possible that spatial and temporal variability in species' presence/absence is due to sampling effects. Typical atlas sampling methodology can result in variable distributions of sampling effort among quadrats as well as, in the case of the OBBA, between the same squares in subsequent atlases (Cadman *et al.*, 2007). The level of sampling effort invested in censusing a square will influence the probability of detecting species. The likelihood of detecting a new species in a square should increase if the time spent sampling is greater in a later atlas. Similarly the likelihood of failing to detect a previously present species should increase if the time spent sampling is lower in the later atlas. To account for this, I also tested predictions of the hypothesis that sampling intensity drives the probability of local species' presence and temporal turnover in species' presence (Table 2.1B).

METHODS

Data

Study area and species distributions

Two Ontario Breeding Bird Atlases (OBBA) (Cadman *et al.*, 1987 & 2007) contain observations of presence/absence of the bird species that breed in Ontario, Canada, censused using consistent methodology from 1981 to 1985 and again from 2001 to 2005. The data were collected within 100 km^2 OBBA squares based on the Universal Transverse Mercator (UTM) grid system. I included data only from OBBA squares that had at least 20 hours of sampling effort in both atlases (all in southern Ontario, corresponding to atlas regions 1 to 33). I excluded squares containing more than 10% lake area (e.g. squares bordering the Great Lakes and Lake Nipissing) and wedge-shaped UTM quadrats to minimize pure area effects. This left 622 OBBA squares (Figure 2.2). The geographical data were processed in ArcInfo Grid 9.3 (ESRI, 2008).

Habitat area

I determined which land covers in the Ontario Provincial-Scale Land Cover data set were potentially suitable for each species based on its habitat description in The Birder's Handbook (Ehrlich *et al*., 1988;see Appendix C for a table of suitable land covers for each species.). I used a land cover map produced by the Ontario Ministry of Natural Resources (OMNR, 2002) from Landsat Thematic Mapper (TM) scenes captured primarily in the 1990's (re-sampled by OMNR from 30 m to 25 m resolution). Land cover was divided into 28 land cover classes including five human-dominated classes (recent cutovers; mine tailings, quarries and bedrock outcrops; settlement and developed land, cropland, and pasture and abandoned field), nine forest classes (including older forest clear-cuts and forest fires), seven wetland classes, and alvar (dry grassland found over limestone substrate with thin soils). Water and unclassified land cover were excluded from the analyses and four land cover classes did not occur in the study area. I assessed species-specific habitat area as the total area of potentially suitable land covers (in square kilometres) for a given species in each square. This measure of habitat area, because it was taken as the total area of potentially suitable land covers, represents a liberal measure of habitat area.

Neighbourhood occupancy

To assess neighbourhood occupancy, I tallied the number of neighbouring squares that were occupied in the 1985 OBBA within a neighbourhood extending two squares (20 km) in each direction. Since not all squares met my inclusion criteria (e.g., due to undersampling or water), I expressed neighbouring occupancy as the proportion of occupied neighbouring squares among those censused.

Sampling effort

The intensity of sampling may impact species detection and thereby the observed level of patchiness in a species' distribution therefore I also tested the hypothesis that sampling intensity drives the probability of local species' detection (Table 2.1B). Bird atlas studies are regarded as an effective method to map species' distributions (Bibby, 2004). In avian atlases, individual grid cells are searched for evidence of all bird species breeding within them (Cadman *et al.*, 1987; Väisänen *et al.*, 1998; Martí & del Moral, 2003; Bibby, 2004; Cadman *et al.*, 2007; Lemoine *et al.*, 2007). This increases the likelihood of detecting rare or cryptic species relative to line transects or point counts (Gregory *et al.,* 2004). The standards for breeding evidence are precisely defined and generally consistent among atlases (Bibby, 2004); however the number of hours of sampling effort and the sampling strategy are often not predefined, particularly in earlier atlases (Cadman *et al.*, 1987; Väisänen *et al.*, 1998; Martí & del Moral, 2003).

Sampling effort ($\log_{10}$ transformed) was taken as the total number of observer-hours in each OBBA square for the 2005 atlas. Change in effort was taken as the direction and the absolute value of the change in the total number of hours spent atlassing in each OBBA square between the 1985 and 2005 atlases. The direction and absolute value of effort were used rather than the signed change in effort to distinguish between the expected positive effect of increases in effort on the detection of previously unrecorded species and the expected negative effect of decreases in effort on the detection of previously recorded species (P2.2, Table 2.1B). The expected relationship between the probability of detection and signed change in effort is positive regardless of the direction of change. The effect of sampling effort and change in sampling effort may also be confounded by a propensity for observers to search more actively for species observed in the first atlas than for species that were absent in 1985.

Statistical analysis

Tests of the predictions

Direction and magnitude of effects

To test the predictions regarding the direction and magnitude of the effects of habitat amount, neighbourhood occupancy, sampling effort and change in effort on the probability of individual species' local presence (predictions 1.1, 1.2 &1.3 and 2.1 & 2.2), I fit a generalized linear model (GLM) for each species. The GLMs (binomial family using a logit link function) included these four variables as main effects, as well as previous presence as a main effect and interactions between previous presence and each of the four continuous variables. A single full model was fitted to test the predictions so that the direction and magnitude of the effects of each variable could be assessed while holding the other variables constant. I standardized the four continuous independent variables (by mean-centering and dividing by the standard deviation) so that the coefficient estimates for the main effects and interactions could be directly compared, allowing me to assess the relative strength of each main effect and interaction. The full model fit for each species was:

$$P_{05} \sim P_{85}+H+P_{85}:H+N_{85}+P_{85}:N_{85}+H:N_{85}+P_{85}:H:N_{85}+E+P_{85}:E+\Delta E+P_{85}:\Delta E+D:\Delta E+P_{85}:D:\Delta E \quad (1)$$

where P_{05} is species presence in the 2005 OBBA, P_{85} is species presence in the 1985 OBBA, H is the area of habitat, N_{85} is the proportion of neighbouring squares occupied by conspecifics in 1985, E is $\log_{10}$(effort in 2005), ΔE is the absolute value of the change in effort and D is the direction of the change in effort. Variables connected by colons represent multiplicative interactions. Species whose GLM results showed large standard errors relative to the size of the associated coefficients were removed from the analysis because these indicate numerical problems such as complete separation, collinearity and numerous zero cell counts (Hosmer & Lemeshow, 2000). This resulted in the final sample size of 151 species that occurred within the study area in both OBBAs (Cadman *et al*., 2007). I excluded 44 species that occupied very few (or all but a few) atlas quadrats. See Tables 1A and 1B for a complete description of the predictions and

Appendix D for a worked example of the interpretation of model coefficients for Swainson's Thrush.

I pooled the regression results for all 151 species and conducted Bonferroni-corrected Wilcoxon signed rank tests to determine if the median coefficients for the main effects and interactions as well as the slopes relating to change in effort differed significantly from zero.

Deviance explained

To test predictions 1.4 and 1.5, that the deviance explained by previous presence and habitat area or neighbourhood occupancy is greater than deviance explained by previous presence alone, I fit simplified models for each species that included only previous presence (model 2) and compared the deviance explained to that explained by models including previous presence and habitat area (model 3) or neighbourhood occupancy (model 4).

$$P_{05} \sim P_{85} \tag{2}$$

$$P_{05} \sim P_{85} + H \tag{3}$$

$$P_{05} \sim P_{85} + N_{85} \tag{4}$$

To test the prediction that presence pooled over both censuses (i.e. present in either the 1985 OBBA or the 2005 OBBA) should be more strongly related to area of habitat than presence in single censuses (P1.6), I fit three models to evaluate the deviance in local presence explained by habitat area, when presence was pooled over both OBBA (P_{85U05}), taken from only the first OBBA (P_{85}) and taken from only the second OBBA (P_{05}):

$$P_{85U05} \sim H \tag{5}$$

P_{85}~H (6)

P_{05}~H (7)

Comparisons of median deviances explained were made using Wilcoxon rank sum tests.

Accounting for autocorrelation

I did not account for spatial autocorrelation explicitly in the individual species' GLMs for two reasons. First, I was primarily interested in the coefficients from the GLMs (rather than their associated p-values) and no method for accounting for spatial autocorrelation in regressions of presence/absence data has been found to produce consistently reliable coefficients (Dormann *et al.*, 2007). The second, and more important, reason is that I was specifically interested in the spatial structure in the presence/absence of each species and have hypothesized that it is governed by the proportion of neighbouring sites that are occupied by conspecifics. I have also hypothesized that the spatial structure in presence/absence is due to the distribution of the amount of habitat, which is spatially autocorrelated. Including neighbourhood occupancy and habitat area as explanatory variables should account for the spatial structure in presence/absence, resulting in residuals that are not spatially autocorrelated.

The explanatory power of the hypotheses

I evaluated the explanatory power of the main hypothesis that the probability of local presence depends on metapopulation-like processes as well as the secondary hypothesis that the probability of presence depends on sampling effects. The explanatory power of the main hypothesis, that metapopulation-like processes determine local species presence, was taken as the deviance explained by a model including previous presence, habitat area, neighbours and their associated interactions (model 8).

$$P_{05} \sim P_{85}+H+P_{85}:H+N_{85}+P_{85}:N_{85}+H:N_{85}+P_{85}:H:N_{85} \qquad (8)$$

Similarly the explanatory power of the sampling effects was taken as the deviance explained by previous presence, effort, change in effort and their associated interactions (model 9).

$$P_{05} \sim P_{85} +E+P_{85}:E+\Delta E+P_{85}:\Delta E+D: \Delta E+P_{85}:D:\Delta E \qquad (9)$$

I also examined the deviance explained by each of habitat area, neighbourhood occupancy, sampling effort and change in sampling effort. The total effects of habitat area, neighbourhood occupancy, effort and change in effort were taken as the deviance explained by each variable's main effect and any interactions in which it was included. This was measured as the deviance explained by the model including only the main effects and interaction(s) as well as the change in deviance explained when they (and their associated interactions) were removed from the full model (model 1).

To evaluate overall trends across all species, I conducted a Kruskal-Wallis one-way ANOVA followed by Bonferroni-corrected multiple comparisons to determine if and how the median deviances explained differed among factors.

The empirical effect of metapopulation-like processes on species richness–environment relationships

The hypothesis that the relationship between observed richness and environment is weaker than expected because of temporarily unoccupied sites within species distributions makes the following additional predictions: 1) species richness evaluated using presence pooled over both OBBAs should be more strongly related to environment than richness evaluated using presence in either OBBA alone; and 2) species richness predicted from the metapopulation models (model 8), taken as the probability of local presence (the GLM fitted values) for each species, summed over all species, should be more strongly related to environment than richness in 1985 or richness in 2005.

To test these latter predictions, I regressed each measure of species richness against the proportion of natural land cover in the OBBA square. The proportion of natural land cover was found to be the best environmental predictor of avian richness in Ontario (Chapter 1; Desrochers *et al*., 2011). Natural land cover was determined from the Ontario Provincial-Scale Land Cover data set (OMNR, 2002) as the proportion of each OBBA square covered by natural land covers including forests (9 classes including older forest clear-cuts and forest fires), wetlands (7 classes), and alvar (dry grassland found over limestone substrate with thin soils). I grouped the small amounts of coniferous plantation in southern Ontario with natural cover because plantations likely share more bird species with natural forests than with human-dominated land cover.

All statistical analyses were performed in R, version 2.12.1 (R Development Core Team, 2010). I tested for spatial autocorrelation in the GLM residuals using the spdep package (Bivand *et al.*, 2010).

RESULTS

Tests of the predictions

All results suggest that metapopulation-like processes strongly affect regional variation in species presence. Local species presence tended to be positively related to the area of species-specific habitat (one-way Wilcoxon signed rank test to compare the median coefficient to zero, p-value < 0.0001; P1.1; Table 2.2) and neighbourhood occupancy (one-way Wilcoxon signed rank test, p-value < 0.0001; P1.2). As predicted, the interaction term was significantly less than zero (one-way Wilcoxon signed rank test, p-value = 0.003; P1.3). Therefore the effect of habitat amount was stronger when fewer neighbouring squares were occupied in the 1985 OBBA indicating that larger habitat area represents a larger target for rescuers from neighbouring sites. Also, consistent with the hypothesis that metapopulation-like processes determine local species presence, habitat area and the frequency of neighbours both account for significant deviance beyond that explained by previous presence alone (using one-way Wilcoxon rank sum tests to compare the median deviances explained, p-value < 0.0001 for habitat area (P1.4) and p-value < 0.0001 for neighbourhood occupancy (P1.5); Table 2.3). Habitat amount explained more deviance in presence pooled over both censuses than presence in either OBBA; however the difference was only significant for the comparison with presence in the first OBBA (one-way Wilcoxon rank sum test, p-value = 0.041 for comparison with presence in the 1985 OBBA and p-value = 0.123 for comparison with presence in the 2005 OBBA; P1.6).

Sampling effort varied considerably and influenced local presence (one-way Wilcoxon signed rank test to compare the median coefficient to zero, p-value < 0.0001; P2.1; Table 2.2), but the effect size was significantly smaller than for neighbourhood occupancy (one-way Wilcoxon rank sum test to compare the median coefficients, p-value < 0.001). However, change in sampling effort was not the explanation for observed local extinctions and colonisations. Changes in presence/absence were unrelated to changes in sampling effort and no associated interaction was significant: changes in sampling effort did not depend upon whether or not the species was initially present or of the direction of the change in effort. The slope of the relationship between the probability of local presence and the absolute change in sampling effort was not significantly different from zero ($p > 0.05$ using one-way Wilcoxon signed rank tests to compare the median slopes to zero) for negative changes in sampling regardless of whether or not the species was previously present as well as for positive changes in effort (Table 2.4).

The explanatory power of the hypotheses

Processes that I believe reflect metapopulation dynamics were about twice as important as differences in sampling intensity. The deviance explained by the metapopulation hypothesis (model 8) was significantly greater than the deviance explained by the sampling hypothesis (model 9; one-way Wilcoxon rank sum test to compare the median deviances explained, p-value < 0.0001; Table 2.3). Among the metapopulation processes considered here, neighbourhood occupancy exerted the strongest effect. Effort and change in effort explained little additional deviance above previous presence, which was common to the models for both hypotheses.

The pattern observed above, that the effects of habitat area and neighbourhood occupancy were stronger than those for sampling effort or change in sampling effort, is mirrored in the pattern in the rank of the importance of habitat area, proportion of neighbours, effort and change in effort per species. Neighbourhood occupancy was consistently the most important effect (mean = 3.51, median = 4, standard deviation = 0.81) followed by the area of habitat (mean = 2.72, median = 3, standard deviation = 1.05), sampling effort (mean = 2.07, median = 2, standard deviation = 0.90) and change in sampling effort (mean = 1.70, median = 2, standard deviation = 0.75). The median ranks for each factor differed significantly (Kruskal-Wallis chi-squared = 227.40, df = 3, p-value < 0.001) for all multiple comparisons ($p < 0.001$).

The empirical effect of metapopulation-like processes on species richness–environment relationships

I found that, as predicted, the richness-environment relationship was stronger for measures of species richness that account for the effect of metapopulation dynamics on local presence and the resulting pattern of richness. Richness predicted from the metapopulation models was more strongly associated with environment, measured here as the proportion of natural area, than richness from presence pooled over both OBBA ($R^2 = 0.62$ and $R^2 = 0.48$, respectively; Figure 2.3). Pooled richness was in turn more strongly associated with environment than richness taken from either OBBA individually ($R^2 = 0.36$ for 2005 OBBA and $R^2 = 0.34$ for 1985 OBBA).

DISCUSSION

This analysis suggests that processes typically associated with metapopulation dynamics that affect local distributions of individual species “scale up” to modify regional species richness patterns. The evidence is consistent with the hypothesis that the patchiness in regional-scale species distributions reflects metapopulation-like processes of local extinction and colonization. All the six predictions derived from the hypothesis were supported, and the deviance explained by the metapopulation hypothesis was significantly greater than the deviance explained by the sampling hypothesis, explaining nearly twice the deviance in local presence compared to the sampling hypothesis.

Moreover, the relationship between species richness and the proportion of natural area, previously found to be the best environmental predictor of bird richness in this region (Chapter 1; Desrochers *et al*., 2011), strengthened from 36% of the variance in richness being explained to 62% after accounting for the metapopulation processes. This is similar to the strength of continental or global richness–environment relationships (e.g., Currie, 1991; Francis & Currie, 2003; Hawkins *et al*., 2003; Field *et al*., 2009). This suggests that the reason why regional patterns are more difficult to predict is because metapopulation processes have a substantial effect on local presence beyond the effect that environmental controls have on determining species' distributions. It is the reflection of the resulting temporary local absences in the data used for regional studies that weakens observed richness–environment relationships.

The results were consistent with the expectation from metapopulation theory that larger, less isolated patches are more likely to be occupied at any given time (Hanski, 1999). Less isolated patches are more likely to be colonized or recolonized, while larger patches, by supporting larger local populations, are more likely to be consistently occupied and provide larger targets for immigrants (Hanski, 1999). As expected, OBBA quadrats with greater area of species-specific habitat were more likely to be occupied than those with less habitat and provided a larger target for immigrants, which was particularly important when fewer neighbouring sites were previously occupied by conspecifics (potential immigrants). And, as would be expected for less isolated patches, OBBA quadrats were more likely to be occupied if more neighbouring sites were occupied by conspecifics in the first OBBA.

Applying a metapopulation framework to predict species' distributions across landscapes at such broad extents is unusual: most metapopulation research focuses within landscapes, rather than across regions. Furthermore, habitat "patches" in this study were not necessarily spatially distinct, nor could I measure bird species abundances within them. Yet, the detailed bird observations available in Ontario permit tests of fundamental metapopulation predictions, such as the effect of neighbourhood occupancy on changing species presence. Moreover, the inclusion of metapopulation perspectives at macroecological scales greatly improved prediction of bird species presence and absence across this region. These results suggest that metapopulation theory may provide a viable bridge linking landscape-to-macroecological patterns at the species level and provide a biological explanation why macroecological hypotheses begin to break down at more local spatial scales.

Sampling effects appear to contribute relatively little to the apparent patchiness of species' regional distributions. Though sampling effort was related to the likelihood of a species being detected, change in effort was not related to local appearance or disappearance. Sampling effort and change in sampling effort had the weakest and least important effects on the detection of species presence. This suggests that the apparently patchy distributions of bird species at the regional scale of Ontario, Canada are a biological phenomenon and not an artefact of the sampling protocol.

Observer behaviour may confound the effect of sampling intensity on species detection. It is possible that observers, rather than searching their assigned squares randomly, deliberately seek out breeding evidence for species known to have been previously present. If so, the number of observer hours spent in an atlas square may be a biased measure of effort. Some evidence of this is reflected in the interaction between sampling effort and previous presence, which indicates that the effect of sampling effort was slightly stronger if the species was recorded as present in the first atlas (Table 2.4). An increase in sampling effort increased the likelihood that a previously observed species was re-observed by more (1.46 times) than the likelihood of observing a previously unobserved species (1.31 times).

The role of metapopulation-like processes in determining local presence has consequences for conservation and management. The effects of neighbourhood occupancy and habitat area (evaluated by their odds ratios; Table 2.4) increased when the species was absent from a given location in the first atlas, suggesting that neighbourhood occupancy and, to a lesser extent, the extent of available unoccupied habitat area increase chances of colonization. Consequently, it is advisable for conservation practitioners to protect and manage suitable, though unoccupied, habitat near extant populations.

Perhaps most notably, this analysis reveals that there is spatial and temporal variability in the local distributions of individual bird species and consequently in regional patterns of species richness that is not due to deterministic environmental or sampling effects. This is potentially also of great importance for conservation. Even after considering sampling effects, the spatial patterns of avian distributions are quite dynamic temporally. Through time, original species complements of mobile organisms might turn over substantially. Selecting areas on the basis of species that are present today is sensible but turnover is to be expected, even in the absence of major environmental change. The possibility of species losses and the arrival of new species should figure into the decisions for conservation. Protected area management must account for such substantial temporal and spatial variability. Strategies should include 1) assessing species richness by pooling species presences over repeated surveys, 2) protecting and/or managing habitat in areas that may be presently unoccupied but are likely to be occupied in the future, namely areas with large amounts of habitat surrounded by sites occupied by conspecifics, and 3) including locally absent species that could potentially inhabit the area in estimates of species richness (called “dark diversity” by Pärtel *et al*., 2010; Morlon *et al*., 2011).

ACKNOWLEDGEMENTS

I am grateful to the official sponsors of the Ontario Breeding Bird Atlas (Bird Studies Canada, Canadian Wildlife Service, Federation of Ontario Naturalists, Ontario Field Ornithologists, and Ontario Ministry of Natural Resources) for supplying Atlas data, and to the thousands of volunteer participants who gathered data for the Ontario Breeding Bird Atlases. In particular, I would like to thank Mike Cadman, Denis Lepage and Peter Blancher for providing the Ontario Breeding Bird Atlas data as well as considerable advice regarding analysis of the data. Finally I would like to thank Adam Algar for assistance with the statistical analysis as well as helpful comments.

TABLES

Table 2.1: A) The predictions derived from the hypothesis that metapopulation-like processes of local extinction and colonization determine local species presence with the associated rationales, statistical models and tests of the predictions. B) The predictions derived from the hypothesis that sampling determines local species presence as well as local extinction and colonization with the associated rationales, statistical models and tests of the predictions.

A	Metapopulation-like processes of local extinction and colonization determine local species presence.			
	Rationale	Prediction	Statistical Model	Test
1.1	Sites with larger areas of habitat support larger populations that are consequently less likely to go locally extinct.	The probability of individual species' local presence is positively related to the area of its habitat.	Full model, evaluated for each species (model 1)	The median coefficient (among all species) for the effect of habitat is positive. One-tailed Wilcoxon signed rank test.
1.2	Species are more likely to be consistently present at sites surrounded by sites occupied by conspecifics because there are more potential rescuers to maintain the local population and recolonize the site if it becomes uninhabited due to local extinction.	The probability of individual species' local presence is positively related to neighbourhood occupancy.	Full model, evaluated for each species (model 1)	The median coefficient (among all species) for the effect of neighbourhood occupancy is positive. One-tailed Wilcoxon signed rank test.
1.3	Larger habitat area represents a larger target for rescuers therefore the effect of habitat area is stronger when there are fewer neighbours.	The effect of habitat area is stronger when there are fewer neighbours.	Full model, evaluated for each species (model 1)	The median interaction term between habitat and neighbourhood occupancy is negative. One-tailed Wilcoxon signed rank test.

A	Metapopulation-like processes of local extinction and colonization determine local species presence.			
	Rationale	Prediction	Statistical Model	Test
1.4	Previous presence indicates that the site is potentially occupiable. However some suitable sites will be unoccupied during any given census due to demographic or environmental stochasticity. The suitability of these unoccupied sites will be related to area of habitat.	Deviance explained by previous presence and habitat area is greater than deviance explained by previous presence alone.	P_{05}~P_{85} (model 2) P_{05}~P_{85} + H (model 3)	The median deviance explained for model 3 is greater than the median deviance explained by model 2. One-tailed Wilcoxon rank sum test.
1.5	Presence/absence of a species at a given site should be related to neighbourhood occupancy, which influences the likelihood of colonization.	The deviance explained by previous presence and neighbours is greater than deviance explained by previous presence alone.	P_{05}~P_{85} (model 2) P_{05}~P_{85} + N_{85} (model 4)	The median deviance explained for model 4 is greater than the median deviance explained by model 2. One-tailed Wilcoxon rank sum test.
1.6	Presence in any census indicates that the site is adequate to support at least one breeding pair. Pooled presences over more than one census will reflect less demographic stochasticity than single censuses. Therefore, presence pooled over both censuses should be more strongly related to area of habitat than presence in single censuses.	Deviance explained in presence pooled over both censuses is greater than the deviance explained in presence in the first or second census.	P_p~H (model 5) P_{85}~H (model 6) P_{05}~H (model 7)	The deviance explained by model 5 is greater than the deviance explained by models 6 or 7. One-tailed Wilcoxon rank sum test.

B	Local species presence and local extinction and colonization are determined by sampling effort.			
	Rationale	Prediction	Statistical Model	Test
2.1	The likelihood of local species presence is positively related to the number of hours spent sampling.	The probability of individual species' local presence is positively related to sampling effort.	Full model, evaluated for each species (model 1)	The median coefficient for the effect of habitat is positive. One-tailed Wilcoxon signed rank test.
2.2	The likelihood of detecting a previously absent species increases with an increase in effort from the previous census. Similarly, the likelihood of detecting a previously present species decreases with a decrease in effort from the previous census. An increase in effort should not increase the likelihood of detecting a previously present species and a decrease in effort should not decrease the likelihood of detecting a previously absent species.	The slope of the relationship between the probability of local presence and change in effort is positive if effort increased and the species was locally absent, and the slope is negative if effort decreased and the species was locally present. The slope is equal to zero otherwise.	Full model, evaluated for each species (model 1)	The median slopes are in the predicted directions. One-tailed Wilcoxon signed rank tests.

Table 2.2: The median (among 151 species) coefficients (A) or slopes (B) relating presence in 2000-2005 to presence in 1980-1985 (P_{85}), and the proportion of neighbouring cells occupied by conspecifics in 1985 (N_{85}), habitat area (H), sampling effort (E) and change in effort(ΔE). Medians were compared with zero using Wilcoxon signed rank tests, for which the related prediction (detailed in Table 2.1), statistical conclusion and associated p-value are presented. The Bonferroni-corrected alpha level is 0.0038.

A	Term	Median Coefficient	Related Prediction	Statistical conclusion	P-values	Prediction rejection
	P_{85}	0.98	N/A	> 0	< 0.001	
	H	0.45	1.1	> 0	< 0.001	Not rejected
	P_{85}:H	-0.09	N/A	≤ 0	0.139	
	N_{85}	0.92	1.2	> 0	< 0.001	Not rejected
	P_{85}:N_{85}	-0.12	N/A	≤ 0	0.031	
	H:N_{85}	-0.10	1.3	< 0	0.003	Not rejected
	P_{85}:H:N_{85}	0.15	N/A	≤ 0	0.026	
	E	0.28	2.1	> 0	< 0.001	Not rejected
	P_{85}:E	0.06	N/A	≤ 0	0.214	

B	Term	Presence in first OBBA	Median Slope	Related Prediction	Statistical conclusion	P-values	Prediction rejection
	Negative ΔE	Absent	0.09	2.2	= 0	0.051	Rejected
		Present	0.06	2.2	= 0	0.823	Rejected
	Positive ΔE	Absent	0.01	2.2	= 0	0.452	Rejected
		Present	-0.06	2.2	= 0	0.447	Rejected

Table 2.3: A) Deviance in local presence explained by species-specific habitat amount alone when presence was pooled over both OBBA (P_{85U05}), taken from only the first OBBA (P_{85}) and taken from only the second OBBA (P_{05}). B) Deviance explained the effects of previous presence, habitat amount, neighbourhood occupancy, all terms relating to the metapopulation dynamics hypothesis, sampling effort, change in sampling effort, and all species presence in the 1985 OBBA, H is the area of habitat, N_{85} is the proportion of neighbouring squares occupied by conspecifics, E is log10(Effort), ΔE is the absolute value of the change in effort and D is the direction of the change in effort. Variables linked by a colon represent a multiplicative interaction. In both A) and B) medians for effects with the same letter do not differ significantly (α=0.05), these are only shown for comparisons related to predictions.

A	Effect	Model	Related Prediction	Median deviance explained	Significant differences	Prediction rejection
	Habitat	P_{85U05}~H (5)	1.6	0.13	a	Not rejected
	Habitat	P_{85}~H (6)	1.6	0.07	b	Not rejected
	Habitat	P_{05}~H (7)	1.6	0.10	a,b	Rejected

B	Effect	Model	Related Prediction	Median deviances explained	Significant Differences	Prediction rejection
	All effects	$P_{05} \sim P_{85}+ H+ P_{85}:H +N_{85}+ P_{85}:N_{85} +H:N_{85} + P_{85}:H:N_{85} + E+P_{85}:E + \Delta E + P_{85}:\Delta E +D:\Delta E+ P_{85}:D:\Delta E$ (1)		0.33		
	Previous presence alone	$P_{05}\sim P_{85}$ (2)	1.4, 1.5	0.14	a	Not rejected
	Habitat	$P_{05}\sim P_{85}+H$ (3)	1.4	0.21	b	Not rejected
	Habitat	$P_{05}\sim P_{85}+H+P_{85}:H$		0.21		
	Neighbours	$P_{05}\sim P_{85}+N_{85}$ (4)	1.5	0.24	b	Not rejected
	Neighbours	$P_{05}\sim P_{85}+N_{85} +P_{85}:N_{85}$		0.26		
	Metapopulation dynamics	$P_{05}\sim P_{85}+H+P_{85}:H+ N_{85}+P_{85}:N_{85}+ H:N_{85}+ P_{85}:H:N_{85}$ (8)		0.3		
	Effort	$P_{05}\sim P_{85}+E$		0.16		
	Effort	$P_{05}\sim P_{85}+E +P_{85}:E$		0.16		
	Change in Effort	$P_{05}\sim P_{85}+\Delta E$		0.14		
	Change in Effort	$P_{05}\sim P_{85}+\Delta E+ P_{85}:\Delta E$		0.15		
	Sampling methodology	$P_{05} \sim P_{85}+E+ P_{85}:E +\Delta E+ P_{85}:\Delta E + D: \Delta E+ P_{85}:D:\Delta E$ (9)		0.16		

Table 2.4: The median slopes and odds ratios for previous presence, and the proportion of neighbours, habitat area and sampling effort. Slopes for different levels of interacting variables were calculated using the equations resulting from the GLMs for both levels of presence in the 1985 Ontario Breeding Bird Atlas (present/absent), for a proportion of neighbours equal to 0 and 1, and for both directions of change in effort (positive and negative) to derive slopes for each combination of factors. P_{85} is species presence in the 1985 OBBA, H is the area of habitat, N_{85} is the proportion of neighbouring squares occupied by conspecifics, E is $\log_{10}$(Effort), ΔE is the absolute value of the change in effort and D is the direction of the change in effort.

Slope	Presence in the 1985 OBBA	Levels of Additional Terms	Median Slope	Median Odds Ratio
P_{85}		All others = 0	0.97	2.65
H	Absent	All others = 0	0.43	1.54
H	Present	All others = 0	0.40	1.49
N_{85}	Absent	All others = 0	0.89	2.44
N_{85}	Present	All others = 0	0.80	2.23
H	Absent	N_{85}=1	0.30	1.35
H	Present	N_{85}=1	0.30	1.35
E	Absent	All others = 0	0.27	1.31
E	Present	All others = 0	0.38	1.46

FIGURES

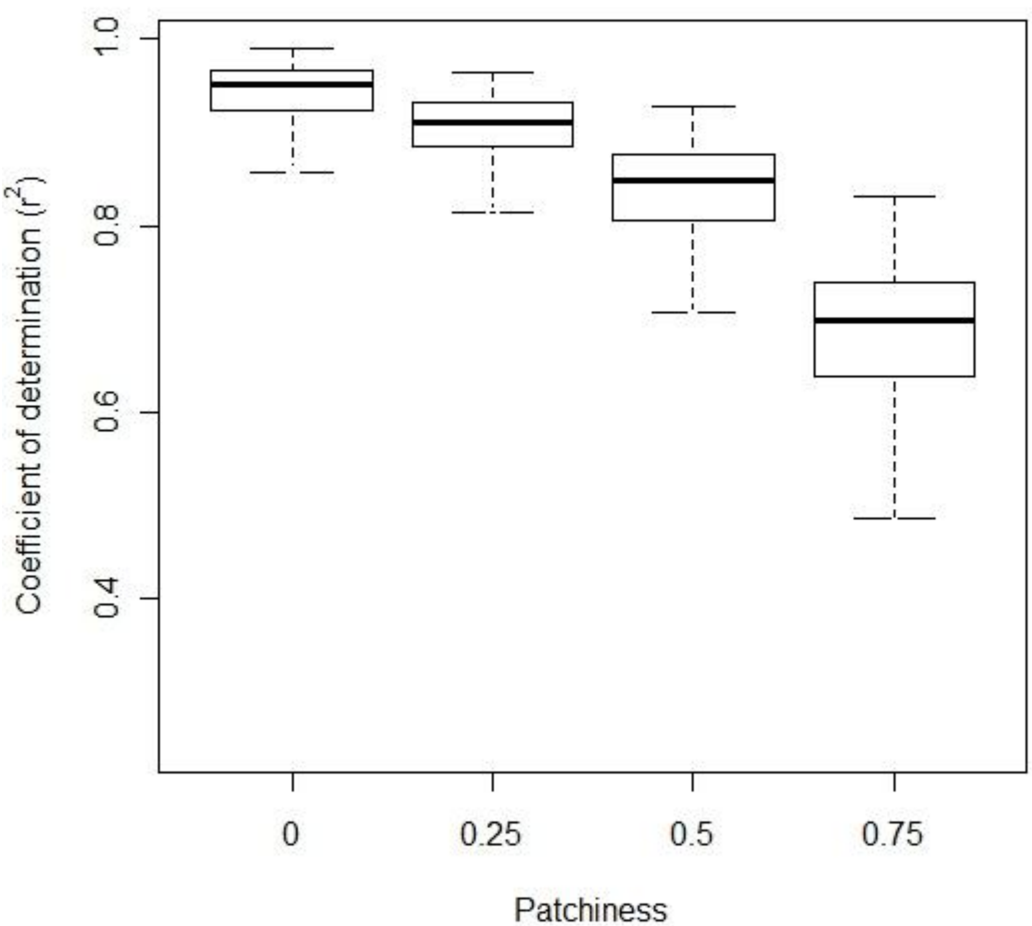


Figure 2.1: Consider a simulated species richness gradient constructed by placing species' ranges stochastically along a hypothetical environmental gradient, with increasing probability toward the high end of the environmental gradient. As expected, the resulting pattern of richness is strongly correlated with the environmental gradient. Then, progressively convert presences to absences at random spots with species' ranges. The relationship between species richness and the environmental gradient weakens as

patchiness (the proportion of presences randomly replaced by absences within the species range) increases, even though the process that determined the placement of ranges with respect to the environmental gradient remained unchanged.

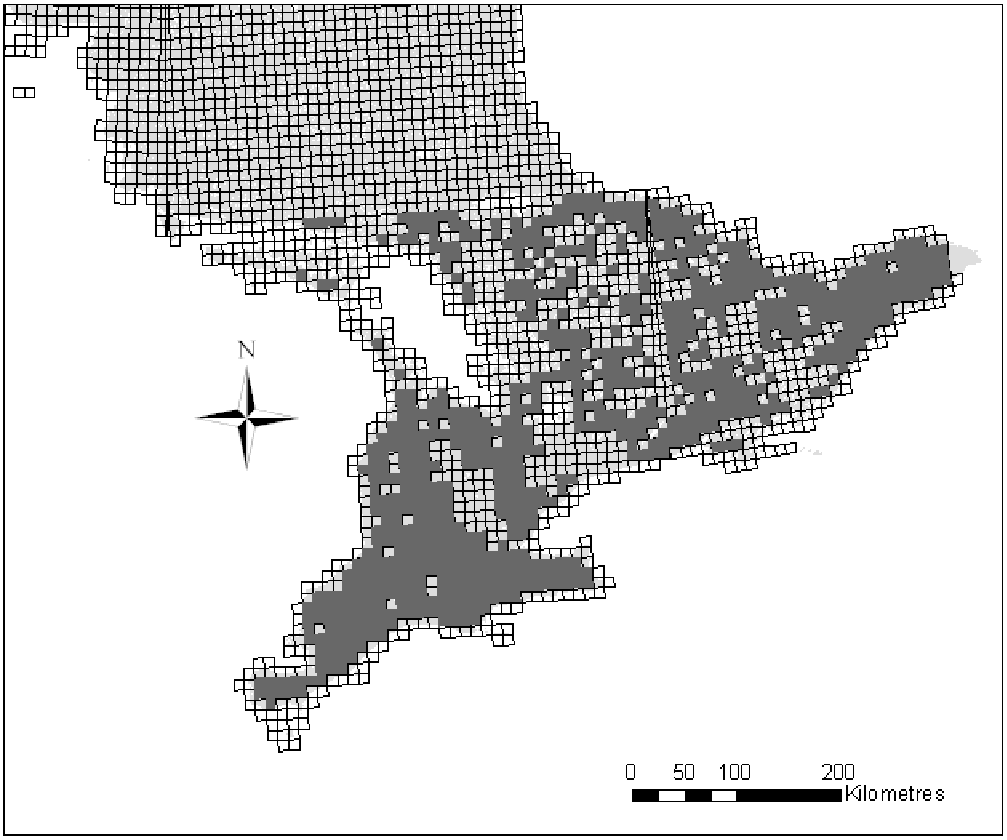


Figure 2.2: Study area in the southern portion of Ontario. Breeding Bird Atlas squares are outlined in black. Atlas squares included in the study (those with at least 10 hours of effort in both atlases and less than 10% area covered by water) are shown in medium gray, excluded squares are shown in light gray. The projection is Lambert Conformal Conic.

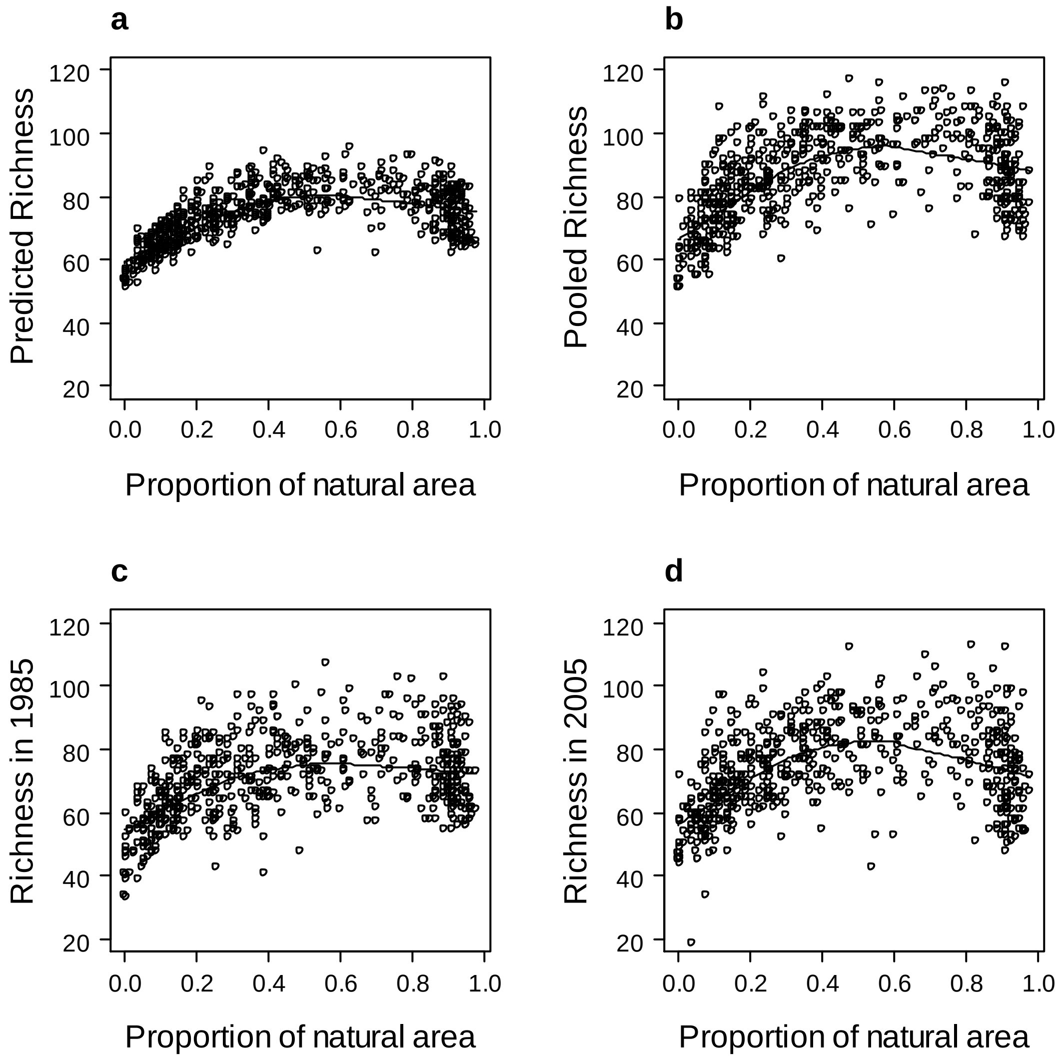


Figure 2.3: The richness–environment relationships for a) species richness predicted from the metapopulation models (model 8), b) species richness for presence pooled over both Ontario Breeding Bird Atlases (OBBA), c) species richness from the 1985 OBBA and d) species richness from the 2005 OBBA as a function of the proportion of natural area.

CHAPTER 3: METAPOPULATION DYNAMICS, NOT ENVIRONMENTAL CHANGE, PREDICT CHANGE IN SPECIES RICHNESS

ABSTRACT

Aim: To determine if species richness responded to change in natural area in the directions predicted by the spatial relationship between avian richness and natural area found in the first chapter of this thesis and as predicted by the metapopulation models developed in the second chapter of this thesis.

Location: The greater park ecosystem of St-Lawrence Islands National Park (SLI ecosystem).

Methods: I evaluated change in bird richness between 1985 and 2005 for 85 Ontario Breeding Bird Atlas (OBBA) squares in the SLI ecosystem. I related change in bird richness to change in natural area for sites that had initially less or greater than 56% natural area. I calculated the change in species richness predicted by the metapopulation models to determine if the models predicted the observed changes in species richness.

Results: Species richness did not respond to change in natural area in the directions predicted by the spatial relationship; however species richness did change as predicted by the metapopulation models. Between 1985 and 2005, species richness tended to increase with decreasing natural area regardless of the initial amount of natural area and the species group (forest vs. open habitat species). This occurred for two reasons; first the sites that lost more natural area were those where metapopulation models predicted species were likely to be present. Second, many of the forest species can inhabit open

forest and even human-dominated areas including parks, orchards and residential neighbourhoods.

Main Conclusions: There is some unpredictability inherent in species presence which translates into unpredictability in species richness. Consequently, detecting responses to environmental changes may often be challenged by low “signal to noise” ratios. The plasticity of individual species’ land cover selection suggests that the utility of species – area relationships for estimating species losses due to land cover conversion is likely quite limited in many conservation situations.

INTRODUCTION

Conversion of natural area to human-dominated uses is often viewed as tantamount to habitat loss. However, in many areas of the world the number of species remaining in human-dominated landscapes is high, sometimes even equal to those in natural areas (Pereira & Daily, 2006). Consequently, it is important to understand how species affiliated with both natural and human-dominated land covers will respond to land cover changes. In Europe, where much of the landscape is human-dominated, farmland birds are declining while forest and woodland bird populations remain stable (Gregory *et al*., 2005). Although much less of the land area of Canada has been converted from natural to human-dominated land uses than in Europe, bird species that prefer open habitats (including grasslands and fields) are often relegated to areas that have substantial human impact, like agriculture, because open habitats rarely escape human modification in southern Canada (Kerr & Cihlar, 2003). Fifteen of the 51 bird species that are endangered or threatened in Canada prefer open habitat and are in need of active conservation efforts (COSEWIC, 2010).

Spatial relationships between species richness and environmental characteristics are commonly reported. These spatial relationships will also hold through time if they are causal and the lag in response to environmental change is brief. As environments change, richness should change as predicted by the spatial relationship. The need for this space – for – time assumption is due in part to the difficulty of obtaining time series species richness and land cover data at commensurate spatial and temporal resolutions with which to assess temporal responses of species richness to environmental changes (White & Kerr, 2006; Kerr *et al*., 2007; Fisher *et al*., 2010).

In Ontario, spatial variation in bird species richness is a peaked function of natural area (Chapter 1; Desrochers *et al.*, 2011). The sum of the species–area curves for species that prefer natural habitats (mostly forest species) and those that prefer human-dominated habitats (mostly agricultural and urban species) reaches a maximum at 56% natural area (Chapter 1; Desrochers *et al.*, 2011; Figure 3.1). This discovery leads to the interesting conservation prediction that conversion of forested landscapes to include mixtures of natural and human-modified, open land covers will increase bird richness with few losses of forest-obligate species. This prediction relies on the space – for – time assumption, specifically that the spatial relationship between habitat area is also observed as habitat area changes through time.

Yet, the temporal response of species richness to changing extents of natural area may differ from its spatial response. First, the space – for – time substitution may fail if the independent variable in the spatial relationship, natural habitat area, happened to be strongly collinear with other variables that affect richness in space but the nature of the collinearity breaks down in time. For example, natural area loss could lead to increased habitat heterogeneity or an increase in the amount of edge habitat, either or both of which could lead to increased species richness. Second, many species that prefer natural land cover for habitat can tolerate human-dominated land covers and many species that prefer open, and consequently human-dominated, habitats can tolerate natural land covers as well (see Wood Thrush and American Kestrel in Appendix C as examples).

Consequently, large changes in natural area may be required to observe changes in species richness.

If changing extents of habitat area through time do not lead to similar species richness – area relationships as those observed spatially, many conservation predictions could become less reliable. Species–area curves have often been used to forecast species loss following habitat loss (Pimm & Askins, 1995; Brooks & Balmford, 1996; Pimm & Raven, 2000; DeFries *et al.*, 2005; Sala *et al.*, 2005). Similarly, the expectation that more species will be found in larger areas of habitat is (or should be) central to conservation and land management decisions (Beatley, 2000; Dale *et al*., 2000; Margules & Pressey, 2000). Failures of the space–for–time substitution have been found elsewhere in ecology (Fisher *et al*., 2010 and references therein) and can be as striking as a reversal in the direction of the observed effect (White & Kerr, 2006).

In the second chapter of this thesis, I found that there is considerable temporal variability in site occupancy by the breeding birds of Ontario, consistent with the hypothesis that metapopulation-like processes determine the likelihood of local species presence (Chapter 2). As would be expected from metapopulation theory for isolated habitat patches (Hanski, 1999), the local presence of a species related strongly to the proportion of neighbouring sites that were occupied by conspecifics in the earlier time period (herein called neighbourhood occupancy). Also, as would be expected for larger habitat patches, local presence of a species was strongly related to the area of species-specific habitat at a given site.

If species presence at a site is a function of neighbourhood occupancy and species-specific habitat area, as suggested by metapopulation theory (Hanski, 1999) and the findings in Chapter 2, then models that include these two key landscape characteristics should correctly predict change in richness (the net change in local species appearances and disappearances) through time. The sites where previously locally absent species had a high likelihood of being present (based on neighbourhood occupancy and habitat area) are likely to increase in richness and the sites where previously locally present species had a low probability of being present are likely to decrease in richness. To predict change in richness, one can predict current richness as the sum of the probabilities at a given time that each species in the regional species pool is present minus previously observed richness. The change in richness predicted by the metapopulation models should be a strong, positive predictor of the observed change in species richness.

In this study, I determined if avian richness in a portion of Ontario responded to change in natural area in the directions predicted by the spatial relationship between avian richness and natural area, which makes specific predictions regarding not only the response of species richness to change in natural area, but also the differential responses of species groups. The peaked relationship predicts that, at sites with greater than 56% natural area initially, loss of natural area should lead to little change in forest bird richness, but an increase in open habitat bird richness so long as natural area was not reduced below the peak. Conversely, in areas with less than 56% natural area initially, loss of natural area would lead to a decrease in forest bird richness and little change in open habitat bird richness (again so long as natural area was not reduced below the peak). I also tested if avian richness changed as predicted by the metapopulation models and assessed the relative contributions of the land cover change and the metapopulation dynamics in determining how avian richness has changed through time.

METHODS

Attempts to test macroecological theories have been hindered by the difficulty of conducting broad-scale manipulative experiments to test causal relationships (Kerr *et al.*, 2007). However, the increasing availability of long-term datasets of species richness and remotely-sensed data on land cover now allow for broad-scale pseudo-experiments testing how land cover extent affects species richness. The data used to assess the regional spatial relationship between bird richness and natural area in Chapter 1 (the 2005 Ontario Breeding Bird Atlas (OBBA)) is the follow-up to the 1985 OBBA (Cadman *et al.*, 2007). This made it possible to study changes in bird distributions and bird richness in Ontario. Fraser *et al.* (2009) developed time-series land cover change data for the area encompassing St. Lawrence Islands National Park and its greater park ecosystem (herein referred to as the SLI ecosystem; Figure 3.2) as part of a federal government initiative to use earth observation for national park monitoring. The SLI ecosystem (approximately 22,000 km^2, roughly the size of Israel or West Virginia) occurs within the study area examined in Chapter 1. From these data, change in natural area in the OBBA squares in the SLI ecosystem was measured. I used the two Ontario BBAs (1985 and 2005) and the time-series land cover change observations (1990-2005) for the SLI ecosystem to test if the space–for–time substitution holds for the regional richness–natural area relationship.

Bird richness

I assessed change in bird richness in 85 OBBA squares in the SLI ecosystem from individual bird species' distribution data from the 1985 and 2005 OBBAs (Cadman *et al.*, 1987 & 2007; Figure 3.2). I tallied the number of breeding bird species present within each 100 km^2 OBBA square in each atlas. The OBBA squares are based on the Universal Transverse Mercator (UTM) grid system. I included data only from OBBA squares that had at least 20 hours of sampling effort in both atlases (Cadman *et al.*, 1987 & 2007). I excluded squares containing more than 10% lake area (e.g., squares bordering the Great Lakes) and wedge-shaped UTM quadrats to reduce confounding area effects.

Using the species classification in Cadman *et al*., (2007), species were classified as either forest / woodland species, wetland species, shrub / early successional species, or open habitat species. The open habitat classification was modified by combining the original grassland, agricultural and open habitat category with the urban and suburban habitat category. The Turkey Vulture (the only unassigned species in the dataset) was included in the open habitat classification. Species richness was calculated individually for forest and open habitat species to test the predictions of the space–for–time substitution (listed in Table 3.1). Individual species are referred to by common name only. The common and scientific names for all species can be found in Appendix A.

Time-series land cover dataset

The time-series land cover dataset for the SLI ecosystem consists of four satellite land cover maps covering the time period from 1990 to 2005 at 5-year intervals. Satellite data were from Landsat 5 Thematic Mapper (TM) at 30 m resolution. Data from each TM scene were adjusted to top-of-atmosphere reflectance using published parameters on solar irradiance, earth-sun distance given the scene date, and sensor gain and offset in each spectral band used for change detection (including red, near infrared, and shortwave infrared bands). This scene normalization procedure reduces the likelihood that scene-to-scene differences could be spurious effects resulting from sensor degradation through time or variations in solar output. Atmospheric haze was eliminated using the Haze Optimized Transform (Zhang *et al.*, 2002). The time-series was created by producing a baseline land cover map for 2000 and updating (or backcasting) this map for 1990, 1995 and 2005 using change detection with signature extension (Fraser *et al.*, 2009 and Fraser, pers. comm.). In the SLI ecosystem there are 13 tree-dominated (forest) classes, two shrub and herb-dominated classes, and one wetland class. There are also four human-dominated classes including two agricultural crop classes, a class representing urban and built-up and a disturbance class.

Change in the amount of natural area

The amount of natural area was measured as the area of each OBBA square that was covered by natural land cover types including forests, wetlands and non-agricultural field. Change for each square was measured by subtracting the area of natural land cover in 1990 from the area of natural land cover in 2005 within each OBBA square (ignoring changes among individual classes).

Confounding potential drivers of species richness change

I measured habitat heterogeneity by calculating the Shannon diversity of land cover classes for each OBBA square in 1990 and 2005 using the Shannon index (Pielou, 1969),

$$H = -\Sigma p_i \log_2 p_i \qquad (1)$$

where p_i is the proportion of the square occupied by land cover i. Change in Shannon diversity was assessed by subtracting the value for 1990 from the value for 2005. I also measured the total length of edge in meters of natural area (where all natural land covers were pooled together) within each square for 1990 and 2005 and measured change between the two time periods.

I resampled all raw land cover data to 100 m resolution to match the data used in Chapter 1. All geographic data were processed using ArcInfo Grid 9.3 (Environmental Systems Research Institute, 2008).

The effect of metapopulation dynamics

Metapopulation processes of local extinction and colonization are expected to continue despite potential trends in habitat loss or gain within any individual grid cell. As a consequence of metapopulation processes, a species may be absent from a grid cell during the 1981-1985 atlas period because of stochastic local extinction and regardless of the availability of extensive suitable habitat. If so, this species may be likely to appear despite some losses of its suitable habitat. If local species presence depends on metapopulation-like processes of local extinction and colonization that are related to neighbourhood occupancy and habitat area, metapopulation models should predict observed richness change. To test the prediction that metapopulation processes drive change in species richness, I first calculated predicted species richness for each square in the SLI ecosystem in 2005 by summing the probability that each species would be present in a given square in 2005. The probabilities were derived by fitting a generalized linear model (family = binomial and link = logit) for each species individually using data from the 537 OBBA squares outside the SLI ecosystem. The models included the species' presence in the previous OBBA (1985), its neighbourhood occupancy, the species-specific habitat area and all possible interactions:

$$P_{05} \sim P_{85}+H+P_{85}:H+N_{85}+P_{85}:N_{85}+H:N_{85}+P_{85}:H:N_{85} \qquad (2)$$

where P_{05} is species presence in the 2005 OBBA, P_{85} is species presence in the 1985 OBBA, H is the area of habitat generalized from 1985 to 2005 by using the Ontario Ministry of Natural Resources land cover product (OMNR, 2002), N_{85} is the proportion of neighbouring squares occupied by conspecifics in the first (1985) OBBA. Variables connected by colons represent multiplicative interactions. The equations from these models were used to predict the probability of presence per OBBA square within the SLI ecosystem for each species using the predict.glm function in R (R Development Core Team, 2010).

I assessed neighbourhood occupancy for each species by tallying the number of neighbouring squares occupied by conspecifics in the 1985 OBBA within a neighbourhood extending two squares (20 km) in each direction. Since not all squares met the inclusion criteria (e.g., due to undersampling or water), I expressed neighbouring occupancy as the proportion of occupied neighbouring squares among those censused. The area of species-specific habitat was assessed as the total area of potentially suitable land covers (not simply natural vs. human-dominated cover) in each square using the Ontario Provincial-Scale Land Cover data set (OMNR, 2002). I determined which land covers were potentially suitable for each species based on the habitat descriptions in The Birder's Handbook (Ehrlich *et al*, 1988). I subtracted observed species richness in 1985 from predicted 2005 richness to measure predicted change in species richness. For more details regarding development of the metapopulation models, please refer to the methods section of Chapter 2.

Statistical analysis

I fit ordinary least squares (OLS) regression models to test the predictions in Table 3.1. I included change in effort (number of hours spent recording birds in a given OBBA square) as a covariate in all regression models because it varies spatially and temporally throughout the study area. The direction of the effect of change in natural area was assessed by the sign of the partial slope after accounting for change in effort. OLS models were also used to assess the relationship between change in species richness and the potentially confounding covariates (change in habitat heterogeneity and change in edge length) as well as the relationships between change in species richness, predicted change in species richness and change in natural area.

Failure to account for spatial autocorrelation can lead to incorrect estimates of coefficients as well as incorrect assessment of the relative strength of predictor variables (Diniz-Filho *et al*., 2003; Kühn, 2007). Changes in bird richness are spatially autocorrelated (rho = 0.47), so I also fit conditional autoregressive models (CAR) using the spdep package (Bivand *et al.,* 2010) in R. See Szabo *et al.*, (2009) for more details regarding the methods used for fitting the conditional autoregressive models. All statistical analyses were performed using R, version 2.12.1 (R Development Core Team, 2010).

RESULTS

Response to change in natural area

The spatial relationship between species richness and natural area within the SLI ecosystem, like the broader pattern found in Chapter 1, was peaked at approximately 50% natural area (Figure 3.3). After controlling for effort, the relationships for forest bird richness and open bird richness followed the non-linear responses expected for their respective species–area curves.

I expected bird richness to increase in sites where changes in natural area through time moved toward the 56% peak observed in spatial relationships. Conversely, I expected bird richness to decrease when the extent of natural habitat changed away from that 56% peak. Loss of natural area should cause forest bird species richness to decline, but much more so below the threshold of 56% habitat extent. Similarly, I expected the number of open habitat birds to increase more quickly with natural area loss up until the threshold of 56% natural area was reached. Most of these predictions failed (Table 3.2) because bird species richness increased with natural area loss when the sites initially had greater than 56% natural area. When natural area was less than 56% in 1985, bird richness change, regardless of habitat affiliation, was not significantly related to change in natural area (Figure 3.4). Interestingly, forest bird richness generally increased while open habitat bird richness more often decreased (but decreased less in areas with less natural area) (Figure 3.4). Some spatial autocorrelation remained in the residuals from the OLS models that related change in total species richness to change in sampling effort and change in natural area. However, accounting for space using conditional autoregressive models had little impact on any of the estimated regression coefficients and did not alter the statistical conclusions.

Confounding potential drivers of species richness change

Changes in habitat heterogeneity and length of edge could not account for the unexpected negative relationship between change in richness and change in natural area. Although species richness increased with decreasing natural area, this effect could arise because of confounding effects of changes to habitat heterogeneity or the amount of edge habitat, which could have overwhelmed signals attributable to changing natural area. However, changes in habitat heterogeneity were not significantly related to loss or gain of natural area ($r = -0.08$, $p = 0.46$), which was itself positively related to changes in the length of habitat ($r = 0.41$, $p < 0.0001$). After controlling for sampling effort, changes in species richness were not related to temporal variation in either habitat heterogeneity or edge length (slope = -31.29, $t = -1.24$, $p = 0.22$, df = 82 for change in habitat heterogeneity; slope = -0.08, $t = -1.77$, $p = 0.08$, df = 82 for change in edge length; Figure 3.5). Although some spatial autocorrelation remained in the residuals of the model including change in habitat heterogeneity, the results did not change after accounting for space (slope = -32.5, $p = 0.28$ for change in habitat heterogeneity; slope = -0.02, $p = 0.79$ for change in edge).

To better understand how specific species contributed to the relationship between change in richness and change in natural area, I divided change in natural area into five equally sized bins such that each resulting quintile included 17 quadrats. Change in natural area ranged from -4.43 km^2 to -2.13 km^2 in the first quintile, from -2.13 to -1.15 in the second quintile, -1.15 to -0.76 in the third quintile, -0.76 to -0.30 for the fourth quintile and from -0.30 to 0.67 in the fifth quintile. For each quintile, I tallied for each species (organized by the species classifications described in the methods section) the number of quadrats within which it appeared or disappeared (Table 3.3). Only species that appeared or disappeared in at least five quadrats in any quintile are discussed.

Overall, open habitat species tended to appear in the first and second quintiles and/or disappear in the fourth and fifth quintiles as expected from the spatial species – area relationship for open habitat birds. The open habitat species that contributed the most to the observed pattern were the American Kestrel, Upland Sandpiper, Common Nighthawk, Horned Lark, Purple Martin, Northern Rough-Winged Swallow, Bank Swallow, Cliff Swallow, Vesper Sparrow, Turkey Vulture, House Finch and Eastern Bluebird. The House Finch, an exotic species, increased in all quintiles of change in natural area, but increased more in the first and second quintiles. Only the pattern for the Eastern Bluebird did not conform to expectation as it tended to appear in all quintiles, likely because it is recovering from being quite rare (though there remains concern regarding its status due to competition with European Starlings and House Sparrows; Ehrlich *et al.*, 1988; Cadman *et al.*, 2007).

Many of the forest bird species that contributed the most to the pattern of change in species richness were species that can inhabit or prefer open woodland, forest edges, parks, orchards or residential neighbourhoods. These include Wild Turkey, Northern Goshawk, Broad-Winged Hawk, Eastern Screech-Owl, Great Horned Owl, Ruby-Throated Hummingbird, Red-Headed Woodpecker, Pileated Woodpecker, Olive-Sided Flycatcher, Yellow-Throated Vireo, Common Raven, Golden-Crowned Kinglet, Hermit Thrush, Black-Throated Blue Warbler, Black-Throated Green Warbler, Magnolia Warbler, Pine Siskin and Evening Grosbeak. Of these, many increased (or decreased less) in the first and second quintiles, contributing to the unexpected increase in forest bird richness in the areas that lost the most natural land cover.

A number of forest species responded as expected by increasing in the higher quintiles and/or decreasing in the lower quintiles (Yellow-Rumped Warbler, Blackburnian Warbler, Pine Warbler, and Canada Warbler) despite being able to inhabit open woodland (Northern Parula, Magnolia Warbler and Mourning Warbler). Surprisingly, many species that prefer mixed, dense or mature forest still increased considerably in the first quintile. These include the Yellow-Belied Sapsucker, Solitary Vireo, Winter Wren, Red-Breasted Nuthatch, and Ruby-Crowned Kinglet.

Many forest species did not respond as expected to change in natural area at least in part due to considerable expansions of their distributions and improvements in the conservation status of their populations. The Sharp-Shinned Hawk, Cooper's Hawk and Northern Goshawk are expanding their ranges as their populations are recovering since the ban of DDT (Ehrlich *et al.*, 1988). Similarly, the North American populations of the Red-Shouldered Hawk, who were previously listed as Special Concern under COSEWIC in 1996, are stable or increasing throughout much of their range and are now listed as Not at Risk (COSEWIC, 2010). Perhaps the most impressive recovery has been that of Wild

Turkey. After being extirpated from Ontario by 1909 due to habitat loss and overhunting, Wild Turkey was only observed in a handful of sites in the 1985 OBBA. Wild Turkey is now widespread throughout the mixedwood plains ecozone as a result of a successful restoration program led by the Ontario Ministry of Natural Resources (Cadman *et al*., 2007).

The effect of metapopulation dynamics

The observed changes in species richness were positively and strongly related to (but exceeded somewhat) changes predicted from the metapopulation model ($r^2 = 0.56$, slope = 1.34, $p < 0.001$; Figure 3.6). Change in sampling effort and change in natural area, on the other hand, accounted for 19% and 14% of the variance, respectively. The slope of the relationship between observed change in richness and predicted change in richness was significantly greater than one ($t = 2.66$, $p < 0.05$) meaning that the predictions of change slightly under predict observed change in richness. Interestingly, richness change predicted from the metapopulation model was also negatively related to change in natural area (slope -3.03, $t = -3.12$, $p = 0.002$; Figure 3.6), which suggests that the sites that experienced the greatest losses of natural area were those where previously (in 1985) locally absent species had a high likelihood of being present in 2005. The relationships between predicted change in species richness and observed change in richness as well as change in natural area are similar when looking at only forest birds or open habitat birds. The slopes of the relationships between predicted change in forest bird richness and change in natural area, and predicted change in open habitat bird richness and change in natural area are -1.37 and -0.55, respectively. Both slopes are somewhat shallower than the slopes between observed change in species richness for both groups and change in natural area.

DISCUSSION

Species richness did not respond to natural area loss in the directions predicted by the spatial relationship between species richness and natural area, however species richness did change as predicted by the metapopulation models. Though the spatial pattern between species richness and natural area in the SLI ecosystem was peaked like the broader regional pattern, species richness tended to increase with decreasing natural area regardless of the initial amount of natural area and the species group (forest vs. open habitat species). This seems to have occurred for two reasons; the first is that the sites that lost more natural area were also those where species had a high likelihood of being present based on the proportion of surrounding sites that were occupied by conspecifics in the first OBBA and the amount of species-specific habitat. The second reason is that many forest species that occur in the SLI ecosystem can inhabit more open types of forest and even human-dominated areas, including recreation areas, orchards and residential neighbourhoods. The contributions of both phenomena to the unexpected increase in species richness with loss of natural area carry with them important consequences for conservation and land management.

The role played by metapopulation dynamics in determining local species presence has consequences for species monitoring and the use of species richness as a measure of the biotic response to land cover modification. The results presented here (and in Chapter 2) suggest that there is a certain inherent unpredictability in species presence because it is not only a function of deterministic environmental drivers or sampling effects. The inherent unpredictability in species presence necessarily translates into unpredictability in species richness. Consequently, detecting responses (whether it is in terms of species richness or its individual components) to environmental changes may often be challenged by low "signal to noise" ratios. This further highlights the potential benefits of long-term regular species monitoring to distinguish the signal of the response to environmental change from the inherent variability of species distributions and richness.

The spatial and temporal extent of the land cover changes may have affected the response of forest species to change in that area of natural land cover. The magnitude of the changes in natural area observed here were small (varying between ~ 1 km^2 gains to losses of 4 km^2). Vance *et al*. (2003), in a study regarding the minimum habitat amount necessary for a 50% probability of species' presence, found that 32 of the 41 examined North American forest bird species require more than 100 km^2 (the size of the sampling units in the present study). This indicates that, while small, losses of 4 km^2 of natural area are sufficient to potentially reduce the amount of available habitat below the threshold minimum habitat requirements for many species. Change in species richness was more strongly related to change in natural area than change in habitat heterogeneity, change in the length of natural area edge as well as change in productivity or change in vegetation heterogeneity (results presented in Appendix E). It cannot be ruled out that larger losses of natural area would have resulted in a net loss of forest species. The changes in species richness and natural area occurred over two decades. It is possible that forest species richness at the sites that lost natural area is not yet at equilibrium with the new area of natural land covers. If there remains some extinction debt (Tilman *et al*., 1994), it is possible that a number of additional forest species will become locally extinct.

The analysis presented here cautions that the effects of changing habitat area may readily be masked by interactions across broader landscape regions that reflect metapopulation processes. The unexpected direction of the area effect for many species could be taken to indicate that these species are insensitive to area, but metapopulation processes may be subsidizing local populations and giving them this appearance only. Somewhat ironically, this means that the extinction debt across these landscapes could be much larger than previously thought because it is possible that there are many sink populations (i.e. populations that are only maintained because surrounding areas are occupied by conspecifics). It would be especially imperative to keep the natural area for these surrounding source populations intact. It may also mean something even riskier for conservation: that in some areas species appear to be tolerant of disturbance, but are maintained through metapopulation processes. Such areas may increasingly act as sinks, but the potentially negative effects of habitat loss are masked by immigration from occupied neighbouring sites.

The unexpected increase in forest birds in response to losses of natural area has further important consequences for conservation as it is also a reflection of the plasticity of individual species' land cover selection. Conservation scientists have used species – area relationships to forecast extinction rates from habitat loss (Pimm & Askins, 1995; Brooks & Balmford, 1996; Pimm & Raven, 2000; DeFries *et al.*, 2005; Sala *et al.*, 2005).

However, defining the species pool that corresponds to the specific “habitat” can be quite challenging because many species use a variety of land covers (Pimm *et al*., 1995; see Appendix C as an example). Pimm *et al*. (1995) cautioned against using the species – area relationship to estimate species loss “naïvely”, in part for this reason. In spite of this, the notion that more species are found in larger areas of habitat is central to conservation and land management decisions (Beatley, 2000; Dale *et al*., 2000; Margules & Pressey, 2000). In the SLI ecosystem, only a very small subset of the forest birds responded as expected by disappearing from areas that lost natural cover while many responded in the opposite direction or were unaffected by the change in land cover (Table 3.3). This suggests that the application of the species – area relationship to predict species losses from land cover conversion would have only been successful if the species pool was restricted to exclude any species that can tolerate some human-dominated land cover. This would have reduced the species pool to fewer than ten species, which would render the detection of spatial species – area relationships or temporal changes in richness following change in habitat area difficult. Given the responses of the forest species studied here, these findings suggest that the utility of species – area relationships for estimating species losses due to land cover conversion is likely quite limited in many conservation situations.

Temporal variability in site occupancy poses a substantial challenge for managing and monitoring biodiversity. In the SLI ecosystem, the magnitude of the changes in species richness was greater than could be explained by any of the factors examined here, even metapopulation dynamics. Change in richness varied from losses of 40 species to gains of nearly 60 species. After accounting for change in effort (which varied from an increase of 145 hours to a decrease of 134 hours), one would still expect changes from +49 to -39 species. Although the change in species richness predicted from the metapopulation models explained 56% of the variance in observed change in species richness, it still consistently under predicted the observed change in species richness. Given that there is more variability than can be explained here, I cannot rule out the possibility that further neutral or stochastic processes are operating in the system. In the face of this variability and the pervasive impacts of human land uses on biodiversity across the globe, expanded collection of temporal datasets for both species distributions or abundances and their environmental determinants (at commensurate spatial and temporal scales) will be invaluable to test macroecological theories and improve decision-making regarding land management.

ACKNOWLEDGEMENTS

I am grateful for research support from the Natural Sciences and Engineering Research Council of Canada and the University of Ottawa. Thanks to the official sponsors of the Ontario Breeding Bird Atlas (Bird Studies Canada, Canadian Wildlife Service, Federation of Ontario Naturalists, Ontario Field Ornithologists, and Ontario Ministry of Natural Resources) for supplying Atlas data, and to the thousands of volunteer participants who gathered data for the Ontario Breeding Bird Atlases. In particular I would like to thank Mike Cadman, Denis Lepage and Peter Blancher for providing the Ontario Breeding Bird Atlas data as well as considerable advice regarding analysis of the data. I am grateful to Rob Fraser, Ian Olthof, Darren Pouliot and Andrea Clouston at the Canada Center for Remote Sensing for providing the land cover maps for

St-Lawrence Islands greater park ecosystem.

TABLES

Table 3.1: Predictions from the space–for–time substitution for the relationship between change in species richness and change in natural area based on the initial area of natural land covers and species' habitat affiliations.

	Initially less than 56% natural area	Initially greater than or equal to 56% natural area
All species	1a) Positive	1b) Negative
Forest species	2a) Positive	2b) Unrelated
Open habitat species	3a) Unrelated	3b) Negative

Table 3.2: The response of change in bird richness to change in natural area in 85 Ontario Breeding Bird Atlas (OBBA) squares in the SLI ecosystem of Ontario, Canada. The slope of the effect of change in natural area with the associated p value is presented for sites that initially had less than 56% natural area (Below), sites that initially had greater than or equal to 56% natural area (Above) and all sites after controlling for change in effort. Also presented are the coefficients of determination (R^2) for the models, which included change in sampling effort and change in natural area, and the acceptance or rejection of the related predictions from Table 3.1. The significant slopes ($p<0.05$) and coefficients of determination† for conditional autoregressive models are presented in parentheses. Non-significant slopes are indicated by NS.

Species group		**Slope**	**R^2**	**Prediction**
All species	Below	NS (NS)	0.18 (0.16)	1a: Rejected
	Above	-10.65 (-10.65)	0.45 (0.40)	1b: Not rejected
	All sites	-5.05 (-4.85)	0.28 (0.19)	
Forest species	Below	NS (NS)	0.19 (0.16)	2a: Rejected
	Above	-4.64 (-4.70)	0.32 (0.27)	2b: Rejected
	All sites	-1.93 (-2.10)	0.21 (0.15)	
Open habitat species	Below	NS (NS)	0.10 (0.10)	3a: Accepted
	Above	-1.81 (-1.88)	0.41 (0.40)	3b: Accepted
	All sites	-0.95 (-1.05)	0.23 (0.18)	

†The coefficients of determination for the conditional autoregressive models represent the variance uniquely explained by the predictors (excluding that which is shared with space).

Table 3.3: The individual species contributions to the pattern of change in species as a function of change in natural area. Change in natural area was divided into five equally sized bins such that each resulting quintile included 17 quadrats. Change in natural area ranged from -4.43km^2 to -2.13km^2 in the first quintile, from -2.13 to -1.15 in the second quintile, -1.15 to -0.76 in the third quintile, -0.76 to -0.30 for the fourth quintile and from -0.30 to 0.67 in the fifth quintile. Within each quintile, the number of quadrats within which a given species disappeared (Lost) or appeared (Gained) was tallied for each open habitat bird species and each forest bird species.

	Quintile	First		Second		Third		Fourth		Fifth	
Habitat	Common name	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained
Open	Red-tailed Hawk	0	2	0	0	0	1	1	1	2	0
Open	American Kestrel	0	1	0	0	3	0	6	1	4	0
Open	Gray Partridge	4	0	1	0	0	0	1	0	2	0
Open	Ring-necked Pheasant	1	3	2	1	0	2	2	3	0	4
Open	Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Open	Killdeer	0	0	0	0	2	0	1	0	4	0
Open	Upland Sandpiper	3	1	8	0	3	2	2	2	2	0
Open	Short-eared Owl	0	0	1	0	0	0	2	0	2	0
Open	Common Nighthawk	5	5	9	1	4	2	4	0	8	1
Open	Eastern Phoebe	0	1	0	0	0	0	0	0	0	0
Open	Eastern Kingbird	0	1	0	0	0	0	0	0	1	0
Open	Horned Lark	5	1	5	0	2	3	4	1	4	0
Open	Purple Martin	3	4	2	1	5	3	5	2	5	1
Open	Northern Rough-winged Swallow	1	2	3	5	2	0	7	0	5	1
Open	Bank Swallow	0	4	5	0	6	2	5	1	9	1
Open	Cliff Swallow	2	2	4	2	5	1	4	2	5	0

	Quintile	First		Second		Third		Fourth		Fifth	
Habitat	Common name	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained
Open	Barn Swallow	0	1	0	0	0	0	1	0	0	0
Open	Eastern Bluebird	1	5	0	5	0	7	1	4	2	3
Open	Vesper Sparrow	3	1	5	0	2	1	1	0	4	1
Open	Savannah Sparrow	0	1	0	0	0	0	1	0	2	1
Open	Grasshopper Sparrow	2	3	1	3	0	3	1	2	1	3
Open	Henslow's Sparrow	1	0	0	0	0	0	2	0	2	0
Open	Bobolink	0	1	0	0	1	0	1	0	0	0
Open	Eastern Meadowlark	0	1	0	0	3	0	0	2	1	0
Open	Western Meadowlark	0	0	0	0	1	0	0	0	0	0
Open	Brewer's Blackbird	0	0	0	0	0	0	0	1	0	0
Open	Common Grackle	0	1	0	0	0	0	0	0	0	0
Open	Brown-headed Cowbird	0	1	0	0	1	0	0	0	1	0
Open	Turkey Vulture	0	10	0	6	0	2	2	1	0	0
Open	Rock Pigeon	0	1	0	0	1	1	0	1	0	1
Open	Mourning Dove	0	1	0	0	0	3	1	1	0	3
Open	Chimney Swift	6	1	6	0	3	2	7	0	9	2
Open	American Crow	0	0	0	0	0	0	0	0	0	0
Open	Black-capped Chickadee	0	1	0	0	0	0	0	0	0	0
Open	European Starling	0	0	0	0	0	0	0	0	0	0
Open	House Finch	0	12	0	13	0	7	0	9	0	7
Open	House Sparrow	0	0	0	0	4	1	3	1	2	0
WF	Sharp-shinned Hawk	2	9	1	6	2	6	5	4	5	5
WF	Cooper's Hawk	2	8	2	6	3	5	5	2	6	3
WF	Northern Goshawk	1	5	2	4	2	3	2	2	3	1
WF	Red-shouldered Hawk	1	8	2	6	1	3	1	4	2	8
WF	Broad-winged Hawk	2	6	5	5	3	3	5	4	3	3
WF	Ruffed Grouse	0	0	0	2	0	2	0	1	2	0
WF	Spruce Grouse	0	0	0	0	0	0	0	0	0	0
WF	Wild Turkey	0	16	0	15	0	14	0	11	0	10

	Quintile	First		Second		Third		Fourth		Fifth	
Habitat	Common name	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained
WF	American Woodcock	2	0	1	2	0	3	3	3	3	0
WF	Eastern Screech-Owl	2	3	3	7	2	3	2	1	2	3
WF	Great Horned Owl	6	4	4	2	3	2	6	2	7	2
WF	Barred Owl	1	11	1	4	0	6	4	8	3	6
WF	Long-eared Owl	2	3	3	1	2	2	5	0	3	2
WF	Northern Saw-whet Owl	4	4	5	1	8	3	7	3	10	0
WF	Whip-poor-will	7	1	7	1	6	2	2	2	7	0
WF	Ruby-throated Hummingbird	0	6	1	0	0	2	0	1	1	1
WF	Red-headed Woodpecker	3	0	4	0	4	1	4	1	7	0
WF	Red-bellied Woodpecker	0	1	0	1	0	3	0	2	0	1
WF	Yellow-bellied Sapsucker	1	4	0	0	0	3	0	0	0	2
WF	Downy Woodpecker	0	3	0	0	0	0	0	0	0	0
WF	Hairy Woodpecker	0	2	0	1	0	0	0	0	0	0
WF	Black-backed Woodpecker	0	0	1	3	1	1	0	0	1	0
WF	Northern Flicker	0	1	0	0	0	0	0	0	0	0
WF	Pileated Woodpecker	0	7	1	6	0	0	0	2	0	0
WF	Olive-sided Flycatcher	2	3	3	4	3	0	5	0	2	1
WF	Eastern Wood-Pewee	0	1	0	0	0	0	1	0	0	0
WF	Acadian Flycatcher	0	0	0	0	0	0	0	0	0	0
WF	Least Flycatcher	0	0	0	1	0	0	0	0	0	0
WF	Great Crested Flycatcher	0	1	0	0	0	0	0	0	0	0
WF	Yellow-throated Vireo	1	7	3	2	3	1	6	1	3	2
WF	Solitary Vireo	1	5	1	6	1	6	1	3	0	6

	Quintile	First		Second		Third		Fourth		Fifth	
Habitat	Common name	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained	Lost	Gained
WF	Warbling Vireo	0	1	0	0	0	0	2	0	1	0
WF	Philadelphia Vireo	0	0	1	2	2	2	1	1	0	3
WF	Red-eyed Vireo	0	0	0	0	0	0	0	0	0	0
WF	Gray Jay	0	0	0	1	1	1	1	1	0	0
WF	Common Raven	0	14	0	12	0	6	0	9	1	8
WF	Boreal Chickadee	0	0	0	0	0	0	0	0	0	0
WF	Tufted Titmouse	0	0	0	0	0	0	0	0	0	0
WF	Red-breasted Nuthatch	2	5	0	1	1	4	0	7	0	3
WF	White-breasted Nuthatch	0	1	0	0	0	2	1	0	0	0
WF	Brown Creeper	2	4	2	2	0	5	5	4	2	2
WF	Winter Wren	1	8	0	6	1	3	1	4	3	4
WF	Golden-crowned Kinglet	1	7	2	4	2	4	2	3	0	3
WF	Ruby-crowned Kinglet	3	4	1	3	1	3	5	0	2	0
WF	Blue-gray Gnatcatcher	1	1	0	2	0	2	1	0	0	2
WF	Veery	0	0	0	0	0	0	0	1	0	0
WF	Swainson's Thrush	1	0	0	0	0	3	2	1	1	0
WF	Hermit Thrush	1	6	0	3	0	1	3	4	0	4
WF	Wood Thrush	0	0	0	0	0	0	3	0	0	0
WF	Tennessee Warbler	0	0	0	0	0	2	1	0	0	0
WF	Nashville Warbler	0	1	0	1	1	1	0	2	0	0
WF	Northern Parula	0	1	1	1	1	0	1	2	2	4
WF	Magnolia Warbler	3	6	3	7	1	6	1	7	0	8
WF	Cape May Warbler	0	0	0	0	1	1	0	0	1	1
WF	Black-throated Blue Warbler	2	5	0	8	1	3	0	2	1	3
WF	Yellow-rumped Warbler	1	3	0	1	1	5	1	6	0	4
WF	Black-throated Green Warbler	1	7	2	2	0	4	0	4	0	6

Habitat	Quintile / Common name	First Lost	First Gained	Second Lost	Second Gained	Third Lost	Third Gained	Fourth Lost	Fourth Gained	Fifth Lost	Fifth Gained
WF	Blackburnian Warbler	5	3	3	3	2	1	2	2	1	3
WF	Pine Warbler	0	6	1	6	0	7	0	8	1	7
WF	Bay-breasted Warbler	0	0	0	0	0	2	1	0	0	0
WF	Cerulean Warbler	1	1	0	1	1	3	2	1	2	3
WF	Black-and-white Warbler	0	0	0	1	0	0	0	1	0	0
WF	American Redstart	0	1	2	0	1	0	0	0	0	1
WF	Ovenbird	0	0	0	0	0	0	0	0	0	0
WF	Louisiana Waterthrush	0	0	0	1	0	0	1	0	0	0
WF	Mourning Warbler	6	2	3	3	3	4	3	3	3	2
WF	Hooded Warbler	0	0	0	0	0	0	0	0	0	0
WF	Canada Warbler	7	1	7	1	3	3	4	2	2	3
WF	Scarlet Tanager	0	3	0	2	1	0	2	0	0	0
WF	Chipping Sparrow	0	0	0	0	0	0	0	0	0	0
WF	Rose-breasted Grosbeak	0	0	0	0	0	0	0	0	0	0
WF	Orchard Oriole	0	0	0	0	0	0	0	1	1	1
WF	Baltimore Oriole	0	1	0	0	0	0	2	0	1	0
WF	Purple Finch	0	2	1	2	0	2	1	2	0	3
WF	Red Crossbill	2	0	1	3	3	3	2	1	2	1
WF	White-winged Crossbill	0	1	0	0	0	2	1	1	2	0
WF	Pine Siskin	5	1	2	4	4	0	11	1	9	1
WF	Evening Grosbeak	3	5	4	5	2	5	2	1	3	4

FIGURES

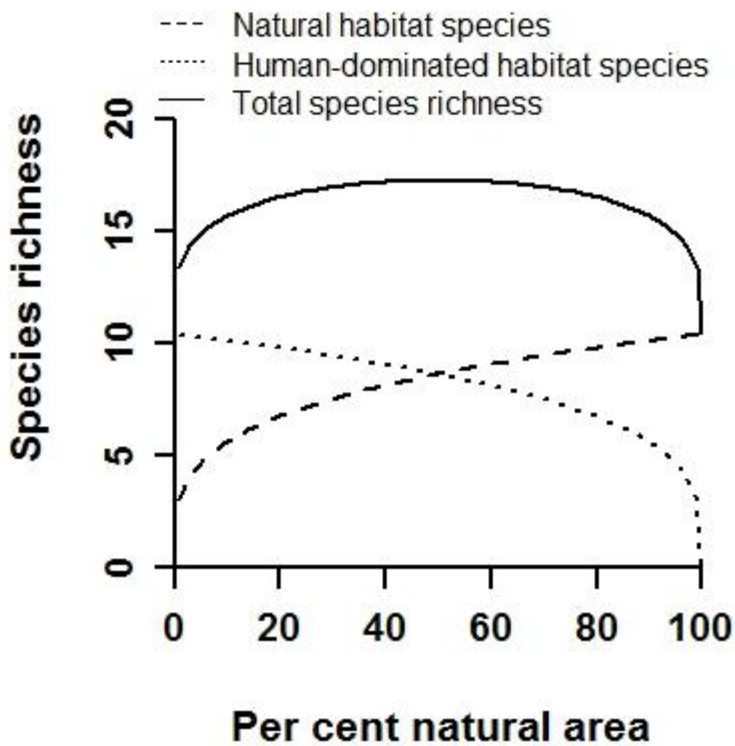


Figure 3.1: Theoretical species–area curves for two broad habitat types, natural habitat and human-dominated habitat (1-natural habitat), and the relationship between total richness and natural area. The species–area curves were generated using $S = cA^z$. I assumed that c for the natural habitat (which is related to the size of the species pool for that habitat) was equal to c for the human-dominated habitat and set it to 3. I used the same scaling coefficient z for both habitat types and set it to 0.27. This is the value used by Preston (1962) and is in the mid-range of empirically derived z values (MacArthur & Wilson, 1967)

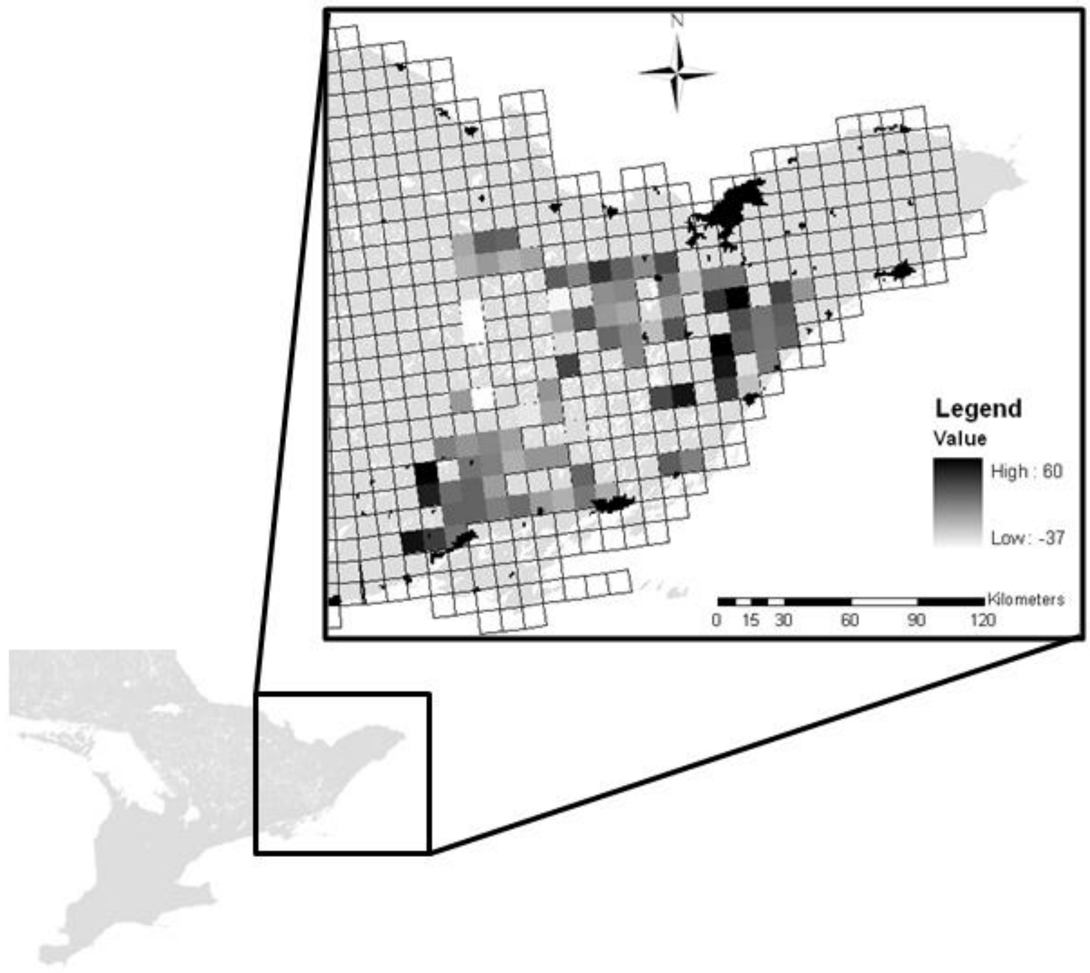


Figure 3.2: Change in bird richness in the SLI (St. Lawrence Islands) ecosystem in Eastern Ontario. Change in richness only appears for squares with at least 20 hours of effort in both Breeding Bird Atlases and less than 10% area covered by water. Breeding Bird Atlas squares are outlined in dark gray for excluded squares, which are shown in light gray. Urban areas appear in black. The projection is Lambert Conformal Conic.

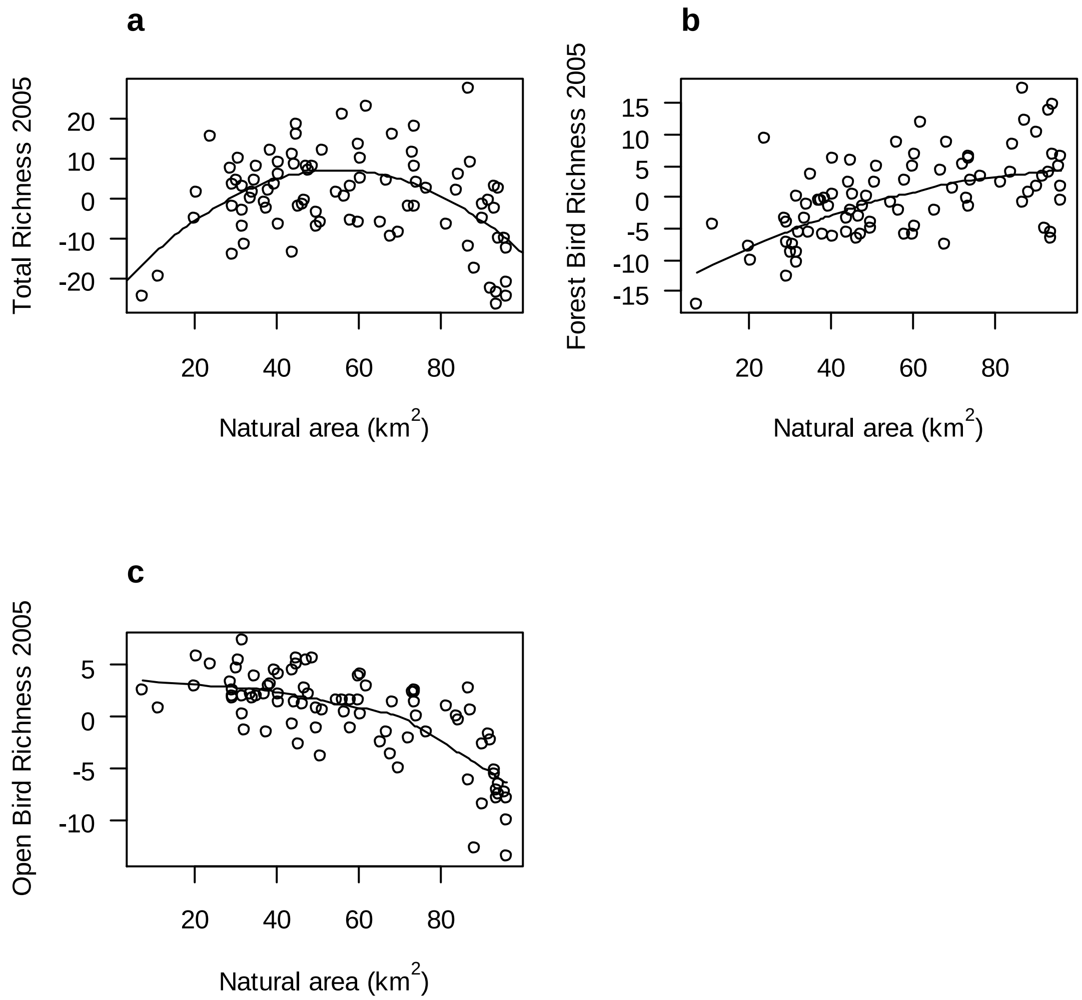


Figure 3.3: The spatial relationship with respect to natural area within the SLI ecosystem for a) total bird richness, b) forest bird richness, and c) open habitat bird richness after controlling for sampling effort. The residuals from linear models including only species richness and natural area were used as the dependent variables shown here for plotting purposes only. This resulted in negative estimates of species richness.

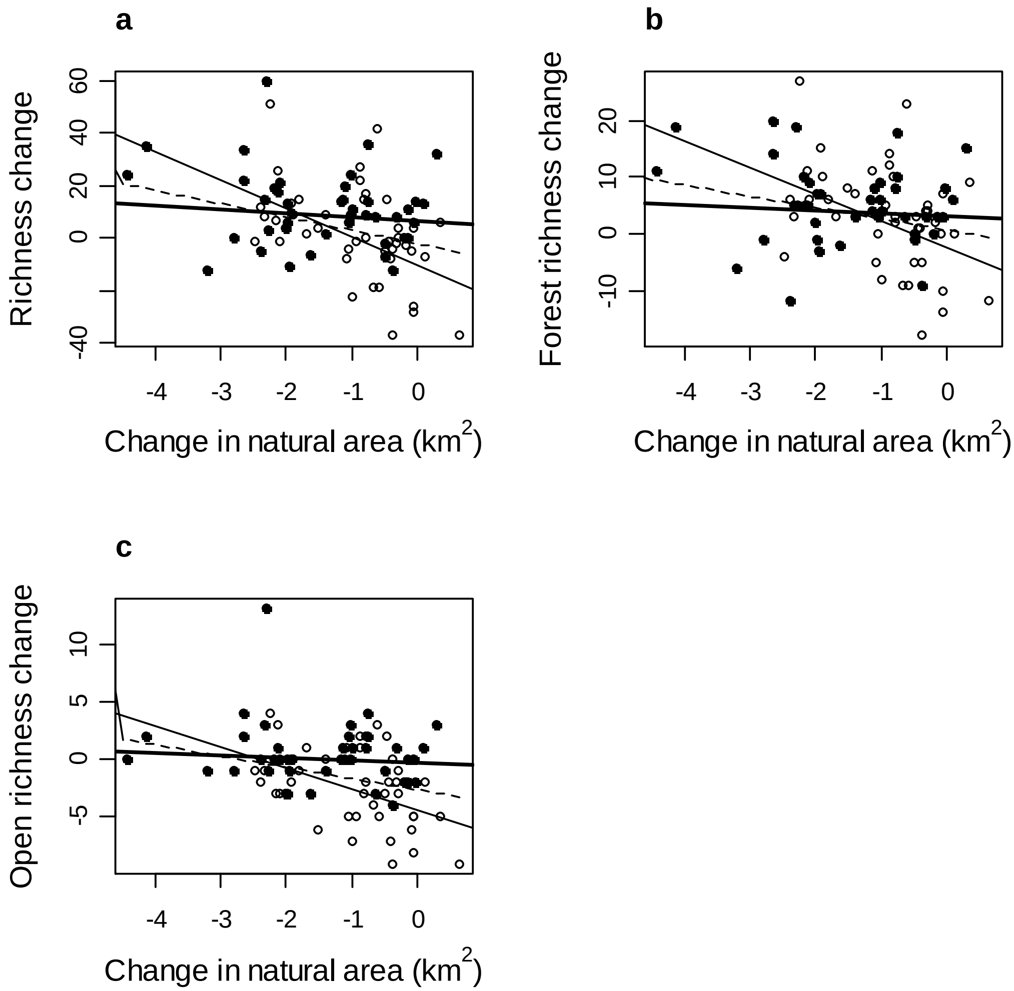


Figure 3.4: Change in bird richness (by habitat affiliation: a) all species, b) forest species and c) open habitat bird species) as a function of change in natural area for sites that initially had greater than 56% natural area (empty circles, fine solid line), sites that initially had less than 56% natural area (filled circles, bold line) and all sites taken together (dashed line). Only the relationships for the sites that initially had greater than 56% natural area and all sites taken together are significant ($p<0.05$).

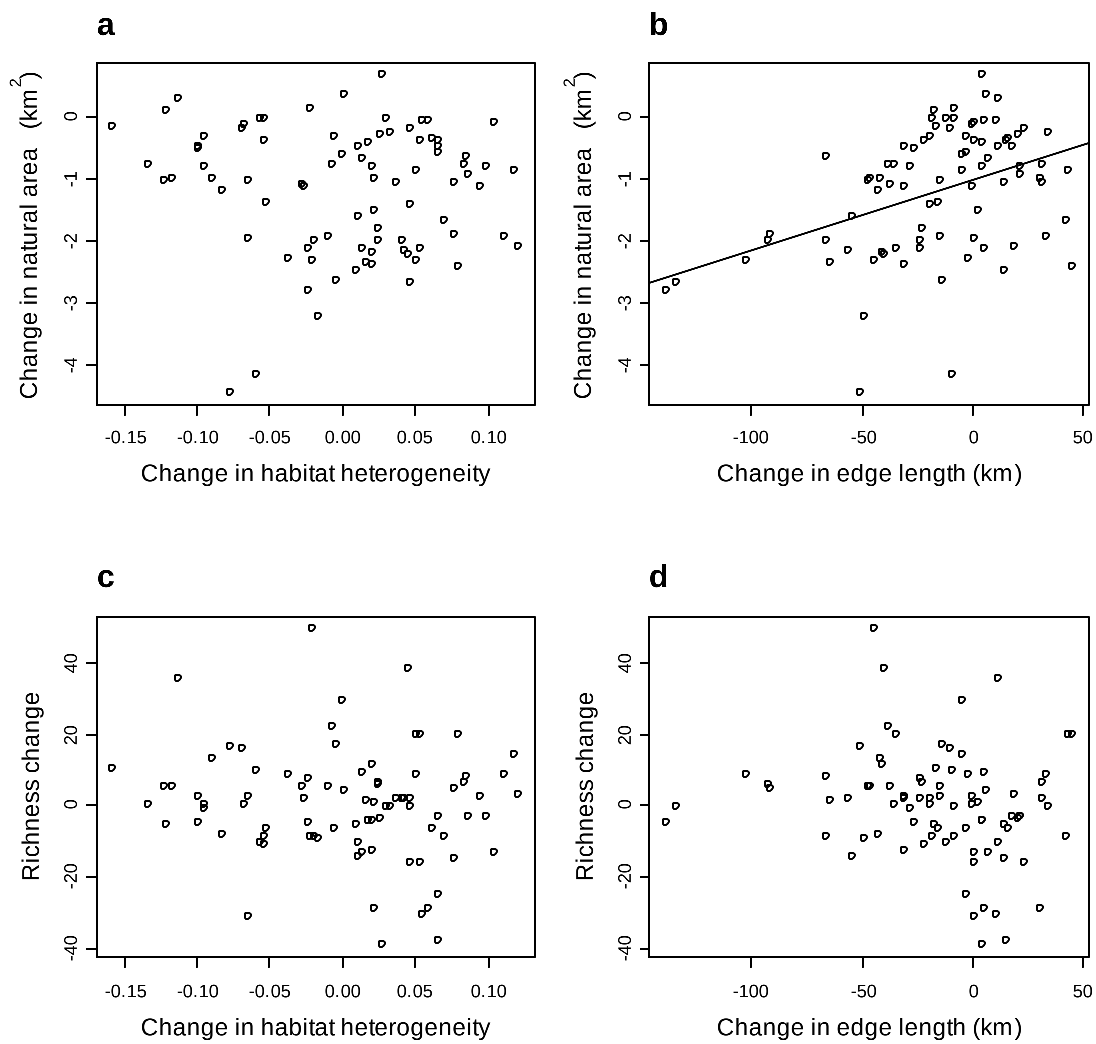
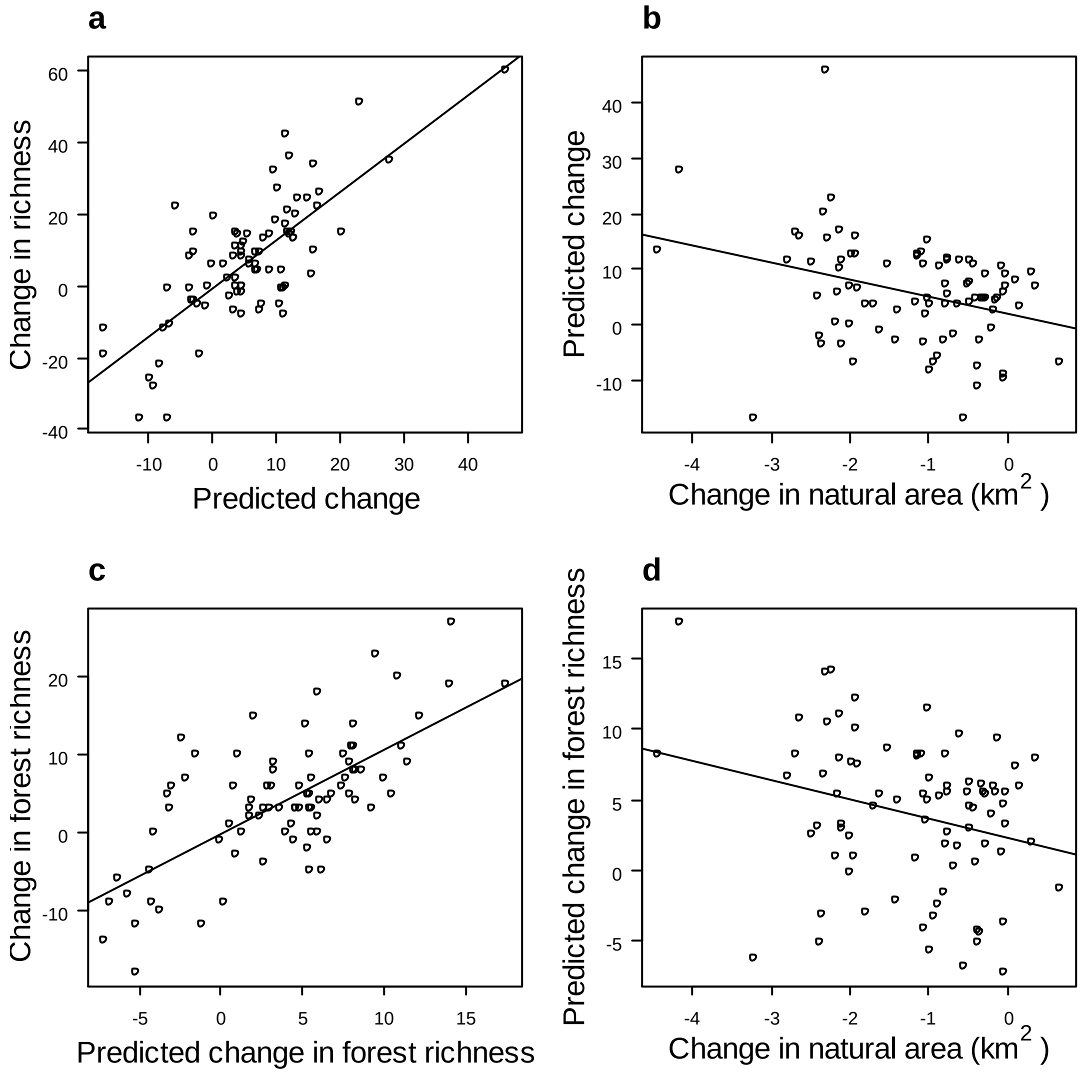
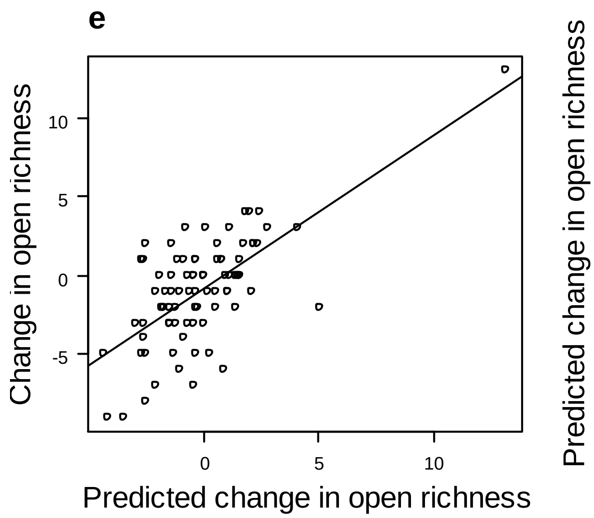


Figure 3.5: The relationship between change in natural area and a) change in Shannon diversity and b) change in edge length fitted with Loess smoothing lines. The response of bird richness to change in c) habitat heterogeneity and d) change in edge length for 85 Ontario Breeding Bird Atlas squares in the greater park ecosystem of St. Lawrence Islands National Park, Ontario, Canada.

Figure 3.6: The relationships between observed change in species richness and the change in richness predicted from the metapopulation models (using richness in 2005 predicted by the models minus observed richness in 1985) for a) all species, c) forest species and e) open habitat species. Also shown are the relationships between predicted change in species richness for b) all species, d) forest species and f) open habitat species as a function of change in natural area. Each is fitted with a linear least squares smoothing line.



a
Change in richness
Predicted change
b
Predicted change
Change in natural area (km^2)
c
Change in forest richness
Predicted change in forest richness
d
Predicted change in forest richness
Change in natural area (km^2)


e
Change in open richness
10
5
0
-5
0
5
10
Predicted change in open richness
f
Predicted change in open richness
10
5
0
-4
-3
-2
-1
0
Change in natural area (km2)

CONCLUSIONS

In this thesis, I set out to gain a better understanding of how avian richness responds to conversion of natural areas to human-dominated forms and how metapopulation dynamics affect the strength of this relationship. To do so, I built upon a key macroecological pattern, the species – area relationship (Rosenzweig, 1995), and the underlying principles of metapopulation theory (Hanski, 1999). The primary goal of this thesis was to test macroecological hypotheses regarding the processes that govern species richness and species distributions. However, the conservation implications of the findings and how they relate to the protection of biodiversity are also of particular interest.

In the first chapter of this thesis, I found that avian richness in Ontario peaked at 56% natural area in a manner that is consistent with the sum of two species – area relationships, one for natural habitat species and one for human-dominated habitat species. In answer to the questions asked in the introduction to this thesis, it seems that yes, natural cover loss can and does lead to increased species richness. In fact, avian richness increased so long as no more than 44% of the natural area was converted to human-dominated land cover. Up until that point, only two forest species were lost on average, but as many as 20 open habitat bird species were gained.

Interestingly, my finding that avian richness peaks at approximately 50% natural area coincides with a recent conservation target set by the International Boreal Conservation Campaign (http://www.interboreal.org/). This target was selected as a challenging but achievable goal. My findings show that there is a more concrete justification for this target, at least for the protection of avian diversity, as they demonstrate that there are benefits of allowing some human-dominated land cover to be introduced in an area, as much as 40%, before species begin to drop out of the regional assemblages. Conservation actions focusing on specific forest species, such as the Bay-breasted Warbler, the Ruby-crowned Kinglet and the Spruce Grouse, will have to consider that these three species rarely occurred in places with less than 80% natural area. However, as a general guideline, the target minimum of 50% natural area seems promising for the conservation of the majority of bird species

In the second chapter of this thesis, I demonstrated that considering the effect of metapopulation-like processes in creating absences within species ranges helps us to understand why regional richness – environment relationships are weaker than at continental scales. The amount of remaining natural area was the best spatial predictor of avian richness and, as is common for regional richness – environment relationships, it explained less than 40% of the variance in species richness (Chapter 1). I found that the unoccupied but suitable sites within species ranges can largely be explained by metapopulation-like processes of local colonization and extinction. It is the reflection of local absences in the data used to assess regional richness – environment relationships that results in weaker relationships.

A snapshot of the pattern of richness at any given time might therefore often provide a rather poor picture of the number of species that could inhabit an area and, consequently, of the regional pattern of species richness. This carries important consequences for tests of macroecological hypotheses, which often seek to explain the patterns of species richness or, more specifically, to uncover the environmental determinants of species richness in a given area. If species are periodically absent from areas that are in fact environmentally suitable, it will necessarily impact our ability to assess the role that environment plays in determining species richness. My findings in Chapter 2 indicate that pooling presence over repeated surveys may provide a way to improve estimations of species richness and our ability to detect relationships with the environment.

The regional context plays an important role for the maintenance of species distributions. I found that the probability of a species occurring in a given location is dependent on, not only the amount of species-specific habitat area available locally, but also on the number of neighbouring sites that are occupied by conspecifics. Moreover, I found that larger areas of habitat are required for species presence if few of the neighbouring sites have been previously occupied by conspecifics. This is consistent with what we expect from metapopulation theory, where larger and less isolated patches are more likely to be occupied and larger patches represent larger targets for immigrants (Hanski, 1999).

Arguably one of the best ways to know if we understand a system is if we can predict how it will change with time (Peters, 1991; Kerr *et al*., 2007; Fisher *et al*., 2010). In the third chapter of this thesis, I demonstrated that avian richness changed in the way that we would expect from metapopulation dynamics. Sites that were predicted to have a high total probability of species' presence (using the metapopulation models from Chapter 2) gained species while sites that were predicted to have lower total probability of species' presence lost species. The ability of these models to strongly predict the observed change in species richness indicates that they capture many of the important processes that govern species distributions and thereby species richness.

My findings reinforce the idea that land and biodiversity management can be made more effective by considering the regional context. Species richness did not respond to changes in the amount of natural area as would have been expected from the spatial richness – natural area relationship. This occurred in part because the spatial and temporal variability in site occupancy induced by metapopulation dynamics was greater than the deterministic response of species to the land cover change. This may mean that, in many ecological systems, a species community may appear to tolerate disturbance, but is in fact being maintained through metapopulation processes. In this case, the maintenance of the local community depends on the maintenance and management of the surrounding sources of immigrants.

In the face of variability in species presence and the pervasive impacts of human land uses on biodiversity across the globe, the continued collection of temporal datasets for both species distributions or abundances and their environmental determinants will likely prove invaluable to test macroecological theories and will improve decision-making regarding land and biodiversity management. My findings have shown that change in species richness is quite predictable from metapopulation processes. However, effective prediction requires knowing not only how much species-specific habitat is locally available, but also how many of the surrounding areas have been occupied by conspecifics. This requires repeated surveys of species distributions. Accounting for metapopulation dynamics through repeated biodiversity surveys will improve our ability to test macroecological hypotheses regarding spatial and temporal of determinants of species richness. Repeated surveys will also be indispensable for detecting species response to human actions despite low “signal to noise” ratios for spatial and temporal relationships between species richness and its environmental determinants caused by metapopulation dynamics. The continued collection of temporal species datasets will help answer the important challenge of detecting community responses to human actions.

REFERENCES

Algar, A.C., Kharouba, H.M., Young, E.R. & Kerr, J.T. (2009) Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography*, **32**, 22-33.

Arbuckle, J.L. (2007) *Amos 17.0 for SPSS. Amos Development Corporation*. Spring House, Pennsylvania, USA.

Beatley, T. (2000) Preserving biodiversity: Challenges for planners. *Journal of the American Planning Association*, **66**, 5-20.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, Populations and Communities*, 3rd edn. Blackwell Science, Oxford.

Belmaker, J. & Jetz, W. (2010) Cross-scale variation in species richness-environment associations. *Global Ecology & Biogeography*, **20**, 464-474.

Bibby, C.J. (2004) Bird diversity survey methods. *Bird Ecology and Conservation, A Handbook of Techniques* (ed. by W.J. Sutherland, I. Newton and R. Green), pp. 1-16. Oxford University Press, Oxford.

Bivand, R. *et al.* (2010) spdep: spatial dependence: weighting schemes, statistics and models. R Package version 0.5-26. Available at: http://www.r-project.org/ (last accessed March 2011).

Brooks, T. & Balmford, A. (1996) Atlantic forest extinctions. *Nature*, **380**, 115.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597-623

Cadman, M.D., Eagles, P.F.J. and Helleiner, F.M. (1987) *Atlas of the Breeding Birds of Ontario*. Federation of Ontario Naturalists and Long Point Bird Observatory. University of Waterloo Press, Waterloo, Canada.

Cadman, M.D., Sutherland, D.A., Beck, G.G., Lepage, D. & Couturier, A.R. (2007) *Atlas of the Breeding Birds of Ontario, 2001-2005.* Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, and Ontario Nature, Toronto, Canada.

Centre for Topographic Information. (2000) *Digital Elevation Map of Canada*. Natural Resources Canada, Ottawa.

Coops, N.C., Wulder, M.A. & Iwanicka, D. (2009) Exploring the relative importance of satellite-derived descriptors of production, topography and land cover for predicting breeding bird species richness over Ontario, Canada. *Remote Sensing of Environment*, **113**, 668-679.

COSEWIC (2010) Canadian Wildlife Species at Risk. Committee on the Status of Endangered Wildlife in Canada. Web site: http://www.cosewic.gc.ca/eng/sct0/rpt/rpt_csar_e.cfm [accessed 5 April 2011]

Currie, D.J. (1991) Energy and large-scale patterns of animal-species and plant-species richness. *The American Naturalist*, **137**, 27-49.

Czech, B., Krausman, P.R. & Devers, P.K. (2000) Economic associations among causes of species endangerment in the United States. *BioScience*, **50**, 593-601.

Daily, G.C. (2001) Ecological forecasts. *Nature*, **411**, 245.

Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.T., Huntly, N., Naiman, R.J., Reibsame, W.E., Turner, M.G.& Valone, T.J. (2000) Ecological principles and guidelines for managing the use of land. *Ecological Applications*, **10**, 639-670.

DeFries, R., Hansen, A., Newton, A.C. & Hansen, M.C. (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications*, **15**, 19-26.

Desrochers, R.E., Kerr, J.T. & Currie, D.J. (2011) How, and how much, natural cover loss increases species richness. Global Ecology and Biogeography, **20,** 857-867.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53-64.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609-628.

eBird. 2011. eBird: An online database of bird distribution and abundance [web application]. Version 2. eBird, Ithaca, New York. Available: http://www.ebird.org. (Accessed: Date [April 15, 2011]).

Ehrlich, P.R., Dobkin, D.S. & Wheye, D. (1988) *The Birder's Handbook: A field guide to the natural history of North American birds*. Simon & Schuster Inc / Fireside Books, New York, USA.

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 589-606.

ERIN Consulting Ltd. (2000) *NCAD – North American Conservation Areas Database*. MS Access database. Accessed December 2009.

ESRI (Environmental Systems Research Institute, Inc). (2000) ArcView Spatial Analyst 2. Redlands, CA, USA.

ESRI (Environmental Systems Research Institute, Inc). (2008) ArcGIS 9.3. Redlands, California, USA.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132-147.

Fisher, J.A.D., Frank, K.T. & Leggett, W.C. (2010) Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography*, **19**, 1-15.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570-574.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, **161**, 523–536.

Fraser, R.H., Olthof, I. & Pouliot, D. (2009) Monitoring land cover change and ecological integrity in Canada's national parks. *Remote Sensing of Environment*, **113**, 1397-1409.

Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Blackwell Science, Oxford.

Gaston, K.J. & Evans, K.L. (2004) Birds and people in Europe. *Proceedings of the Royal Society of London B*, **271**, 1649-1655.

González-Taboada, F., Nores, C. & Álvarez, M.Á. (2007) Breeding bird species richness in Spain : assessing diversity hypothesis at various scales. *Ecography,* **30**, 241-250.

Gregory, R.D., Gibbons, D.W. & Donald, P.F. (2004) Bird census and survey techniques. *Bird Ecology and Conservation, A Handbook of Techniques* (ed. by W.J. Sutherland, I. Newton and R. Green), pp. 17-56. Oxford University Press, Oxford.

Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B*, **360**, 269-288.

Guilhaumon, F., Gimenez, O., Gaston, K.J. & Mouillot, D. (2008) Taxonomic and regional uncertainty in species–area relationships and the identification of richness hotspots. *Proceedings of the National Academy of Sciences USA*, **105**, 15458-15463.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.

Hijmans, R., Garcia, N. & Wieczorek, J. (2009) GADM database of Global Administrative Areas. GIS Shapefile. Accessed November 2009.

Honkanen, M., Roberge, J.-M., Rajasärkkä, A. & Mönkkönen, M. (2010) Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecology and Biogeography*, **19**, 61-71.

Hortal, J., Rodríguez, J., Nieto-Díaz, M. & Lobo, J.M. (2008) Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography*, **35**, 1202-1214.

Hosmer, D.W. & Lemeshow, S. (2000) Applied Logistic Regression, 2nd edn. John Wiley & Sons, New York.

Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 13384-13389.

Insightful Corporation. (2007) S-PLUS 8.0.4 for Windows. Seattle, Washington, USA.

Kerr, J.T. & Cihlar, J. (2003) Land use and cover with intensity of agriculture for Canada from satellite and census data. *Global Ecology and Biogeography*, **12**, 161-172.

Kerr, J.T. & Cihlar, J. (2004) Patterns and causes of species endangerment in Canada. *Ecological Applications*, **14**, 743-753.

Kerr, J.T. & Currie, D.J. (1995) Effects of human activity on global extinction risk. *Conservation Biology*, **9**, 1528-1538.

Kerr, J.T., Kharouba, H.M., & Currie, D.J. (2007) The macroecological contribution to global change solutions. Science, 316, 1581-1584.

Kerr, J.T. & Ostrovsky, M. (2003) From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution*, **18**, 299-305.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences USA*, **98**, 11365-11370.

Koh, C.-N., Lee, P.-F. & Lin, R.-S. (2006) Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Diversity and Distributions*, **12**, 546-554.

Kühn, I. (2007) Incorporating spatial autocorrelation may invert observed patterns. *Diversity and Distributions*, **13**, 66-69.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, **24**, 564-571.

Lemoine, N., Bauer, H.-G., Peintinger, M. & Böhning-Gaese, K. (2007) Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology*, **21**, 495-503.

Lepczyk, C.A., Flather, C.H., Radeloff, V.C., Pidgeon, A.M., Hammer, R.B. & Liu, J. (2008) Human impacts on regional avian diversity and abundance. *Conservation Biology*, **22**, 405-416.

Lichstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, **72**, 445-463.

Lillesand, T.M., Kiefer, R.W. & Chipman, J.W. (2004) *Remote Sensing and Image Interpretation*, 5th edn. John Wiley & Sons, Inc., Hoboken, NJ, USA.

Luck, G.W. (2007) The relationships between net primary productivity, human population density and species conservation. *Journal of Biogeography*, **34**, 201-212.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243-253.

Martí, R. & del Moral, J.C. (2003) *Atlas de las aves reproductoras de España* . Dirección General de Conservación de la Naturaleza –SEO/BirdLife, Madrid.

Mayer, A.L. & Cameron, G.N. (2003) Landscape characteristics, spatial extent, and breeding bird diversity in Ohio, USA. *Diversity and Distributions*, **9**, 297-311.

Miller, J.R., Groom, M., Hess, G.R., Steelman, T., Stokes, D.L., Thompson, J., Bowman, T., Fricke, L., King, B. & Marquardt, R. (2008) Biodiversity conservation in local planning. *Conservation Biology*, **23**, 53-63.

Morlon, H., Schwilk, D.W., Bryant, J.A., Marquet, P.A., Rebelo, A.G., Tauss, C., Bohannan, B.J. & Green, J.L. (2011) Spatial patterns of phylogenetic diversity. *Ecology Letters*, **14**, 141-149.

OMNR (2002) Ontario Land Cover Data [computer file]. The Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Pärtel, M., Szava-Kovats, R. & Zobel, M. (2011) Dark diversity: shedding light on absent species. *Trends in Ecology and Evolution*, **26**, 124-128.

PCI Geomatics. (2009) GeomaticaVersion 10.2. Richmond Hill, Ontario, Canada.

Pereira, H.M. & Daily, G.C. (2006) Modeling biodiversity dynamics in countryside landscapes. *Ecology*, **87**, 1877-1885.

Peters, R.H. (1991) *A critique for ecology*. Cambridge University Press, Cambridge.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, **20**, 503-510.

Pielou, E.C. (1969) *An Introduction to Mathematical Ecology*. Wiley-Interscience, New York, New York, USA.

Pimm, S.L. & Askins, R.A. (1995) Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences USA*, **92**, 9343-9347.

Pimm, S.L. & Raven, P. (2000) Extinction by numbers. *Nature*, **403**, 843-845.

Pimm, S.L., Russell, G.J., Gittleman, J.L., & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347-350.

Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part II. *Ecology*, **43**, 410-432.

R Development Core Team (2008) *R: A language and environment for statistical computing v.2.7.2.* R Foundation for Statistical Computing, Vienna, Austria.

R Development Core Team (2010) *R: A language and environment for statistical computing v.2.12.1.* R Foundation for Statistical Computing, Vienna, Austria.

Ramankutty, N. & Foley, J.A. (1999) Estimating historical changes in land cover: North American croplands from 1850 to 1992. *Global Ecology and Biogeography*, **8**, 381-396.

Ricklefs, R.E. & Lovette, I.J. (1999) The role of island area *per se* and habitat diversity in the species–area relationship of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142-1160.

Rompré, G., Robinson, W.D., Desrochers, A. & Angehr, G. (2007) Environmental correlates of avian diversity in lowland Panama rain forests. *Journal of Biogeography*, **34**, 802-815.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.

Sala, O.E., van Vuuren, D., Pereira, H.M., Lodge, D., Alder, J., Cumming, G., Dobson, A., Wolters, V. & Xenopoulos, M.A. (2005) Biodiversity across scenarios. *Ecosystems and Human Well-Being: Scenarios, Volume2* (ed. Carpenter, S.R., Pingali, P.L., Bennett, E.M. and Zurek, M.B.), pp. 375-408, Island Press Millennium Ecosystem Assessment, Washington, D.C.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891-904.

Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J. Jr., & Link, W. A. (2011) *The North American Breeding Bird Survey, Results and Analysis 1966 - 2009.* Version 3.23.2011 USGS Patuxent Wildlife Research Center, Laurel, MD, Schreiner, S.M. (2003) Six types of species–area curves. *Global Ecology and Biogeography*, **12**, 441:447.

Stiles, A. & Schreiner, S.M. (2007) Evaluation of species–area functions using Sonoran Desert plant data: not all species–area curves are power functions. *Oikos*, **116**, 1930-1940.

Stutchbury, B. (2007) *Silence of the Songbirds*. Walker & Company, New York.

Szabo, N.D., Algar, A.C. & Kerr, J.T. (2009) Reconciling topographic and climatic effects on widespread and range-restricted species richness. *Global Ecology and Biogeography*, **18**, 735-744.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat extinction and the extinction debt. *Nature*, **371**, 65-66.

Vaïsänen, R. A., E. Lammi, and P. Koskimies. 1998. Distribution, numbers and population changes of Finnish breeding birds. [In Finnish with English summary.] Otavan Kirjapaino, Keuruu, Finland.

Vance, M.D., Fahrig, L. & Flather, C.H. (2003) Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology*, **84**, 2643-2653.

Venter, O., Brodeur, N.N. Nemiroff, L., Belland, B., Dolinsek, I.J. & Grant, J.W.A. (2006) Threats to endangered species in Canada. *BioScience*, **56**, 903-910.

Virkkala, R., Luoto, M., Heikkinen, R.K. & Leikola, N. (2005) Distribution patterns of boreal marshland birds: modelling the relationships to land cover and climate. *Journal of Biogeography*, **32**, 1957-1970.

White, P. & Kerr, J.T. (2006) Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. *Ecography*, **29**, 908-918.

Williams, M.R., Lamont, B.B. & Henstridge, J.D. (2009) Species–area functions revisited. *Journal of Biogeography*, **36**, 1994-2004.

Zhang, Y., Guindon, B. & Cihlar, J. (2002) An image transform to characterize and compensate for spatial variations in thin cloud contamination of Landsat images. *Remote Sensing of Environment***,** **82**, 173-187.

APPENDIX A: List of common and scientific bird names.

Table A1: The common and scientific names for the Ontario breeding bird species studied in this thesis (excluding hybrids). Species are grouped by order and family, and ordered by taxonomy of the AOU (American Ornithologists' Union) to follow the order in which they are presented in the 2005 Ontario Breeding Bird Atlas (OBBA; Cadman *et al.*, 2007). Scientific names are given according to the AOU checklist, 7th edition (American Ornithologists' Union 1998 and the supplements through 2006 to maintain consistency with the OBBA; names that have since been updated appear in parentheses).

Order	Family	Common name	Scientific name
Anseriformes	Anatidae	Canada Goose	*Branta canadensis*
		Mute Swan	*Cygnus olor*
		Trumpeter Swan	*Cygnus buccinator*
		Wood Duck	*Aix sponsa*
		Gadwall	*Anas strepera*
		American Wigeon	*Anas americana*
		American Black Duck	*Anas rubripes*
		Mallard	*Anas platyrhynchos*
		Blue-winged Teal	*Anas discors*
		Northern Shoveler	*Anas clypeata*
		Northern Pintail	*Anas acuta*
		Green-winged Teal	*Anas crecca*
		Canvasback	*Aythya valisineria*
		Redhead	*Aythya americana*
		Ring-necked Duck	*Aythya collaris*
		Lesser Scaup	*Aythya affinis*
		Bufflehead	*Bucephala albeola*

Order	Family	Common name	Scientific name
		Common Goldeneye	*Bucephala clangula*
		Hooded Merganser	*Lophodytes cucullatus*
		Common Merganser	*Mergus merganser*
		Red-breasted Merganser	*Mergus serrator*
		Ruddy Duck	*Oxyura jamaicensis*
Galliformes	Phasianidae	Gray Partridge	*Perdix perdix*
		Ring-necked Pheasant	*Phasianus colchicus*
		Ruffed Grouse	*Bonasa umbellus*
		Spruce Grouse	*Falcipennis canadensis*
		Sharp-tailed Grouse	*Tympanuchus phasianellus*
		Wild Turkey	*Meleagris gallopavo*
	Odontophoridae	Northern Bobwhite	*Colinus virginianus*
Gaviiformes	Gaviidae	Common Loon	*Gavia immer*
Podicipediformes	Podicipedidae	Pied-billed Grebe	*Podilymbus podiceps*
		Horned Grebe	*Podiceps auritus*
		Red-necked Grebe	*Podiceps grisegena*
Suliformes	Phalacrocoracidae	Double-crested Cormorant	*Phalacrocorax auritus*
Pelecaniformes	Ardeidae	American Bittern	*Botaurus lentiginosus*
		Least Bittern	*Ixobrychus exilis*
		Great Blue Heron	*Ardea herodias*
		Great Egret	*Ardea alba*
		Cattle Egret	*Bubulcus ibis*
		Green Heron	*Butorides virescens*
		Black-crowned Night-Heron	*Nycticorax nycticorax*
		Yellow-crowned Night-Heron	*Nyctanassa violacea*
Accipitriformes	Cathartidae	Turkey Vulture	*Cathartes aura*

Order	Family	Common name	Scientific name
	Pandionidae	Osprey	*Pandion haliaetus*
	Accipitridae	Bald Eagle	*Haliaeetus leucocephalus*
		Northern Harrier	*Circus cyaneus*
		Sharp-shinned Hawk	*Accipiter striatus*
		Cooper's Hawk	*Accipiter cooperii*
		Northern Goshawk	*Accipiter gentilis*
		Red-shouldered Hawk	*Buteo lineatus*
		Broad-winged Hawk	*Buteo platypterus*
		Red-tailed Hawk	*Buteo jamaicensis*
Falconiformes	Falconidae	American Kestrel	*Falco sparverius*
		Merlin	*Falco columbarius*
		Peregrine Falcon	*Falco peregrinus*
Gruiformes	Rallidae	Yellow Rail	*Coturnicops noveboracensis*
		King Rail	*Rallus elegans*
		Virginia Rail	*Rallus limicola*
		Sora	*Porzana carolina*
		Common Moorhen	*Gallinula chloropus*
		American Coot	*Fulica americana*
	Gruidae	Sandhill Crane	*Grus canadensis*
Charadriiformes	Charadriidae	Killdeer	*Charadrius vociferus*
	Recurvirostridae	Black-necked Stilt	*Himantopus mexicanus*
	Scolopacidae	Spotted Sandpiper	*Tringa macularia*
		Solitary Sandpiper	*Tringa solitaria*
		Upland Sandpiper	*Bartramia longicauda*
		Wilson's Snipe	*Gallinago delicata*
		American Woodcock	*Scolopax minor*
		Wilson's Phalarope	*Steganopus tricolor (Phalaropus tricolor)*

Order	Family	Common name	Scientific name
		Red-necked Phalarope	*Phalaropus lobatus*
	Laridae	Little Gull	*Larus minutes (Hydrocoloeus minutes)*
		Ring-billed Gull	*Larus delawarensis*
		Herring Gull	*Larus argentatus*
		Great Black-backed Gull	*Larus marinus*
		Caspian Tern	*Sterna caspia (Hydroprogne caspia)*
		Black Tern	*Chlidonias niger*
		Common Tern	*Sterna hirundo*
		Forster's Tern	*Sterna forsteri*
Columbiformes	Columbidae	Rock Pigeon	*Columba livia*
		Eurasian Collared-Dove	*Streptopelia decaocto*
		Mourning Dove	*Zenaida macroura*
Cuculiformes	Cuculidae	Black-billed Cuckoo	*Coccyzus erythropthalmus*
		Yellow-billed Cuckoo	*Coccyzus americanus*
Strigiformes	Tytonidae	Barn Owl	*Tyto alba*
	Strigidae	Eastern Screech-Owl	*Megascops asio*
		Great Horned Owl	*Bubo virginianus*
		Northern Hawk Owl	*Surnia ulula*
		Barred Owl	*Strix varia*
		Great Gray Owl	*Strix nebulosa*
		Long-eared Owl	*Asio otus*
		Short-eared Owl	*Asio flammeus*
		Boreal Owl	*Aegolius funereus*
		Northern Saw-whet Owl	*Aegolius acadicus*

Order	Family	Common name	Scientific name
Caprimulgiformes	Caprimulgidae	Common Nighthawk	*Chordeiles minor*
		Chuck-will's-widow	*Caprimulgus carolinensis*
		Eastern Whip-poor-will§	*Caprimulgus vociferus*
Apodiformes	Apodidae	Chimney Swift	*Chaetura pelagica*
	Trochilidae	Ruby-throated Hummingbird	*Archilochus colubris*
Coraciiformes	Alcedinidae	Belted Kingfisher	*Megaceryle alcyon*
Piciformes	Picidae	Red-headed Woodpecker	*Melanerpes erythrocephalus*
		Red-bellied Woodpecker	*Melanerpes carolinus*
		Yellow-bellied Sapsucker	*Sphyrapicus varius*
		Downy Woodpecker	*Picoides pubescens*
		Hairy Woodpecker	*Picoides villosus*
		American Three-toed Woodpecker	*Picoides dorsalis*
		Black-backed Woodpecker	*Picoides arcticus*
		Northern Flicker	*Colaptes auratus*
		Pileated Woodpecker	*Dryocopus pileatus*
Passeriformes	Tyrannidae	Olive-sided Flycatcher	*Contopus cooperi*
		Eastern Wood-Pewee	*Contopus virens*
		Yellow-bellied Flycatcher	*Empidonax flaviventris*
		Acadian Flycatcher	*Empidonax virescens*
		Alder Flycatcher	*Empidonax alnorum*
		Willow Flycatcher	*Empidonax traillii*

Order	Family	Common name	Scientific name
		Least Flycatcher	*Empidonax minimus*
		Eastern Phoebe	*Sayornis phoebe*
		Great Crested Flycatcher	*Myiarchus crinitus*
		Eastern Kingbird	*Tyrannus tyrannus*
	Laniidae	Loggerhead Shrike	*Lanius ludovicianus*
	Vireonidae	White-eyed Vireo	*Vireo griseus*
		Yellow-throated Vireo	*Vireo flavifrons*
		Blue-headed Vireo*	*Vireo solitarius*
		Warbling Vireo	*Vireo gilvus*
		Philadelphia Vireo	*Vireo philadelphicus*
		Red-eyed Vireo	*Vireo olivaceus*
	Corvidae	Gray Jay	*Perisoreus canadensis*
		Blue Jay	*Cyanocitta cristata*
		American Crow	*Corvus brachyrhynchos*
		Common Raven	*Corvus corax*
	Alaudidae	Horned Lark	*Eremophila alpestris*
	Hirundinidae	Purple Martin	*Progne subis*
		Tree Swallow	*Tachycineta bicolor*
		Northern Rough-winged Swallow	*Stelgidopteryx serripennis*
		Bank Swallow	*Riparia riparia*
		Cliff Swallow	*Petrochelidon pyrrhonota*
		Barn Swallow	*Hirundo rustica*
	Paridae	Black-capped Chickadee	*Poecile atricapillus*
		Boreal Chickadee	*Poecile hudsonica*
		Tufted Titmouse	*Baeolophus bicolor*
	Sittidae	Red-breasted Nuthatch	*Sitta canadensis*
		White-breasted Nuthatch	*Sitta carolinensis*

Order	Family	Common name	Scientific name
	Certhiidae	Brown Creeper	*Certhia americana*
	Troglodytidae	Carolina Wren	*Thryothorus ludovicianus*
		House Wren	*Troglodytes aedon*
		Winter Wren	*Troglodytes troglodytes (Troglodytes hiemalis)*
		Sedge Wren	*Cistothorus platensis*
		Marsh Wren	*Cistothorus palustris*
	Regulidae	Golden-crowned Kinglet	*Regulus satrapa*
		Ruby-crowned Kinglet	*Regulus calendula*
	Polioptilidae	Blue-gray Gnatcatcher	*Polioptila caerulea*
	Turdidae	Eastern Bluebird	*Sialia sialis*
		Veery	*Catharus fuscescens*
		Swainson's Thrush	*Catharus ustulatus*
		Hermit Thrush	*Catharus guttatus*
		Wood Thrush	*Catharus mustelinus*
		American Robin	*Turdus migratorius*
	Mimidae	Gray Catbird	*Dumetella carolinensis*
		Northern Mockingbird	*Mimus polyglottos*
		Brown Thrasher	*Toxostoma rufum*
	Sturnidae	European Starling	*Sturnus vulgaris*
	Bombycillidae	Cedar Waxwing	*Bombycilla cedrorum*
	Parulidae	Blue-winged Warbler	*Vermivora pinus (Vermivora cyanoptera)*
		Golden-winged Warbler	*Vermivora chrysoptera*
		Tennessee Warbler	*Vermivora peregrina*
		Nashville Warbler	*Vermivora ruficapilla*
		Northern Parula	*Parula americana*

Order	Family	Common name	Scientific name
		Yellow Warbler	*Dendroica petechia*
		Chestnut-sided Warbler	*Dendroica pensylvanica*
		Magnolia Warbler	*Dendroica magnolia*
		Cape May Warbler	*Dendroica tigrina*
		Black-throated Blue Warbler	*Dendroica caerulescens*
		Yellow-rumped Warbler	*Dendroica coronata*
		Black-throated Green Warbler	*Dendroica virens*
		Blackburnian Warbler	*Dendroica fusca*
		Pine Warbler	*Dendroica pinus*
		Kirtland's Warbler	*Dendroica kirtlandii*
		Prairie Warbler	*Dendroica discolor*
		Palm Warbler	*Dendroica palmarum*
		Bay-breasted Warbler	*Dendroica castanea*
		Cerulean Warbler	*Dendroica cerulea*
		Black-and-white Warbler	*Mniotilta varia*
		American Redstart	*Setophaga ruticilla*
		Prothonotary Warbler	*Protonotaria citrea*
		Worm-eating Warbler	*Helmitheros vermivorus*
		Ovenbird	*Seiurus aurocapilla*
		Northern Waterthrush	*Seiurus noveboracensis*
		Louisiana Waterthrush	*Seiurus motacilla*
		Kentucky Warbler	*Oporornis formosus*
		Connecticut Warbler	*Oporornis agilis*

Order	Family	Common name	Scientific name
		Mourning Warbler	*Oporornis philadelphia*
		Common Yellowthroat	*Geothlypis trichas*
		Hooded Warbler	*Wilsonia citrina*
		Wilson's Warbler	*Wilsonia pusilla*
		Canada Warbler	*Wilsonia canadensis*
		Yellow-breasted Chat	*Icteria virens*
	Cardinalidae	Summer Tanager	*Piranga rubra*
		Scarlet Tanager	*Piranga olivacea*
	Emberizidae	Eastern Towhee†	*Pipilo erythrophthalmus*
		Chipping Sparrow	*Spizella passerina*
		Clay-colored Sparrow	*Spizella pallida*
		Field Sparrow	*Spizella pusilla*
		Vesper Sparrow	*Pooecetes gramineus*
		Savannah Sparrow	*Passerculus sandwichensis*
		Grasshopper Sparrow	*Ammodramus savannarum*
		Henslow's Sparrow	*Ammodramus henslowii*
		Le Conte's Sparrow	*Ammodramus leconteii*
		Song Sparrow	*Melospiza melodia*
		Lincoln's Sparrow	*Melospiza lincolnii*
		Swamp Sparrow	*Melospiza georgiana*
		White-throated Sparrow	*Zonotrichia albicollis*
		Dark-eyed Junco	*Junco hyemalis*
	Cardinalidae	Northern Cardinal	*Cardinalis cardinalis*
		Rose-breasted Grosbeak	*Pheucticus ludovicianus*
		Indigo Bunting	*Passerina cyanea*

Order	Family	Common name	Scientific name
		Dickcissel	*Spiza americana*
	Icteridae	Bobolink	*Dolichonyx oryzivorus*
		Red-winged Blackbird	*Agelaius phoeniceus*
		Eastern Meadowlark	*Sturnella magna*
		Western Meadowlark	*Sturnella neglecta*
		Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
		Rusty Blackbird	*Euphagus carolinus*
		Brewer's Blackbird	*Euphagus cyanocephalus*
		Common Grackle	*Quiscalus quiscula*
		Brown-headed Cowbird	*Molothrus ater*
		Orchard Oriole	*Icterus spurius*
		Baltimore Oriole‡	*Icterus galbula*
	Fringillidae	Pine Grosbeak	*Pinicola enucleator*
		Purple Finch	*Carpodacus purpureus*
		House Finch	*Carpodacus mexicanus*
		Red Crossbill	*Loxia curvirostra*
		White-winged Crossbill	*Loxia leucoptera*
		Pine Siskin	*Carduelis pinus (Spinus pinus)*
		American Goldfinch	*Carduelis tristis (Spinus tristis)*
		Evening Grosbeak	*Hesperiphona vespertina (Coccothraustes vespertinus)*
	Passeridae	House Sparrow	*Passer domesticus*

§Recorded as Whip-poor-will in both OBBA; *Recorded in the 1985 OBBA as the Solitary Vireo; †Recorded in the 1985 OBBA as the Rufous-sided Towhee ‡Recorded in the 1985 OBBA as the Northern Oriole

APPENDIX B: Details of the simulation demonstrating the effect of absences within species ranges on the strength of the richness–environment relationship.

To demonstrate that absences within species distributions weaken the relationship between species richness and an environmental gradient (hereafter the richness-environment relationship), I simulated species distributions for 151 species along a hypothetical one-dimensional gradient that varied systematically from 1 to 100 in 100 cells. Species distributions of random breadth (maximum breadth was set to 25) were placed at random locations along the gradient. The center of the distribution was selected by taking the larger of two random numbers (varying between 0 and 1) multiplied by 125. This procedure favoured placement of species' distributions toward the upper end of the gradient in order to simulate a positive richness-environment relationship. Ranges that extended beyond 100 in the environmental gradient were truncated to end at 100. Richness was calculated for each cell and regressed on the environmental variable. This was repeated 1000 times and the average coefficient of determination was taken as a measure of the strength of the relationship in the absence of patchiness in species distributions. I repeated the process but allowed presences within species' distributions to be randomly converted to absences with probabilities of 0.25, 0.5 and 0.75 to assess the effect of increasing patchiness on the richness-environment relationship.

The simulation of species distributions along a hypothetical environmental gradient is useful for demonstrating how the richness-environment relationship weakens with increasing patchiness within species distributions. The mean coefficient of determination for the richness-environment relationship over 1000 model runs decreased from 0.94 in the absence of patchiness in species distributions to 0.90, 0.83 and finally 0.68 when patchiness (measured as the probability that a presence was randomly converted to an absence) was set to 0.25, 0.5 and 0.75 respectively (Chapter 2, Figure 2.1).

APPENDIX C: Species-specific suitable land cover

Table C1: Land covers in the Ontario Provincial-Scale Land Cover data set deemed to potentially include suitable habitat for each of the 151 avian species from the 1985 and 2005 Ontario Breeding Bird Atlases retained in the statistical analysis in Chapter 2 (*The role of metapopulation-like dynamics in determining regional species richness patterns*). The land covers are: inland marsh (5), deciduous swamp (6), coniferous swamp (7), open fen (8), treed fen (9), open bog (10), treed bog (11), dense deciduous forest (13), dense coniferous forest (14), coniferous plantation (15), mixed forest that is mainly deciduous (16), mixed forest that is mainly coniferous (17), sparse coniferous forest (18), sparse deciduous forest (19), recent cutovers (20), recent burns (21), old cuts and burns (22), mine tailings, quarries and bedrock outcrops (23), settlement and developed land (24), pasture and abandoned fields (25), cropland (26) and alvar (a dry grassland; 27). Species are ordered following the taxonomy of the AOU to follow the order in which they are presented in the 2005 Ontario Breeding Bird Atlas (OBBA; Cadman *et al*., 2007). Suitability was based on the habitat descriptions in The Birder's Handbook (Ehrlich *et al*., 1988). Land covers that potentially include suitable habitat are denoted with 1 and those that do not are denoted with 0. Species are ordered taxonomically based on their American Ornithologists' Union (AOU) numeric code.

Common name	5	6	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Canada Goose	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Wood Duck	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gadwall	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
American Wigeon	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Black Duck	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0		0	0	0	0
Mallard	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Blue-winged Teal	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Northern Shoveler	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Northern Pintail	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Green-winged Teal	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Ring-necked Duck	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hooded Merganser	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Common Merganser	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ruddy Duck	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gray Partridge	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Ring-necked Pheasant	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1
Ruffed Grouse	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1
Common Loon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pied-billed Grebe	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Bittern	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Least Bittern	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Great Blue Heron	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Green Heron	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Common name	5	6	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Black-crowned Night-Heron	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turkey Vulture	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Osprey	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Northern Harrier	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Sharp-shinned Hawk	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Cooper's Hawk	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Northern Goshawk	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0
Red-shouldered Hawk	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Red-tailed Hawk	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1
American Kestrel	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1
Virginia Rail	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sora	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Common Moorhen	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Coot	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spotted Sandpiper	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Upland Sandpiper	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1
Wilson's Snipe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
American Woodcock	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1
Wilson's Phalarope	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Herring Gull	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Common Tern	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Tern	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Common name	5	6	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Rock Pigeon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mourning Dove	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0
Black-billed Cuckoo	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Yellow-billed Cuckoo	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0
Eastern Screech-Owl	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	1	0	1	0	0	0
Great Horned Owl	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	0	0
Barred Owl	0	1	1	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Long-eared Owl	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	0
Northern Saw-whet Owl	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Common Nighthawk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Eastern Whip-poor-will	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Chimney Swift	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0
Ruby-throated Hummingbird	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0
Belted Kingfisher	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Red-headed Woodpecker	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0
Red-bellied Woodpecker	0	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0
Yellow-bellied Sapsucker	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Downy Woodpecker	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	0

Common name	5	6	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Black-backed Woodpecker	0	1	1	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0
Pileated Woodpecker	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0
Olive-sided Flycatcher	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0
Eastern Wood-Pewee	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0
Yellow-bellied Flycatcher	0	0	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0
Alder Flycatcher	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Willow Flycatcher	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0
Eastern Phoebe	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0
Loggerhead Shrike	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0
Yellow-throated Vireo	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0
Blue-headed Vireo	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0
Warbling Vireo	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Philadelphia Vireo	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Gray Jay	0	1	1	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Common Raven	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
Horned Lark	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Purple Martin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Northern Rough-winged Swallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Bank Swallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Cliff Swallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1

Common name	5	6	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Red-breasted Nuthatch	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
White-breasted Nuthatch	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Brown Creeper	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
House Wren	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0
Winter Wren	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sedge Wren	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Marsh Wren	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Golden-crowned Kinglet	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	0	0	0
Ruby-crowned Kinglet	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Blue-gray Gnatcatcher	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1
Eastern Bluebird	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0
Veery	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Swainson's Thrush	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
Hermit Thrush	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Wood Thrush	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0
Northern Mockingbird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1
Brown Thrasher	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0
European Starling	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1
Blue-winged Warbler	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0
Golden-winged Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
Tennessee Warbler	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0

Common name	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
Nashville Warbler	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Northern Parula	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Yellow Warbler	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Magnolia Warbler	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Cape May Warbler	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Black-throated Blue Warbler	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0
Yellow-rumped Warbler	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Black-throated Green Warbler	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Blackburnian Warbler	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Pine Warbler	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0
Bay-breasted Warbler	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Cerulean Warbler	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black-and-white Warbler	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
American Redstart	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Ovenbird	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Northern Waterthrush	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Louisiana Waterthrush	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Mourning Warbler	1	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
Canada Warbler	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Common name	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
Scarlet Tanager	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Eastern Towhee	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0
Clay-colored Sparrow	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0
Field Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0
Vesper Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
Savannah Sparrow	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Grasshopper Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Lincoln's Sparrow	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Swamp Sparrow	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
White-throated Sparrow	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Dark-eyed Junco	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Northern Cardinal	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0
Indigo Bunting	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0
Eastern Meadowlark	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Rusty Blackbird	0	0	1	0	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Brown-headed Cowbird	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Orchard Oriole	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0
Baltimore Oriole	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0
Purple Finch	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Red Crossbill	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
White-winged Crossbill	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Pine Siskin	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0
Evening Grosbeak	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0

Common name	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
House Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0

APPENDIX D: A worked example of the interpretation of model coefficients for Swainson's Thrush

The coefficients from the generalized linear models (GLMs) for the 151 species were used to test predictions 1.1, 1.2, 1.3, 2.1 and 2.2 listed in Table 2.1 (Chapter 2). The coefficients for the main effects indicate the direction and magnitude of the effect of each variable on the probability of local species presence when all other variables are held at zero. Therefore the coefficients for the main effects of habitat area, neighbourhood occupancy and sampling effort represent the magnitude of each variable's effect when the species was not locally present in the first OBBA (i.e. when previous presence equals zero). The coefficients for the interactions between previous presence and each of the other variables (habitat area, neighbourhood occupancy and sampling effort) represent the increase (or decrease if it is negative) in the magnitude of the effect of habitat area, neighbourhood occupancy or sampling effort if the species was locally present in the first OBBA (i.e. when previous presence equals one). The two-way interaction between habitat area and neighbourhood occupancy represents the increase (or decrease) in the effect of habitat area when more neighbouring sites were occupied by conspecifics in the first atlas (or vice versa). For ease of computation, the effects of all interactions were evaluated using zero or one. For example, the coefficients for the GLM for Swainson's Thrush were

$P_{05} = 1.53*P_{85} +1.30*H -0.62*P_{85}:H +1.10*N_{85} +1.28*P_{85}:N_{85} -0.40*H:N_{85} - 0.69*P_{85}:H:N_{85} +0.10*E +0.12*P_{85}:E -0.24*\Delta E +0.20*P_{85}:\Delta E +0.24*D:\Delta E - 0.32*P_{85}:D:\Delta E.$

where P_{05} is species presence in the 2005 OBBA, P_{85} is species presence in the 1985 OBBA, H is the area of habitat, N_{85} is the proportion of neighbouring squares occupied by conspecifics in 1985, E is $\log_{10}$(effort in 2005), ΔE is the absolute value of the change in effort and D is the direction of the change in effort. Variables connected by colons represent multiplicative interactions. The slopes for the effects of habitat area, neighbourhood occupancy and sampling effort were 1.30, 1.10 and 0.10, respectively if Swainson's Thrush was locally absent in the first atlas. The slope of the effect of habitat area decreased to 0.68 if it was locally present in the first atlas while the slopes of the effects of neighbourhood occupancy and sampling effort increased to 2.37 and 0.22, respectively, if it was locally present in the first atlas. For Swainson's Thrush, the slope of the effect of habitat area decreased from 1.30 to 0.90 when neighbourhood occupancy increased from zero to one.

Based on the predictions in Table 2.1, I expected that, across species, the coefficients for area of habitat, neighbourhood occupancy and sampling effort would be positive. The coefficient for the interaction of each of these with previous presence was used to evaluate if the effect of habitat area or neighbourhood occupancy differed if the species was locally present rather than absent in the first OBBA. I also expected that the two-way interaction between habitat area and neighbourhood occupancy (prediction 1.3) would be negative such that the effect of habitat area is greater when fewer neighbouring squares are initially occupied by conspecifics. The three-way interaction between habitat area, neighbourhood occupancy and presence in 1985 OBBA was used to evaluate if the effect of this interaction differed if the species was locally present or absent in the first OBBA.

I assessed how the effect of change in effort differed for species that were locally present or absent in the first atlas depending on whether effort increased or decreased by evaluating the equations resulting from the GLMs to derive the slope for each of the four combinations of previous presence (previously present = 1 or absent = 0) and both directions of change in effort (negative=0 or positive=1). I expected that, across species, the slope of the relationship between the probability of local presence and change in effort would be positive if the species was previously locally absent and effort increased, the slope would be negative if the species was previously locally present and effort decreased, and the slope would be negative otherwise. Returning to Swainson's Thrush, the slope was 0 if it was previously locally absent ($P_{85} = 0$) and effort increased ($D = 1$), 0.44 if it was previously locally present ($P_{85} = 1$) and effort decreased ($D = 0$), -0.24 if it was previously locally absent ($P_{85} = 0$) and effort decreased ($D = 0$), and -0.12 if it was previously locally present ($P_{85} = 1$) and effort increased ($D = 1$).

APPENDIX E: Additional temporal determinants of change in species richness

Vegetation heterogeneity:

Since it is possible that birds do not distinguish between different habitats using a human-derived land cover classification, I used non-classified data from time series remote sensing data for the SLI ecosystem (SLI mosaics; Fraser *et al*., 2009) to calculate a measure of vegetation heterogeneity. I first did a cluster analysis on the SLI mosaics for 1990 and 2005 using the red, near infrared and mid infrared bands used to create the time series land cover maps. This grouped together map pixels with similar spectral signatures, since statistically distinguishable spectral clusters often reflect ecologically different features in the landscape that can also be used as the first step of an ecological land classification (Lillesand *et al*., 2004). The number of spectral clusters is not necessarily collinear with the number of land types, since a single land cover class may have a large number of spectrally distinct pixels. I derived the number of spectral clusters. The cluster analysis was run on the data from the red, near infrared and mid infrared bands, with a maximum number of clusters set at 150. The same bands are used to sense chlorophyll absorption, and to classify vegetation type, and to estimate vigour and moisture content (Lillesand *et al*., 2004). Vegetation heterogeneity was measured as the number of distinct spectral clusters in each OBBA square. Change in vegetation heterogeneity was measured as the change in the number of spectral clusters found within a square over the 15-year period.

Productivity:

The Normalized Difference Vegetation Index (NDVI) is a satellite-derived measure of 'greenness' of land cover (Pettorelli *et al*., 2005). NDVI correlates closely with absorbed photosynthetically active radiation and has become a common estimate of net primary productivity (Kerr & Ostrovsky, 2003). The SLI mosaics for 1990 and 2005 were also used to calculate NDVI using the equation:

$$NDVI = (red - nir)/(red + nir) \tag{2}$$

where red and nir are red radiation and near infrared radiation respectively (Pettorelli et al., 2005). Mean NDVI was estimated for each square. The red and near infrared bands of the time series remote sensing data for the SLI ecosystem were used to calculated NDVI for 1990 and 2005 using equation (2). Change in productivity was measured as the change in mean NDVI for each OBBA square over the 15-year period.

I resampled all raw data from a 30m to 100m resolution to match the DEM data. All geographic data were processed using ArcInfo Grid 9.3(Environmental Systems Research Institute, 2008) and Geomatica 9.0 (PCI Geomatics, 2003). I used ordinary least squares regression to determine the variance explained by each variable above the variance explained by change in effort. All statistical analyses were performed using R (R Development Core Team, 2010).

Results:

Table E1: Coefficients and variances explained by models included additional environmental predictors for the SLI (St. Lawrence Islands) ecosystem. Partial R^2 is variance explained after controlling for change in effort.

	Predictor	**Slope**	**R^2**	**Partial R^2**	**p-value** *
Effort Alone	Change in effort	0.14	0.194		<0.001
Temporal predictors	Productivity: Change in mean NDVI	-35.09	0.204	0.010	0.327
	Heterogeneity: Change in vegetation heterogeneity	-0.006	0.194	<0.001	0.983

*All models have p-values <0.0001, the reported p-values are for individual predictors.