

Community-level Patterns in Boreal Riparian and Wetland Bird Assemblage

by

Julienne Morissette

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Ecology

Department of Biological Sciences
University of Alberta

© Julienne Morissette, 2014

ABSTRACT

Canada's boreal forest is the breeding ground for some 288 species of resident and migratory birds. Approximately 65% of the species that are currently of highest conservation priority in the boreal region are associated with wetlands and riparian areas. Although estimates vary with scale and specific geographic boundaries, wetlands (open water, marshes, fens, bogs and swamps) and other aquatic areas occupy between 20-60% of the boreal landscape. These ecosystems are interspersed with uplands resulting in a heterogeneous landscape hosting a wide variety of transitions, or ecotones, including riparian areas among and within aquatic, wetland and terrestrial systems. Like most ecosystems worldwide, riparian areas within Canada's boreal forests face increasing environmental pressure from the cumulative effects of climate change and unprecedented rates of anthropogenic landscape modification. My objectives were to advance understanding of boreal riparian and wetland-associated bird communities and to evaluate emerging community-level metrics for comparing different habitats and measuring effects of human disturbance. First, I characterized species composition and ecological characteristics of boreal riparian areas associated with open water wetlands which represent a broad spectrum of riparian habitats available to boreal birds. This work demonstrated that riparian zones associated with boreal plain wetlands (shallow lakes and ponds) act as a source of unique bird species and that community dynamics of these ecotones were different from that of upland bird communities. More specifically, I found that bird species composition was more variable in riparian areas than upland sites. I also found that riparian areas supported bird communities that were less specialized in their habitat preferences than those in upland areas.

To explore these findings further, I examined whether applying an accepted wetland classification scheme would refine current understanding of habitat associations for birds. My

analysis showed that despite some overlap in community composition among wetlands of roughly similar habitat structure (*i.e.*, shrubby wetlands), boreal riparian bird communities were structured differently among a broad suite of wetland classes. This work also showed that wetland communities were distinct from upland communities of similar structure created by forest harvesting. Using indices of ecological function and resilience based on ecological traits of the bird community to compare riparian and upland bird communities, I found riparian bird assemblages possess a different suite of functional traits, higher functional diversity, and greater resilience than the other areas of the landscape I examined.

Finally I used, Threshold Indicator Taxa Analysis (TITAN), a technique developed specifically for identifying community-level thresholds (Baker), to explore species-level changes at wetlands along a gradient of agricultural conversion. I compared two spatial scales (local and landscape level) and two geographic regions one in Northeastern Alberta with extensive relatively intact boreal forest immediately to the north and another forested landscape in South western Manitoba embedded in a matrix of agricultural conversion. Community-level changes appeared more abrupt at the landscape than wetland scales but tended to occur over a wide portion of the disturbance gradient, providing only equivocal evidence for community-level thresholds. Species responding positively to agricultural conversion were more typical of open country regions. Species that responded negatively were generally those for which loss of forest cover represented direct loss of habitat. For species common to both regions, specific change points differed but direction of response (+ or -) was consistent.

Taken together evidence presented here supports other boreal studies that have shown that for bird communities riparian areas are ecologically unique. They support species rich and subsequently, functionally rich bird communities structured to be more resilient than upland

communities. However, even when forest is retained around the periphery of boreal wetlands, conversion to agriculture in the surrounding landscape resulted in species assemblages more typical of open prairie landscapes. Thus my work clearly describes patterns community composition and points to future research necessary to ensure conservation of boreal wetlands and associated bird communities. Greater consideration of ecological traits and community level approaches will compliment species-level work and assist in developing effective conservation and sustainable land use strategies. Data from long term studies of boreal forest bird communities that strategically consider both species- and ecosystem-level changes in boreal bird assemblages in response to environmental gradients over time and including human disturbances will be critical to this effort.

PREFACE

Some of the research conducted for this thesis forms part of a research collaboration, led by Dr. Keith Hobson at Environment Canada with Dr. Erin Bayne being the lead collaborator at the University of Alberta. Data analyses and interpretation are my original work. Introductory and concluding chapters are my synthesis of the significance of the chapters within. Chapter 3 has been published as: Morissette, JL, KJ Kardynal, EM Bayne, KA Hobson. *Wetlands* 33(4): 653-665.

In all cases the format of the remaining data chapters reflects that they have been or will be submitted for publication with a journal. I was responsible for data collection and analysis as well as manuscript composition. E.M. Bayne and K. Hobson were supervisory authors and were involved in concept formation and manuscript composition.

FOR TYLER

ACKNOWLEDGEMENTS

When I considered starting this degree my “super”visor E. Bayne warned me it wouldn’t be easy doing a PhD while working full time. You understood the risks and then took me on anyways- thank you Erin for your sound advice, good teaching and for giving me a little push (or a big one) when I was getting in my own way! Thanks also to you Keith Hobson for co-advising this project – I always appreciate your wit and wisdom – doing a PhD at times, was indeed a little “like ordering fish and chips”! I would also like to thank the various committee members along the way that have provided challenging and thoughtful comments Stan Boutin, Susan Hannon, Cindy Paszcowski, Lee Foote and also my external examiner, André Desrochers. Kevin Devito also provided invaluable insight and support selecting field sites at the Utikuma Study area.

The many moving parts of the “Riparian Bird Project” were supported financially and logistically by the Alberta Conservation Association, Ducks Unlimited Canada, Environment Canada -Western Boreal Conservation Initiative, Louisiana Pacific Swan Valley Division, Sustainable Forest Management Network, and the University of Alberta.

Boreal riparian areas and wetlands are challenging and sometimes dangerous places to work and I am grateful to the many people who braved “the swamps” and assisted with field logistics, data collection and management. Kevin Kardynal (thanks for the serenades too!), Tracy Lanson and Colleen Stevens were with me for the long haul and each of Julia Burger, Derek Keeping, Sean Haughian, Lisa Flaman, Sara Bumstead, Steven Smith, Neil McLaughlin, and Maureen Wetsch collected their fair share of data over the years. Thanks also to Vern Bauman for showing us how to get anywhere we wanted to go in the Duck Mountain!

I must also extend my gratitude to my colleagues at DUC and elsewhere; those who supported the PhD idea in the first place (Eric Butterworth, Gary Stewart); helped me crunch numbers (Llwellyn Armstrong, Michael Robin programmer extra-ordinaire!); analyze spatial information and make maps (Michael Robin, Lindsay McBlane, Stéphane Laroche), those who provided moral support and took on extra work (especially Chris Smith, Wally Price) or who later gave we some wiggle room (Dave Howerter, Kevin Smith) so I would have the time to complete. Special thanks to Stuart Slattery who understood “the process”, provided genuine

mentorship and knew just what to say during pivotal moments, to Glenn Mack for listening...and listening and listening, and to Danna Schock, Donna Kopecky and Samantha Song for friendship and invaluable conversations.

Completing this Ph.D. has definitely taken a few more years than I originally thought it would and I am blessed with wonderful family and friends who have stood by me during personal and professional challenges and continued to believe I would persevere and eventually complete this degree. There is not enough room on these pages to properly express my gratitude!

Last and certainly not least, dearest Tyler, hubby, best friend, tireless editor, coach and inspiration in perseverance to face obstacles with grace and courage, thank you for the privilege of being your wife.

“Only those who will risk going too far can possibly find out how far one can go.”

~ T.S. Eliot

Thanks to everyone who helped me figure out just how far that was.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION.....	1
1.1 Boreal forests, birds and wetlands	1
1.2 Defining and delineating the riparian bird community.....	3
1.3 Community ecology – quantifying diversity and specialization.....	6
1.4 From measuring diversity to measuring function: indices for assessing ecological function using bird communities	8
1.5 Effects of human disturbance on riparian and wetland associated bird community diversity and function	10
1.6 Thesis Outline	12
1.7 References.....	13
CHAPTER 2: COMPOSITION AND ECOLOGICAL CHARACTERISTICS OF RIPARIAN BIRD ASSEMBLAGES ASSOCIATED WITH BOREAL WETLANDS	25
2.1 Introduction.....	25
2.2 Methods.....	28
2.2.1 Study area.....	28
2.2.2 Site selection and study design	29
2.2.3 Bird surveys	30
2.2.4 Vegetation composition of transects	31
2.2.5 Community and species- level difference between upland, lowland and riparian sites.....	31
2.2.6 Multivariate dispersion as a measure of beta diversity	32

2.2.7 Quantifying specialization (or plasticity).....	33
2.3 Results.....	34
2.3.1 Community and species-level differences between upland, lowland and riparian sites	35
2.3.2 Multivariate dispersion as a measure of beta diversity	35
2.3.3 Species specialization index.....	36
2.3.4 Comparing community specialization (CSI).....	36
2.4 Discussion	37
2.4.1 Species richness and indicators of riparian areas	37
2.4.2 Multivariate dispersion as a measure of beta diversity	39
2.4.3 Specialization	41
2.4.5 Implications for conservation and future research	43
2.5 References.....	58
CHAPTER 3: COMPARING BIRD COMMUNITY COMPOSITION AMONG BOREAL WETLANDS: IS WETLAND	
CLASSIFICATION A MISSING PIECE OF THE HABITAT PUZZLE?.....	65
3.1 Introduction.....	65
3.2 Methods.....	67
3.2. 1 Study area.....	67
3.2.2 Wetland Classification	68
3.2.3 Site Selection	69
3.2.4 Bird Surveys.....	70
3.2.5 Data analysis	70
3.2 Results.....	73

3.2.1 Differences in Bird Community Composition among Wetland Classes.....	73
3.2.2 Characteristic Bird Communities of Wetland Classes.....	73
3.2.3 Species Characteristic of Wetland Classes.....	74
3.3 Discussion.....	75
3.3.1 Management Implications.....	77
3.4 References.....	79
CHAPTER 4: ECOLOGICAL CHARACTERISTICS OF BOREAL RIPARIAN BIRD ASSEMBLAGES: A TRAIT-BASED APPROACH.....	92
4.1 Introduction.....	92
4.2 Methods.....	95
4.2.1 Study area.....	95
4.2.2 Bird surveys.....	96
4.2.3 Site selection and study design.....	96
4.2.4 Functional Diversity and Resilience Measures.....	97
4.3 Results.....	101
4.4 Discussion.....	103
4.5 References.....	122
CHAPTER 5: REGIONAL VARIATION IN THRESHOLD RESPONSES OF WETLAND-ASSOCIATED BIRD COMMUNITIES TO CONVERSION OF BOREAL FOREST TO AGRICULTURE.....	130
5.1 Introduction.....	130
5.2. Methods.....	134
5.2.1 Description of Study areas.....	134

5.2.2 Landscape selection, quantifying total human disturbance and conversion to agriculture	136
5.2.3 Wetland selection.....	136
5.2.4 Wetland-scale disturbance calculations	137
5.2.5 Bird Surveys.....	137
5.2.6 Statistical Analysis.....	138
5.3. Results.....	140
5.3.1 Landscape-level community thresholds and species change points.....	140
5.3.2 Wetland- level community thresholds and species change points	141
5.4. Discussion	142
5.4.1 Community-level effects.....	143
5.4.2 Species-level effects.....	143
5.4.3 Landscape-level vs. wetland-level effects.....	146
5.4.4 Regional responses to agricultural conversion.....	147
5.5 Conclusions and management implications	148
5.6 References.....	157
CHAPTER 6: SYNTHESIS	164
6.1 Habitat associations of boreal birds	164
6.2 Community-level metrics complement species-level work	166
6.2.1 Detectability.....	171
6.3 Conclusions & Further research.....	171
6.4 References.....	173

BIBLIOGRAPHY	182
APPENDIX 1: SUPPLEMENTARY MATERIALS FOR ASSESSING THE COMPOSITION OF RIPARIAN ASSEMBLAGES (CHAPTER 2).....	210
APPENDIX 2: SUPPLEMENTARY MATERIAL SUPPORTING THE CHARACTERIZATION OF BIRD ASSEMBLAGES AMONG BOREAL WETLAND CLASSES IN CHAPTER 3	215
APPENDIX 3: SUPPLEMENTARY MATERIALS USED FOR CALCULATING FUNCTIONAL DIVERSITY AND RESILIENCE INDICES IN CHAPTER 4.....	220
APPENDIX 4: INDIVIDUAL SPECIES RESULTS FROM TITAN IN RESPONSE TO A GRADIENT IN TOTAL DISTURBANCE BY AGRICULTURE IN NEAB AND DMMB STUDY AREAS	234

LIST OF TABLES

Table 2.1 Description of three habitat types examined in the Utikuma Lake, Alberta study area (2002 and 2003).....45

Table 2.2 Habitat categories used to calculate Species Specialization Index (SSI) values...46

Table 2.3 Indicator values (% of perfect indication) for bird species in riparian compared to upland and lowland transects Utikuma, Alberta..... 47

Table 2.4 Results of MRPP analysis among habitat types when complete transects (a) and when only the upland/shoreline forest portion of riparian transect is compared to ½ of the upland transect (b)..... 49

Table 2.5 Post-hoc pairwise comparisons of multivariate dispersions (within group distance from centroid) in PERMDISP2 (Anderson 2006) for (a) whole transects and (b) only the upland/shoreline forest portion of transects in each of riparian, upland and lowland transects (Bray-Curtis distance on untransformed data; Permutation test- 9999 randomizations; Anderson 2006).....50

Table 2.6 Comparison of CSI among habitat types (Oneway Anova; Figure 2.6). Variances were equal (a) and unequal (b-Bartlett’s prob > *chi2* =0.04), and tests for heteroscedasticity (Levene’s) and normality (KS) were not significant.....51

Table 3.1 Wetland classes as modified from the Canadian Wetland Classification System (CWC) and the classification scheme used by Ducks Unlimited Canada to map wetlands via remote sensing in the Boreal Plains ecozone (Smith *et al.*, 2007). † Moisture and hydrodynamic (vertical or lateral water movement) characteristics are outlined below and modified from Smith *et al.*, (2007).....85

Table 3.2	Results from Multiple Response Permutation Procedures to compare bird community composition among wetland classes. Statistical significance level after Bonferoni correction is $p < 0.002$. Unless otherwise indicated, all comparisons were significant $p < 0.0001$ (* indicates $p < 0.002$ and “ns” is non-significant)...87
Table 3.3	Significant indicator species ($p < 0.01$) of each wetland class (results apply to the wetland class; sub-classes are presented for reference). IV is Indicator Value, n is number of sites surveyed. * IV represents the Indicator Value when harvested areas were excluded from the analysis. Scientific names and total number of birds counted are included in Appendix 2.....88
Table 4.1	Sample sizes and descriptions of transect placement for each of the three habitat types sampled.....108
Table 4.2	Functional traits used to calculate indices of functional diversity and resilience (as per sources in table 4.3).....109
Table 4.3	Selected measures of functional diversity and resilience used to distinguish functional attributes and contributions of riparian areas (Modified from:Petchev and Gaston 2006; Schleuter <i>et al.</i> , 2010).....110
Table 4.4	Results of foraging trait–level indicator species analysis (ISA) among the three habitat types described in Table 4.1.....112
Table 4.5	Results of ANOVAs comparing FD indices among three habitat types. FD indices were dependent variables, habitat type was entered as a fixed factor and year as a random factor.113

Table 4.6	Results of ANOVAs for resilience measures as dependent variables; habitat type was entered as a fixed factor and year as a random factor.....	116
Table 5.1	Community change-point (cp) results for TITAN at landscape, 500 m and 100 m scales along an agricultural gradient in NEAB and DMMB. Values for 5 %, 10 %, 50 %, 90 % and 95 % quantiles are included. For comparison, results of typical change- point analyses that examine ecological distances without considering direction of the species responses are also included.....	151
Table A1.1	Complete Indicator Species Analysis results and associated Species Specialization Index (SSI) values.....	210
Table A2.1	Table number of birds counted for each species in each wetland class during the study.....	215
Table A3.1	Species list and functional traits and weight classes assigned to each species. The full list was used to assess potential FD relative to actual FD and so that Weight class clusters could be used for other components of the thesis.....	220
Table A3.2	Complete results for trait-based Indicator Species Analysis.....	233
Table A4.1	Species codes, English names scientific names, indicator scores (IndVal), change points (env.cp) and percentiles (5 %, 50 %, 95 %), for declining (-) and increasing taxa (+) in response to increasing agricultural conversion at the landscape and 500 m scales in NEAB. Note that all significant indicator species are shown but that only species that met significance criteria for $P (\leq 0.05)$, purity (≥ 0.95), and reliability (≥ 0.95 , and ≥ 0.9 for at 0.05, and 0.01, respectively) are included in the figures. P is the probability of getting an equal or larger IndVal	

using 250 random permutations. IndVal is the unstandardized indicator score, z is the standardized indicator value and N= frequency of species occurrence among blocks/wetlands sampled.234

Table A4.2 Species codes, English names scientific names, indicator scores (IndVal), change points (env.cp) and percentiles (5 %, 50 %, 95 %), for declining (-) and increasing taxa (+) in response to increasing agricultural conversion at the landscape and 500m scales in DMMB. Note that all significant indicator species are shown but that only species that met significance criteria for $P (\leq 0.05)$, purity (≥ 0.95), and reliability (≥ 0.95 , and ≥ 0.9 for at 0.05, and 0.01, respectively) are included in the figures. P is the probability of getting an equal or larger IndVal using 250 random permutations. IndVal is the unstandardized indicator score, z is the standardized indicator value and N= frequency of species occurrence among blocks/wetlands sampled.....242

LIST OF FIGURES

Figure 2.1	Location of riparian, upland and lowland edge transects and the Utikuma Lake (Alberta, Canada) study area.....	52
Figure 2.2	Schematic diagram of transect and point count layout along riparian and lowland edge ecotones.....	53
Figure 2.3	Species accumulation curves for birds recorded from both years (2002-2003) in three habitat types: riparian, upland, and lowland edge for whole transects (A) and for only the upland portion of transects (B).....	54
Figure 2.4	NMS (Nonmetric Multidimensional Scaling) ordination of transects from riparian, upland and lowland edge transects. Symbols indicate transects and 4 letter codes indicate bird species (full names associated with four letter codes are located in Appendix 2).....	55
Figure 2.5	Mean community (multivariate) dispersion among riparian, upland and lowland edge habitat types for complete transect and upland only portion of transect. The panel on the right represents only shoreline forest portion of transect compared to one half of upland transects.....	56
Figure 2.6	Mean Community Specialization Index (landbirds only) by habitat type for Utikuma Lake, AB, comparing entire transects (A) and only the upland portion of transects (B). Different letters represent statistically significant differences (Scheffe test; $p < 0.001$).....	57

Figure 3.1	Location of Duck Mountain study area in Manitoba and Saskatchewan and locations of wetland classification survey points.....	90
Figure 3.2	Two- dimensional solution for Non-Metric Multidimensional Scaling analysis of bird community composition among pre-assigned wetland classes. Four letter codes and scientific names of bird species are included in Appendix 2.....	91
Figure 4.1	Distribution of transect locations in the Utikuma study area.....	118
Figure 4.2	Diagram representing placement of transect survey line in transition zone between habitat types.....	119
Figure 4.3	Comparison of mean FD measures among the three habitat types. Error bars represent \pm SE. Based on Tukey’s post hoc test, bars marked with the same letter are not significantly different at $\alpha < 0.03$	120
Figure 4.4	Comparison of mean resilience measures among the three habitat types. Error bars represent \pm SE. Based on Tukey’s post hoc test, bars marked with the same letter are not significantly different at $\alpha < 0.03$	121
Figure 5.1	Overview map of the study areas relative to one another a) and North Eastern Alberta (NEAB) study area (b) and Duck Mountain study area in west central Manitoba (DMMB) (c).....	153
Figure 5.2	Thresholds Indicator Taxa Analysis(TITAN; Baker and King 2010) of bird community responses to proportion total human disturbance (conversion of forest to agriculture, roads) for NEAB study site the landscape scale (5 wetlands in 5 by 5 km area), and within 500m of a wetland respectively. Figures in the first	

column represent community-level thresholds. Peaks in sum (z) values represent points at which synchronous species increases (z+) or declines (z-) are occurring. Solid and dashed lines represent cumulative frequency distribution of change points (x_{cp} thresholds among 100 bootstrap replicates). Figures in the second column represent species-level thresholds to total disturbance gradient. Species are plotted in increasing order of change point and solid symbols correspond to negative indicator species (z-) while open symbols correspond to positive indicator species (z+). Symbols are sized in proportion to the magnitude of the response (higher the z-value the bigger the symbol). Lines through the symbols represent the extent of the 5th and 95th percentiles. See Appendix 4 for species names, and numerical values associated with this figure. Scatter plots of the abundance of each species against a gradient of agricultural conversion are found in Appendix 4: Table A4.1 (negative) and Table A4.2 (positive).....154

Figure 5.3 Thresholds Indicator Taxa Analysis (TITAN; Baker and King 2010) of bird community response to proportion total disturbance (conversion of forest to agriculture, roads) for DMMB study site at 2 scales: Block scale (5 wetlands in 5 by 5 km area), and within 500 (m) of a wetland respectively. See Figure 2 for additional interpretive details.156

Figure A1.1 Comparison of SSI for landbirds and waterbirds counted during the study.....214

Figure A4.1 Scatter plots representing abundance of species that were significant negative (z-) indicators of a gradient of increasing agricultural conversion NEAB and DMMB at landscape and wetland scales.....253

Figure A4.2 Scatter plots representing abundance of species with significant positive (z+) responses to a gradient of increasing agricultural conversion for NEAB and DMMB at landscape and wetland scales.....264

CHAPTER 1: INTRODUCTION

1.1 Boreal forests, birds and wetlands

Biodiversity is a key component of environmental sustainability (*e.g.*, Väckär *et al.*, 2012) and maintaining biodiversity and ecosystem function alongside rising environmental pressure from economic development and human population growth are challenges faced worldwide (Fischer *et al.*, 2007). Canada's boreal forests are no exception and the cumulative effects of climate change and increasing anthropogenic disturbance are leading to unprecedented levels and rates of landscape modification (Schneider *et al.*, 2003). In addition to climate change, current threats to biodiversity in the boreal region include habitat loss and alteration due to activities associated with oil and gas exploration and extraction (*e.g.*, pipelines, wells, seismic lines), mining, forestry, agricultural conversion (Hobson and Bayne 2000; Hobson *et al.*, 2002) and urbanization (Schneider *et al.*, 2003). However, relative to other parts of the world, opportunities for innovative approaches to conservation and sustainable development are also potentially greater. Industrialization is relatively recent and large areas are still relatively intact especially in its northern portions (Foote and Krogman 2006; Niemi *et al.*, 1998). Wetlands in particular are considered stable, productive and relatively intact throughout much of the boreal, but these ecosystems are also among those least well studied and most susceptible to climate change (Foote and Krogman 2006).

Although estimates vary with scale and specific geographic boundaries, wetlands (open water, marshes, fens, bogs and swamps) and other aquatic areas occupy between 40-60% of the boreal landscape (Foote and Krogman 2006; Tarnocai 2001). These ecosystems are interspersed with uplands and due to a complex combination of factors such as natural disturbances (*e.g.*, fire, insect pest out-breaks, beaver activity, wind, tree disease, *etc.*), soil types, landforms, climate,

slope, and varying successional pathways, the resulting boreal landscape is a heterogeneous mosaic (Environment Canada 2013; Foote and Krogman 2006). Evidence of this heterogeneity can be observed at relatively small spatial scales which highlight a wide variety of transitions, or ecotones, between site types such as riparian areas between and within aquatic, wetland and terrestrial systems.

Canada's boreal forest is also one of the world's last vast wilderness areas (Foote and Krogman 2006) and recognized internationally for its role as the breeding ground for some 288 species of resident and migratory birds (Environment Canada 2013). Approximately 66% of the species that are currently of highest conservation priority in the boreal region are associated with wetlands and riparian areas (Environment Canada 2013). Spanning two decades, analysis of bird populations among different forest stand age classes and types (Hobson *et al.*, 2000; Kirk *et al.*, 1996) and studies of the effects of natural and anthropogenic disturbances on bird behaviour, individual species and communities (*e.g.*, Desrochers and Hannon 1997; Hannon 2005; Hobson 1996; Morissette *et al.*, 2002; Norton *et al.*, 2000 and many others) has undoubtedly augmented our understanding of habitat requirements of boreal birds (Cumming *et al.*, 2010). However, analogous work for wetlands and riparian-associated birds is relatively scarce (*e.g.*, Calmé *et al.*, 2002; Kardynal *et al.*, 2011; Kardynal *et al.*, 2009; Morissette *et al.*, 2013; Whitaker and Montevecchi 1997). Moreover, much of the work on wetland and riparian-associated birds has focussed on examining the efficacy of retaining forest buffers of various widths on individual upland bird species (*e.g.*, Darveau *et al.*, 1995; Hannon *et al.*, 2002) or has tended to emphasize aquatic birds in the strictest sense (*e.g.*, Epnors *et al.*, 2010; Lemelin 2007; McParland 2004; Paszkowski and Tonn 2006; Pierre 2001). As information to support land-use management and conservation planning decisions in boreal landscapes becomes increasingly essential, ecological

studies of species at the interface of terrestrial and aquatic ecosystems are needed to achieve a more complete understanding of habitat requirements for the full suite of boreal bird communities.

1.2 Defining and delineating the riparian bird community

Species are a fundamental unit of currency in biodiversity. However, maintaining and managing for biodiversity requires complementary approaches that combine species-level and ecosystem based concepts (Lindenmayer *et al.*, 2007). Thus community level studies that examine biodiversity composition, distribution and dynamics provide a conceptual framework for generalization (McGill *et al.*, 2006 Keith). Communities are collections of species that co-occur at a given place and time (Magurran 2003; Morin 1999). For avian community ecology, Wiens (1989) recommends the use of an operational definition of "assemblages of individuals of several species that occur together". Thus, there are a variety of approaches for delineating communities including geography, habitat, life-form, taxonomic, statistical clustering, and interactions among organisms or combinations of these (Morin 1999; Wiens 1989). As a result, delineations are often study- or context-specific and thus when discrete entities must be identified and delineated such as with land-use planning or in a regulatory context, the nature of communities challenges their utility for this purpose (Keith 2010).

In the case of riparian areas, defining a riparian bird community is further complicated by the difficulty of applying a clear spatial delineation. The Latin word "*Riparius*" meaning "of or belonging to the bank of a river" (Naiman *et al.*, 2005) clearly places flowing (lotic) water at the root of the word but this term is also frequently used to describe areas adjacent to lentic or non-flowing systems. Naiman *et al.*, (2005) provides a generalized definition of riparian areas as a "transitional or semi-terrestrial areas regularly influenced by freshwater, usually extending from

the edges of water bodies to the edges of upland communities”. A more precise definition that considers not only scale but also the interactions that can occur between terrestrial and aquatic systems was proposed by Ilhardt *et al.*, (2000) stating that riparian areas are “... 3 dimensional ecotones of interaction that include terrestrial and aquatic ecosystems, and extend down to the ground water, up above the canopy, outward across the floodplain, up the near slopes that drain to the water, laterally into the terrestrial ecosystem, and along the water course at variable width”. Defined this way, key attributes of riparian areas become apparent including (1) proximity to a body of water, (2) temporal and spatial (horizontal and longitudinal) variability, and (3) the probability of an area being considered riparian decreases with increasing distance from water but widths can be location- and species-specific (Lee *et al.*, 2004). The limitations of this type of complex definition for riparian areas become immediately apparent in a forest management or regulatory context where consistency and ease of enforcement are necessarily as much a concern as minimizing potential effects.

The task of classifying communities is also not as simple as using vegetation classes. First, vegetation classes typical of riparian areas do not occur exclusively in riparian areas. For example, many vegetation classes occur elsewhere on the landscape as early successional habitat, as mature forests away from water or as larger expanses of treed or shrubby wetland classes. In addition, bird species may be related to a variety of coarse vegetation classes depending on study context or purpose. For example, the White-throated Sparrow (*Zonotrichia albicollis*) has been described as each of a forest interior, understory, early-successional and generalist species (Hannah 2001; Poole 2005).

Nevertheless, quantitative approaches have been used to determine whether species should be considered “riparian”. For example, the USGS (Bureau of Land Management 2013)

defined riparian species as either riparian obligate or dependent. Riparian obligate species were those with "...at least 90% of nests or with > 90% of abundance in riparian vegetation during the breeding season", while for riparian dependent species these criteria are set at between 60 and 90% (Bureau of Land Management 2013). By this definition other species are considered as either "upland" or "aquatic" birds.

Arguably any species could be considered "riparian" if (1) it occurs exclusively or reaches maximum densities in habitats that are transitional between aquatic and terrestrial systems, (2) it requires riparian areas as an essential part of its life history (*e.g.*, nesting or foraging), or (3) it uses a combination of habitats found exclusively in riparian zones (*e.g.*, shorelines). Many species typically thought of as riparian species fit at least one of these criteria such as Northern Waterthrush (*Parkesia noveboracensis*) or Common Yellowthroat (*Geothlypis trichas*). However, these criteria would also apply to species typically considered wetland obligates or aquatic such as waterfowl, particularly those species that nest along the wetland periphery, (*e.g.*, Blue-winged Teal - *Anas discors*) or who require large cavity trees (*e.g.*, Common Goldeneye - *Bucephala clangula*) and shorebirds. Consequently, most riparian bird studies do not explicitly state quantitative methods of determining whether species are "riparian" but rather rely on species accounts (*e.g.*, Poole 2005) or other expert opinion to make this determination.

In the chapters that follow, I have opted not to pre-classify birds as "riparian" or otherwise but rather to examine the use of riparian areas by boreal bird assemblages while including as many species as the assumptions of selected survey and analytical methods in each chapter allow. I based this decision on two primary factors. First, the natural heterogeneity of the boreal forest and its extreme climate suggest birds should demonstrate some plasticity in their

habitat requirements (Mönkönnen and Welsh 1994; Simon *et al.*, 2003). Second, the riparian ecotone often represents the spatial juxtaposition of many vegetation classes providing an opportunity to measure some of this plasticity. Together, these factors subsequently raise some interesting questions. Are riparian bird communities simply structured by overlapping resource-use among species? Is there such a thing as a riparian specialist within boreal bird communities? To explore these questions, I selected metrics that place species on a generalist-to-specialist continuum allowing for a quantitative comparison of specialization among communities (Devictor *et al.*, 2008; Julliard *et al.*, 2006; Pandit and Kolasa 2012).

1.3 Community ecology – quantifying diversity and specialization

The number of species in a community and the distribution pattern of individuals among those species represent community structure and its defining properties (Keith 2010; Kelly *et al.*, 2008). Species diversity comprises abundance and frequency of occurrence and many techniques have been proposed for its measurement (*e.g.*, Shannon, Simpson, Chao *etc.*, Magurran 2003). Whitakker (1960) was the first to define community parameters by partitioning diversity into three components, alpha (α), beta (β) and gamma (γ) diversity. Alpha diversity is the number of species within a site or sampling unit (Magurran 2003), while gamma diversity, sometimes referred to as regional diversity, is the total number of species within a geographic boundary (Anderson *et al.*, 2006) or set of communities (Lande 1996). Beta diversity, on the other hand, has a number of definitions and as a result is also calculated in a variety of ways (Anderson *et al.*, 2006). The most commonly understood definitions of beta diversity are those by Whitakker (1960) and MacArthur (1962). Whitakker (1960) defined beta diversity as the proportion that a given area is richer than the average of samples within it ($\beta = \gamma/\bar{\alpha}$). MacArthur (1962) proposed an additive method ($\gamma = \beta + \bar{\alpha}$) which was revived by Lande

(1996) and has since stimulated a renewed interest in diversity partitioning (e.g., Crist and Veech 2006; Flohre *et al.*, 2011; Schmera and Podani 2013; Veech *et al.*, 2002).

However, Anderson *et al.*, (2011) differentiate among definitions within two categories of beta diversity which are turnover and variation and provide guidelines for their use, calculation and interpretation in ecological studies. Turnover measures the change in identity, relative abundance (cover) or biomass of individual species from one sampling unit to another along a spatial temporal or environmental gradient (Anderson *et al.*, 2011). Variation, on the other hand, refers to variability in these same factors among sampling units such as among habitat types or experimental treatments. Statistical methods to calculate beta diversity and their relationship to the various definitions have been discussed in detail and debated elsewhere (Anderson *et al.*, 2011; Legendre *et al.*, 2005) and new statistical methods continue to be developed (Anderson *et al.*, 2006; Bacaro *et al.*, 2007; Schmera and Podani 2013).

Variation in species composition among locations is generally calculated using selected multivariate measures of ecological distance (Anderson *et al.*, 2006). This particular method has been used to interpret community dynamics in a number of ways. For example, high species turnover can be the result of seasonal cycles in species composition or indicate a community with a high number of transient species (Thrush *et al.*, 2008). High species turnover can also be an indication that a particular habitat patch is unable to sustain the original community (Pearson and Manuwal 2001) and has been shown to increase in communities along disturbance gradients (Houseman *et al.*, 2008). Since riparian areas are thought to be heterogeneous and stochastic relative to other portions of the landscape, interpretations similar to those above are possible. That is, multivariate dispersion may be higher in riparian than upland forests. On the other hand, riparian areas may be one of many types of ecotones in the boreal forest and given the many

factors intrinsic to the heterogeneity of boreal systems (*e.g.*, natural disturbances) non-riparian forests may plausibly be as stochastic as riparian areas (Macdonald *et al.*, 2006; Whitaker and Montevocchi 1997).

1.4 From measuring diversity to measuring function: indices for assessing ecological function using bird communities

Biodiversity ecosystem function (BDEF) research is motivated by the loss of biodiversity and wanting to understand potential ecosystem consequences (Hillebrand and Matthiessen 2009). Two major premises drive research related to diversity and ecological function. The first is that higher-level ecological function in all ecosystems is controlled, at least in part, by the species present such that loss of species leads to reduced functional capacity in some way (Elmqvist *et al.*, 2003) The second premise, implies that functions are known and can be measured directly or indirectly (Petchey and Gaston 2002). Studies have measured function directly by looking at productivity (*e.g.*, nutrients, biomass as in Tilman *et al.*, 2001) and indirectly via changes in representation of functional traits in assemblages inferring changes in function (*e.g.*, resource use, pollinators, food webs)

The contribution of birds to ecological function is not always well recognized and is certainly less well understood in temperate than in tropical systems (Sekercioglu 2006). Ecological functions of birds include pollination, decomposition, seed dispersal, pest control, nutrient cycling and ecosystem engineering (Sekercioglu 2006). For instance, insectivorous birds have been shown to suppress populations of insect herbivores which otherwise would reduce crop yields (Marquis and Whelan 1994), and are implicated in reducing the likelihood of insect pest outbreaks (Dickson *et al.*, 1979); waterfowl may be important nutrient vectors inputting up to 40% of nitrogen and 75% of phosphorous (Post *et al.*, 1998) entering a wetland

when present in large numbers (Hahn *et al.*, 2008). Arguably, the range of ecological functions is more diverse in birds than in any other vertebrate group and some functions have no ecological equivalents in other taxa (e.g., cavity makers, Sekercioglu 2006). However, quantifying the effects of birds on ecosystem function remains challenging.

For birds, ecological function can be measured directly (e.g., number of nesting holes, nutrient levels, pollen deposition rates), but in community level studies function is most often inferred from traits (Fischer *et al.*, 2007). To be appropriate for quantifying function, a trait must strongly influence an organism's ecological performance and is therefore preferably measured at the individual level, averaged and used comparatively across species (McGill *et al.*, 2006). However for birds, most authors have combined factors such as foraging guilds (Petchey *et al.*, 2007; Petchey and Gaston 2002), measures of resource quantity (body mass, clutch size), diet, feeding substrate, and foraging period (Fischer *et al.*, 2007) into measures of functional diversity. As a result, methodologies combining these factors into a continuous variable representing function of birds can then be used to test relationships and look for patterns with the advantage of increasing the number of functional traits that can be used at once to differentiate functional contributions of species within a community and compare functional diversity among communities (Petchey and Gaston 2006). The interest in measuring functional diversity has steadily increased over the last decade and new methodologies are reviewed as quickly as they are being developed (e.g., Mouchet *et al.*, 2008; Petchey and Gaston 2006; Schleuter *et al.*, 2010).

The primary impetus for these efforts is to measure and make predictions regarding effects of species loss on ecosystem function over time due to climate change or human disturbances (Hillebrand and Matthiessen 2009; Sundstrom *et al.*, 2012). Thus an extension of

trait-based approaches is that these metrics of function also yield insight into functional redundancy and ecosystem resilience (Gamfeldt *et al.*, 2008; Sundstrom *et al.*, 2012). Resilience is defined as “the ability of ecosystems to absorb disturbances while maintaining their characteristic functions and feedbacks (Holling 1973). While conceptually simple, resilience has been criticized for being a theoretical construct that is difficult to measure and quantify (Allen *et al.*, 2011; Carpenter *et al.*, 2001; Fischer *et al.*, 2007). Attempts to quantify resilience rest on two of its key components: 1) ecological functions and 2) the distribution of functions across scales (Allen *et al.*, 2005; Fischer *et al.*, 2007). Functional richness or the diversity and range of functional traits are thought to contribute to the resilience of ecosystems. First functional richness and diversity may contribute to functional redundancy, when a function is performed by multiple biologically unique species (*e.g.*, insurance hypothesis- Yachi and Loreau 1999). Others have suggested a mechanism for increased resilience might be via species complementarity where increasing the number of species increases the use of non-overlapping resources (Wohl *et al.*, 2004). Authors have also postulated that resilience should also be greater when functions are performed across spatial scales (Peterson *et al.*, 1998).

1.5 Effects of human disturbance on riparian and wetland associated bird community diversity and function

Although there are many anthropogenic disturbances occurring in the boreal forest, the most cumulative of landscape level changes are in its southern fringe due to agricultural conversion in combination with roads and other related infrastructure (Hobson *et al.*, 2002). In many areas the conversion of land to agricultural use often produces a pattern of forest remnants that are concentrated along waterways (Rodewald and Bakermans 2006). While these forest remnants are thought to offer some protection for aquatic resources, research related to effects

of forestry has shown that the value of forest remnants and buffers as habitat for forest dependent boreal birds is reduced in strips that are < 200 m wide (Hannon *et al.*, 2002). However, general guidelines for buffer widths are typically much narrower (usually 100 m or less; Lee *et al.*, 2004) and apply only to landscapes where forestry is a primary disturbance. In addition such guidelines overlook the landscape matrix in which the shoreline forest is embedded (Marczak *et al.*, 2010) a factor that authors have demonstrated affects riparian bird assemblages. For example, Saab (1999) found that bird species richness in riparian areas was positively associated with the amount of natural vegetation in the surrounding landscape. Similarly, Bakermans (2003) found that the Acadian Flycatcher (*Empidonax virescens*) required riparian forests 25% wider in urban than in rural landscapes. While there may be interactions between the width of forest retained adjacent to riparian systems and the surrounding matrix, Groom and Grubb (2002) found that woodland area within the landscape was a better predictor of riparian bird communities than width.

Agricultural conversion has known negative effects on boreal bird species; reducing the abundance of forest interior birds and increasing nest predation and brood parasitism of ground and shrub nesting birds (Hobson and Bayne 2000). However, effects of agricultural conversion on abundance and occurrence riparian and wetland associated birds have not been quantified. Thus the extent of agricultural conversion in the surrounding landscape that can occur while maintaining the avian wetland associated communities typical of boreal forest systems is currently unknown. Community level responses to cumulative effects may occur gradually over the disturbance gradient or as thresholds (Baker and King 2010; With and King 2004). Thresholds are described as sudden or steep changes in an ecological variable (*e.g.*, abundance of a population, or complete change in community type) occurring across a narrow range of values,

or a single value (Huggett 2005). Generally evidence for thresholds is limited however, to species that exhibit a strong preference for particular habitat types that are more likely to exhibit a threshold response (Swift and Hannon 2010).

1.6 Thesis Outline

I have organized this dissertation around the thesis that boreal birds are effective indicators of ecological function, that community-level metrics are useful for differentiating boreal avian assemblages, and that together these can be used to measure effects of land-use change. My purpose is two-fold. First, I aim to advance understanding of boreal riparian and wetland-associated bird communities and my second goal is to evaluate applicability of emerging community-level metrics for comparing different habitats and measuring effects of human disturbance.

In the first two chapters following this one, I focus largely on describing “what a species needs” as represented by the habitats in which it is found. Chapter 2 examines whether riparian zones associated with boreal plain wetlands (shallow ponds) act as a source of unique bird species and whether community dynamics (*i.e.*, variability in composition, relative composition of generalists and specialists) of these ecotones are unique relative to that of upland bird communities. In Chapter 3, I use data collected in boreal Manitoba to specifically examine the potential for applying accepted wetland classification schemes to refine current understanding of habitat associations for birds. Then, I shift focus to explore “what a species does” in Chapter 4 which examines the use of ecological traits as an index of ecological function and resilience and compares these in riparian and upland bird communities. Chapter 5 provides an examination of community-level responses of riparian birds to the agricultural conversion of habitats using a recent technique developed specifically for identifying community-level thresholds. Finally,

Chapter 6 provides a synthesis of key findings of the dissertation with some recommendations for practical application, biodiversity conservation and further study.

1.7 References

- Allen, C. R., G. S. Cumming, A. S. Garmestani, P. D. Taylor, and B. H. Walker. 2011. Managing for resilience. *Wildlife Biology* 17:337-349.
- Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958-966.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of α diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19-28.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693.
- Bacaro, G., C. Ricotta, and S. Mazzoleni. 2007. Measuring beta-diversity from taxonomic similarity. *Journal of Vegetation Science* 18:793-798.
- Baker, M. E. and R. S. King. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* 1:25-37.
- Bakermans, M. H. 2003. Hierarchical habitat selection by the Acadian flycatcher: implications for conservation of riparian forests. The Ohio State University.

- Bureau of Land Management. 2013. Birds as indicators of riparian vegetation condition in the western U.S. Bureau of Land Management, Partners in Flight, Boise, Idaho.
- Calmé, S., A. Desrochers, and J.-P. L. Savard. 2002. Regional significance of peatlands for avifaunal diversity in southern Quebec. p. 273-281.
- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4:765-781.
- Crist, T. O. and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species-area relationships: unifying alpha-, beta- and gamma-diversity with sample size and habitat area. *Ecology Letters* 9:923-932.
- Cumming, S. G., K. L. Lefever, E. M. Bayne, T. Fontaine, F. K. A. Schmiegelow, and S. J. Song. 2010. Toward conservation of Canada's boreal forest avifauna: design and application of ecological models at continental extents. *Avian Conservation and Ecology* 5:-8.
- Darveau, M., P. Beauchesne, L. Bélanger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. *Journal of Wildlife Management* 59:67-77.
- Desrochers, A. and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11:1204-1210.
- Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17:252-261.

- Dickson, J. G., R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll. 1979. The role of insectivorous birds in forest ecosystems. Academic Press, New York.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488-494.
- Environment Canada. 2013. Bird Conservation Strategy for Bird Conservation Region 6: Boreal Taiga Plains. Canadian Wildlife Service, Environment Canada, Edmonton, Alberta.
- Epner, C. A., S. E. Bayley, J. E. Thompson, and W. M. Tonn. 2010. Influence of fish assemblage and shallow lake productivity on waterfowl communities in the Boreal Transition Zone of western Canada. *Freshwater Biology* 55:2265-2280.
- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. A. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- Flohre, A., C. Fischer, T. Aavik, J. Bengtsson, F. Berendse, R. Bommarco, P. Ceryngier, L. W. Clement, C. Dennis, S. +. Eggers, M. Emmerson, F. Geiger, I. Guerrero, V. Hawro, P. Inchausti, J. Liira, M. B. Morales, J. J. O+|ate, T. P+ñrt, W. W. Weisser, C. Winqvist, C. Thies, and T. Tschardtke. 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications* 21:1772-1781.
- Foote, L. and N. Krogman. 2006. Wetlands in Canada's western boreal forest: agents of change. *The Forestry Chronicle* 82:825-833.

- Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89:1223-1231.
- Groom, J. D. and T. C. Grubb. 2002. Bird Species Associated with Riparian Woodland in Fragmented, Temperate-Deciduous Forest
Especies de Aves Asociadas con Zonas Riparias Arboladas Fragmentadas de Bosque Templado Caducifolio. *Conservation Biology* 16:832-836.
- Hahn, S. S., S. S. Bauer, and M. Klaassen. 2008. Quantification of allochthonous nutrient input into freshwater bodies by herbivorous waterbirds. *Freshwater Biology* 53:181-193.
- Hannah, K. C. 2001. Patterns in habitat quality for the white-throated sparrow (*Zonotrichia albicollis*) in a recently logged landscape. University of Alberta.
- Hannon, S. J. 2005. Effect of stand vs. landscape level forest structure on species abundance and distribution. Sustainable Forest Management Network, Edmonton, Alberta.
- Hannon, S. J., C. A. Paszkowski, S. Boutin, J. DeGroot, S. E. Macdonald, M. Wheatley, and B. R. Eaton. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. *Canadian Journal of Forest Research* 32:1784-1800.
- Hillebrand, H. and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12:1405-1419.
- Hobson, K. 1996. The influence of forest management practices on boreal forest bird habitat use and productivity: a community approach., Prince Albert Model Forest Association Inc.

- Hobson, K. A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixedwoods of western Canada. *Wilson Bulletin* 112:373-387.
- Hobson, K. A., E. M. Bayne, and S. L. Van Wilgenburg. 2002. Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. *Conservation Biology* 16:1530-1541.
- Hobson, K. A., D. A. Kirk, and A. R. Smith. 2000. A multivariate analysis of breeding bird species of western and central Canadian boreal forests: stand and spatial effects. *Ecoscience* 7:267-280.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-23.
- Houseman, G. R., G. G. Mittlebach, H. L. Reynolds, and K. L. Gross. 2008. Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology* 89:2172-2180.
- Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124:301-310.
- Ilhardt, B. L., E. S. Verry, and B. J. Palik. 2000. Defining riparian areas. p. 23-42. *In* E. S. Verry, J. W. Hornbeck, and A. Dolloff (eds.) *Riparian management in forests of the continental eastern United States*. Lewis Publishers, Boca Raton, Florida.
- Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters* 9:1237-1244.

- Kardynal, K. J., J. L. Morissette, S. L. VanWilgenburg, E. M. Bayne, and K. A. Hobson. 2011. Avian response to experimental harvest in southern boreal mixedwood shoreline forests: implications for riparian buffer management. *Canadian Journal of Forest Research* 41:2375-2388.
- Kardynal, K., K. A. Hobson, S. L. Van Wilgenburg, and J. L. Morissette. 2009. Moving riparian management guidelines towards a natural disturbance model: an example using boreal riparian and shoreline forest bird communities. *Forest Ecology and Management* 257:54-65.
- Keith, D. A. 2010. The interpretation, assessment and conservation of ecological communities. *Ecological Management and restoration* 10:S3-S15.
- Kelly, C. K., M. G. Bowler, O. Pybus, and P. H. Harvey. 2008. Phylogeny, niches and relative abundance in natural communities. p. 962-970.
- Kirk, D. A., A. W. Diamond, K. A. Hobson, and A. R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Canadian Journal of Zoology* 74:1749-1770.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5-13.
- Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. *Journal of Environmental Management* 70:165-180.

- Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435-450.
- Lemelin, L.-V. 2007. L'habitat de la sauvagine en nidification dans le Québec forestier. Université du Québec.
- Lindenmayer, D. B., J. Fischer, A. Felton, R. Montague-Drake, A. D. Manning, D. Simberloff, K. Youngentob, D. Saunders, D. Wilson, A. M. Felton, C. Blackmore, A. Lowe, S. Bond, N. Munro, and C. P. Elliott. 2007. The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos* 116:1220-1226.
- Macdonald, S. E., B. Eaton, C. S. Machtans, C. Paszkowski, S. Hannon, and S. Boutin. 2006. Is forest close to lakes ecologically unique? Analysis of vegetation, small mammals, amphibians, and songbirds. *Forest Ecology and Management* 223:1-17.
- Magurran, A. E. 2003. *Measuring Biological Diversity*. Blackwell Science, Malden, MA.
- Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. R. Wood, and J. S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecological Applications* 20:126-134.
- Marquis, R. J. and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007-2014.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution* 21:178-185.

- McParland, C. E. 2004. Food web interactions of waterbirds and fish in eutrophic wetlands of Alberta's aspen parkland. University of Alberta (Canada).
- Mönkönen, M. and D. A. Welsh. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. *Annales Zoologici Fennici* 31:61-70.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, Malden, MA.
- Morissette, J. L., K. J. Kardynal, E. M. Bayne, and K. Hobson. 2013. Comparing bird community composition among boreal wetlands: is wetland classification a missing piece of the puzzle? *Wetlands* 33:653-665.
- Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research* 32:2169-2183.
- Mouchet, M., F. Guilhaumon, S. Villeger, N. W. H. Mason, J.-A. Tomasini, and D. Mouillot. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117:794-800.
- Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia - ecology, conservation, and management of streamside communities*. Elsevier Academic Press, Burlington, MA.
- Niemi, G., J. Hanowski, P. Helle, R. Howe, M. Mönkkönen, L. Vernier, and D. Welsh. 1998. Ecological sustainability of birds in boreal forests. *Conservation Ecology* 2:17.

- Norton, M. R., S. J. Hannon, and F. K. A. Schmiegelow. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. *Ecography* 23:209-223.
- Pandit, S. N. and J. Kolasa. 2012. Opposite effects of environmental variability and species richness on temporal turnover of species in a complex habitat mosaic. *Hydrobiologia* 685:145-154.
- Paszkowski, C. A. and W. M. Tonn. 2006. Foraging guilds of aquatic birds on productive boreal lakes: environmental relations and concordance patterns. *Hydrobiologia* 567:19-30.
- Pearson, S. F. and D. A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed pacific northwest Douglas-fir forests. *Ecological Applications* 11:840-853.
- Petchey, O. L., K. L. Evans, I. S. Fishburn, and K. J. Gaston. 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology* 76:977-985.
- Petchey, O. L. and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402-411.
- Petchey, O. L. and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741-758.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Pierre, J. P. 2001. Effects of forest harvesting disturbance on aquatic birds in the boreal forest of Alberta. University of Alberta (Canada).

- Poole, A. e. 2005. The birds of North America Online. Cornell Laboratory of Ornithology, Ithaca, New York.
- Post, D. M., J. P. Taylor, J. F. Kitchell, M. H. Olson, D. E. Schindler, and B. R. Herwig. 1998. The Role of Migratory Waterfowl as Nutrient Vectors in a Managed Wetland. *Conservation Biology* 12:910-920.
- Rodewald, A. D. and M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? *Biological Conservation* 128:193-200.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9:135-151.
- Schleuter, D., M. Daufresne, F. Massol, and C. Argiller. 2010. A user's guide to functional diversity indices. *Ecological Monographs* 80:469-484.
- Schmera, D. and J. Podani. 2013. Components of beta diversity in hierarchical sampling designs: a new approach. *Ecological Indicators* 26:126-136.
- Schneider, R. R., J. B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land-uses in the western Canadian sedimentary basin: a modelling approach. *Conservation Ecology* 7:8.
- Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. *Trends in Ecology & Evolution* 21:464-471.

- Simon, N. P., A. W. Diamond, and F. E. Schwab. 2003. Do northern forest bird communities show more ecological plasticity than southern forest bird communities in eastern Canada? *Ecoscience* 10:289-296.
- Sundstrom, S. M., C. R. Allen, and C. Barichiev. 2012. Species, Functional Groups, and Thresholds in Ecological Resilience. *Conservation Biology* 26:305-314.
- Swift, T. L. and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. *Biological Reviews* 85:35-53.
- Tarnocai, C. 2001. Eastern Cereal and Oilseed Research Centre Research Branch, Agriculture and Agri-Food Canada, Ottawa, Canada.
- Thrush, S. F., Hallida Jane, J. E. Hewitt, and A. M. Lohrer. 2008. The effects of habitat loss, fragmentation, and community homogenization on resilience in estuarries. *Ecological Applications* 18:12-21.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843-808.
- Väckär, D., B. ten Brink, J. Loh, J. E. M. Baillie, and B. Reyers. 2012. Review of multispecies indices for monitoring human impacts on biodiversity. *Ecological Indicators* 17:58-67.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99:3-9.

- Whitaker, D. M. and W. A. Montevercchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a Balsam fir ecosystem. *Canadian Journal of Forest Research* 27:1159-1167.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.
- Wiens, J. A. 1989. The ecology of bird communities. Volume 1. Foundations and patterns. University Press, Cambridge.
- With, K. A. and A. W. King. 2004. The effect of landscape structure on community self-organization and critical biodiversity. *Ecological Modelling* 179:349-366.
- Wohl, D. L., S. Arora, and J. R. Gladstone. 2004. Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. *Ecology* 85:1534-1540.
- Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences* 96:1463-1468.

CHAPTER 2: COMPOSITION AND ECOLOGICAL CHARACTERISTICS OF RIPARIAN BIRD ASSEMBLAGES ASSOCIATED WITH BOREAL WETLANDS

A version of this chapter is in preparation for publication: Morissette, J.L., E.M. Bayne and K.A. Hobson. *In Prep.* Composition and ecological characteristics of riparian bird assemblages associated with boreal wetlands.

2.1 Introduction

Riparian areas are ecotones between aquatic and terrestrial ecosystems (Naiman *et al.*, 2005) and frequently have higher species richness, diversity and abundance than the neighbouring uplands. Consequently, riparian areas are often considered to be disproportionately important (Sanders and Edge 1998) or unique (Naiman and Descamps 1997) habitat relative to adjacent terrestrial areas. Higher richness and diversity in riparian areas are believed to be caused by increased levels and diversity of resources. However, diversity patterns of riparian ecosystems are not always consistent. An extensive meta-analysis of studies comparing terrestrial and riparian habitats across different taxa and ecosystems found that significant differences in mean or cumulative species richness are not always present but that riparian areas are consistently a source of unique species and thus an important contributor to regional (gamma) diversity (Sabo *et al.*, 2005). The lack of a consistent pattern of difference in species richness and abundance between riparian and upland areas has been attributed to a number of factors such as a natural heterogeneity of vegetation (Macdonald *et al.*, 2006), or to the degree of variation in resource gradients in mesic forests compared to more arid areas (Whitaker and Montevicchi 1997). In addition, differences in study design and challenges associated with delineation or even definition of riparian areas can explain such complex

findings. For example, some studies of birds in riparian areas have emphasized only one type of water body (*e.g.*, Boulet *et al.*, 2003) while others have emphasized shoreline forest of only one forest type (*e.g.*, mixed wood). Such approaches facilitate comparisons among treatments (*e.g.*, harvested vs. unharvested) but shoreline forests and ecotone types are varied and basic descriptions of bird assemblages that broadly consider this variation are lacking, particularly in the boreal forest.

In boreal forests, wetlands can make up between 20-60 % of the landscape (National Council for Air Stream Improvement 2007). Depending on the hydrologic, soil and landscape context, the riparian ecotone between open water and upland forests can encompass a broad range of vegetation classes ranging from early successional forests typical of terrestrial systems to a variety of wetland classes such as treed or shrubby swamps, bogs and fens. In addition, different zones of transition are possible including wetland to wetland ecotones such as between open-water wetlands and vegetated wetland classes (*e.g.*, between an open-water body and conifer swamp) or wetland to upland ecotones demarking the transition to true terrestrial forests (*e.g.*, between a treed wetland and mature deciduous forest). The spatial complexity of these transitions varies and can occur over as little as 10 m or over several hundred meters perpendicular or parallel to the shoreline of a water body.

Such zonal transitions often result in a number of different types of vegetation existing in close proximity. Community theory suggests that such heterogeneity should be reflected in the ecological characteristics of species within an assemblage such as whether generalists or specialists dominate (Pandit and Kolasa 2012). Environmental heterogeneity should increase species richness but also might favour generalists over specialists which are thought to benefit from greater consistency in their environment (Julliard *et al.*, 2006). Pandit and Kolasa (2012)

found that higher environmental variability resulted in decreased species richness of specialists. Thus, riparian assemblages might have both higher species richness and species that are more plastic in their habitat preferences (generalists) than species occurring in relatively more contiguous areas. Interestingly, communities with high species richness and dominated by generalists are also expected to exhibit lower beta-diversity (turnover and variation) (Naiman *et al.*, 2005).

Definitions of *beta*-diversity generally fall into two camps, variation in species composition among sites and turnover along an environmental or temporal gradient (Anderson *et al.*, 2011; Schmera and Podani 2013). For example, high levels of species turnover along an environmental gradient, suggest that spatial and environmental heterogeneity at multiple scales are important for maintaining a diverse regional species pool (Anderson *et al.*, 2006; Pollock *et al.*, 1998). However, higher levels of species turnover among sites of a single vegetation class or landscape position might also indicate unstable communities such as those in areas with a high frequency of disturbances (Houseman *et al.*, 2008; Julliard *et al.*, 2006). Thus, despite favouring generalists, if riparian areas do not represent optimal habitat for birds relative to other areas on the landscape, then it is reasonable to expect less predictable community composition among riparian sites relative to upland sites and little differences in turnover along the riparian to upland environmental gradient.

We examined riparian zones associated with boreal plain wetlands (shallow ponds) to determine whether their periphery contains characteristic bird assemblages and to identify whether some species are unique to these areas. We limited our comparisons to species other than waterfowl. In addition, we compared beta-diversity (as multivariate dispersion) among riparian and upland sites and relate these results to overall specialization within and among

boreal bird communities in riparian and upland areas. We hypothesize that as ecotones with heterogeneous vegetation composition, riparian areas associated with wetlands act as a source of regionally unique bird species, are more variable in their species composition and contain a less specialized community composition relative to that of upland bird communities.

2.2 Methods

2.2.1 Study area

We conducted this study near Utikuma Lake, AB, Canada, which is approximately 400 km north of Edmonton, AB (Figure 2.1; 56°, 52'N, 115° 27' W). The area is situated in the boreal mixedwood region of the Boreal Plains ecozone of north central Alberta. The area is dominated by three geological formations, a moraine area that runs north to south from Utikuma Lake, an outwash area to the west of the moraine and a lowland lacustrine plain to the east. Five major wetland classes (marsh, swamp, fen, bog and open water) account for between 30-60 % of the total study area. Depending on geologic formation and hydrologic regime, the transition zone and shoreline forest of typical boreal ponds or lakes may contain elements of several wetland classes and/or several upland classes often resulting in a structurally heterogeneous shoreline. Further some areas exhibit two transitions, one from aquatic to a treed wetland and another several hundred meters away from open water separating treed wetlands (lowland edge) from upland forests (Figure 2.2).

Riparian areas adjacent to open-water wetlands and lakes were generally characterized by a gradient from the water's edge of aquatic grasses, sedges (*Carex* spp.), rushes (*Juncus* spp.), cattails (*Typha latifolia*), and lowland shrubs (*Alnus* spp., *Salix* spp.), to more xeric shrub species (e.g., *Cornus canadensis*) and trees in the upland. The most common tree species in transition

areas of forested wetland (lowland) sites included balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*). The shoreline forest and upland forests, depending on soil characteristics, disturbance history and topography were pure or mixed stands of any combination of trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and jack pine (*Pinus banksiana*). In addition to variability introduced by changes over time in the moisture regime, in both study areas, tree harvest by beaver (*Castor canadensis*) was common adjacent to most wetlands where hardwood tree species were present (Morissette *et al.*, unpubl. data). Occasionally, dead trees also stood in open water within ponds created or maintained by beaver activity.

2.2.2 Site selection and study design

In 2002, we selected 24 open-water wetlands and ponds between 2.5 and 16 ha distributed among three geomorphologic areas typical of the western boreal plain (Ferone and Devito 2004). In 2003, we expanded our surveys to 64 ponds (Table 2.1). Where possible, each riparian transect was paired with an upland transect of equal length, and similar forest type at least 200 m away from the riparian transect and any other pond. In one geomorphologic area (*e.g.*, the clay plain), the transition between upland and aquatic was greater than 200 m wide. In these cases, another transect representing the transition between treed wetland and upland (lowland edge) was also added ($n = 13$). Thus, we included 2 types of transitions (riparian = aquatic to terrestrial transition; lowland edge = treed wetland to upland transition) to each other and to upland forest (no ecotone). The start point and direction of travel for each transect were randomly situated with the only limiting factor being that a 400 m transect could fit. In some cases, we used two separate randomly placed 200 m transects. The design and survey method

also permitted an additional set of comparisons between only the shoreline forest (upland) portions of each transect type and half of the upland transect. These comparisons were made to establish whether bird communities in shoreline forest (mature forested portion of ecotone) were unique from mature forests of similar composition in the upland.

2.2.3 *Bird surveys*

Our bird survey method combined a 400 m variable-width transect with two, 10 minute, variable-radius point counts (Figure 2.2; Kardynal *et al.*, 2009). Each transect was surveyed at a rate of 10 min/100 m (Hobson and Schieck 1999; Kardynal *et al.*, 2009). A 5-minute playback for marsh birds was also conducted (North American Marsh Bird Monitoring Protocol (Conway 2002)). We placed transects parallel to the shoreline between the ecotone and the shoreline forest (Figure 2.2). Each point count was placed 50 m from the water's edge and 200 m apart typically at the 50 m and 350 m mark of the transect. Although individual birds may have been detected on both transect and point count, these were counted as single birds in all subsequent analyses. For both types of surveys, "distance to bird" was estimated in bands of 0–25 m, 26–50 m, 51–100 m or >100 m from the observer. During the survey, observers assigned each bird to one of eighteen predetermined vegetation classes based on the best estimate of the bird's actual position when it was counted. In 2002, each site was surveyed three times whereas in 2003 each site was surveyed only once to accommodate the larger sample size. Observers underwent a period of training prior to surveys and were randomly assigned to survey locations to avoid confounding observer effects and effects of habitat type. Surveys were conducted 1-30 June 2002 and 2003, began 30 minutes before sunrise, ended within 5 hours, and only took place on days free of rain with low wind (< 4 on a Beaufort scale).

2.2.4 Vegetation composition of transects

We used a remotely sensed vegetation inventory (LANDSAT TM 30 m resolution; 2001-2002 imagery) to assess the relative composition of vegetation within transects in each habitat type. Using GIS each transect was buffered by 100 m and the proportional composition of each vegetation class was assessed. Remotely sensed vegetation classes corresponded to those used during surveys as outlined in Table 2.2.

2.2.5 Community and species-level difference between upland, lowland and riparian sites

Data for two point counts and corresponding transects were combined for analysis (*i.e.*, to reflect the bird community composition in any given riparian, lowland or upland site). For all analyses, we used the mean number of birds at a site in 2002 (each site was visited 3 times) and the total counted per site in 2003 (sites were only visited once). To compare the complete upland transect with the complete riparian transect, we limited observations to birds counted within 100 m. To compare only the shoreline forest portion of the riparian ecotone to upland forest, only birds detected within 100 m on the upland half the transect were included.

Because the number of individuals differed among the three habitat types, we measured differences in richness by individual-based rarefaction (Gotelli and Colwell 2001). We used a Monte Carlo simulation procedure and Chao1 estimates (EcosimVersion 9.0; Gotelli and Entsminger 2000) because the sample size and number of individuals differed among the three habitat types. Species unique to any particular habitat type were those counted on only that transect type.

We used indicator species analysis (ISA; Duf r ne and Legendre 1997; McCune and Grace 2002) to identify whether species were significantly associated with either upland, lowland or riparian areas (4999 randomizations, software package - PCORD; R). This technique

is useful for evaluating the association between site classifications and species and "good indicator species" are those found to be exclusive to a group and detected at most of the sites within that group (Legendre and Legendre 2002). Indicator values are based only on combined within-species-abundances and occurrences comparisons and therefore are not affected by the abundance of other species.

We used nonmetric multidimensional scaling (NMS; Clarke 1999; McCune and Grace 2002) and multi-response permutation procedures (MRPP; McCune and Grace 2002) to qualitatively and quantitatively examine differences in community composition. In both cases, we applied a Bray-Curtis distance metric. MRPP tests the hypothesis of no multivariate difference between groups and the accompanying NMS provides a visual assessment of the separation among groups and the association of species with these groups (McCune and Grace 2002). Both procedures are non-parametric, an advantage with species occurrence and abundance data that are potentially non-linear and with skewed frequency distributions.

2.2.6 Multivariate dispersion as a measure of beta diversity

We tested the degree of community dispersion among riparian, upland and lowland community types using permutation analysis of dispersion (PERMDISP2; Anderson *et al.*, 2006). A multivariate analogue of the Levene's test, PERMDISP2 measures the distance of samples from the group centroid and allows for unequal sample sizes. We removed singletons, and used a Bray-Curtis distance measure. For consistency, we used this ecological distance measure in all multivariate analyses. We tested for effects of habitat type using 9999 permutations.

2.2.7 Quantifying specialization (or plasticity)

We quantified "habitat specialization" for each species by determining the number of habitat classes in which a species is known to be present relative to the available habitat classes (Devictor *et al.*, 2010; Julliard *et al.*, 2006). The degree of habitat specialization is the variance of the average densities among all habitat classes considered (Devictor *et al.*, 2008). This measure is continuous and allows the ordering of species from most specialized (occurring in few vegetation classes) to least specialized (occurring in many vegetation classes). Thus, a Species Specialization Index (SSI) is the coefficient of variation of abundances among vegetation classes (Julliard *et al.*, 2006). This measure not only incorporates the presence and absence of species among vegetation classes, but also accounts for density variation among vegetation classes. SSI can also be calculated using presence and absence data by assuming equal density in all occupied vegetation classes where H is the number of possible classes and h is the number of classes where a species is counted (Devictor *et al.*, 2008; Julliard *et al.*, 2006).

$$SSI = \left(\frac{H}{h} - 1 \right)^{1/2}$$

A species is considered more specialized to a particular class where its density is highest and more of a generalist where its density varies little among habitat classes (Devictor *et al.*, 2008).

To reduce potential biases due to small sample sizes when developing specialization indices, we combined data from this and three other studies that used the same habitat assignment protocols (see *Bird Surveys*) to best reflect the SSI for each species (Appendix 1: TableA1.1). We used 19 habitat classes (Table 2.2) and calculated SSI's for species detected at least 50 times using 48,050 detections and surveys of over 600 wetlands from a larger regional dataset. We used the SSI to quantify the relative specialisation of species in riparian and upland

communities as well as the overall community specialization index (CSI) for riparian and upland bird communities. The CSI was calculated from the average SSI of the individuals counted in the community (*i.e.*, at each pond; Julliard *et al.*, 2006). The formula used is as follows

$$\frac{CSI_j = \sum_{i=1}^n a_{ij} (SSI_i)}{\sum_{i=1}^n a_{ij}},$$

where n is the total number of species recoded, a_{ij} is the abundance of individuals of species in plot j and SSI is its specialization index (Devictor *et al.*, 2008). To compare the riparian community to the upland community, only landbirds were included in the CSI calculations.

2.3 Results

A total of 11,868 individuals representing 86 species were recorded in the study area over 2 years. We did not analyze differences in detection due to habitat differences, but to reduce these potential effects, we used only data for birds detected within 50 m of the observer (Nur *et al.*, 2008). For riparian and upland habitats, accumulation curves indicated that very few new species could be expected in each of the habitat types with more sampling because each curve approached its asymptote (Figure 2.3). Species richness was significantly higher in riparian areas than in the other two habitat classes (Figure 2.3).

Twenty-four species were unique to riparian areas, while only one species was unique to lowlands and none were unique to uplands. If waterbirds, were included these numbers obviously increased (35 species were unique to riparian areas, one to lowland and one to upland areas, respectively). When only the forested portion of transects was considered, riparian areas were a source of only seven unique species relative to the other two habitat types we examined. Many of these species occurred less than five times throughout the entire study. Indicator Species Analysis showed that when the entire assemblage was considered, there were 16

indicator species of riparian areas and four and six indicator species for lowland and upland areas, respectively (Table 2.3). However, when only the upland portions of transects were included in the analyses (*e.g.*, shoreline forest compared to upland forest), the number of significant indicator species was reduced to three in riparian, two in upland, and one in lowland transects (Table 2.3).

2.3.1 Community and species-level differences between upland, lowland and riparian sites

Results of the NMS showed separation of riparian, upland and lowland sites (Figure 2.4). Vectors representing the remotely sensed vegetation composition of each transect suggest that community differences are partly explained by differences in vegetation composition. When the complete riparian transect was compared to the complete upland transect, the final two-dimensional NMS explained 71 % of cumulative variance (the 1st axis explained 27 % of the variance and the second axis 44.3 % of the variance) with a stress value of 17.1. Some differences still remained when only the forested portions of transects were compared among site types, with 54 % of the cumulative variance explained by the resulting ordination (axis 1, 0.08 %; axis 2, 13.4 %; axis 3, 33.8 %). However, a three-dimensional solution was recommended with a stress of 28.9 suggesting some difficulty in the NMS settling on a repeatable solution. MRPP analysis further supported this result, demonstrating that the species composition of the three habitat types were distinct for both types of comparisons (full transect and partial transect), but the magnitude of the difference was smaller when only the upland portions of transects were compared (Table 4a and 4b).

2.3.2 Multivariate dispersion as a measure of beta diversity

Beta diversity measured as multivariate dispersion within habitat types, varied significantly among treatments ($F_{2, 135} = 11.33, p < 0.0001$). That is, riparian areas were less

similar to one another than to either upland areas or lowland transitions (Figure 2.5; Table 2.5a). However, comparing only the forested upland portions of transects to one another among transect types, upland forests had the highest multivariate dispersion ($F_{2, 135} = 5.82, p < 0.004$), but were no longer significantly different from shoreline forest (*i.e.*, including only the mature forest part of transects) and were more variable than upland forests adjacent to lowlands (Figure 2.5, Table 2.5b).

2.3.3 Species specialization index

Among the 54 species of landbirds detected in this study, SSI ranged from 0.261 for the American Robin (*Turdus americanus*) to 1.98 for the Yellow-bellied Flycatcher (*Empidonax flaviventris*). The SSI for shorebirds ranged from 0.54 for Wilson's Snipe (*Gallinago delicata*) to 3.8 for Common Tern (*Sterna hirundo*). SSI values for all species detected in this study are presented in Table A.1 and for significant indicator species in Table 2.4. Comparison of SSI for passerines and non-passerines is presented in Figure A1.1.

2.3.4 Comparing community specialization (CSI)

Using only passerine species, our community specialization index (CSI) showed that birds within the combined upland and riparian portion of transect were significantly less specialized than the upland bird community (Figure 2.5; Table 2.6). When the all species were considered (*i.e.*, including all waterbirds), the results became non-significant. During preliminary analyses, bird species considered to be facultative or obligate aquatic, such as shorebirds were found to be most specialized (Figure A1.1) a pattern that was partly due to the limited number classes attributed to these areas (water, shoreline). Our findings suggest that non-passerines are more likely to be specialized on the aquatic zones of vegetation characteristic

of wetland periphery (*i.e.*, not available in upland transects) thus, only passerines were included in our assessment of CSI.

2.4 Discussion

We found that bird assemblages in wetland-associated riparian areas were unique relative to those in upland and lowland edges. Differences were attributable not only to the non-forested and wetland portions of riparian areas, but also to the forested upland sometimes referred to as shoreline forest (Hunt and Haider 2004; Steedman *et al.*, 2001). Though not always exclusive to riparian areas, fifteen species were significant riparian indicators. Riparian bird assemblages had higher cumulative species richness and multivariate dispersion (beta-diversity) and contained unique species, particularly when known wetland or shoreline obligate species such as Lesser Yellowlegs (*Tringa flavipes*) and Solitary Sandpiper (*Tringa solitaria*) were considered. However, considering only landbirds, riparian bird assemblages had a lower overall index of community specialization relative to assemblages in either lowland edges or upland forests. This suggests that at least among landbirds, riparian areas favour generalists capable of using the complex juxtaposition of habitat types within riparian areas.

2.4.1 Species richness and indicators of riparian areas

Riparian areas adjacent to boreal open water wetlands and ponds had higher species richness than either upland forest or the interface between uplands and lowlands (Figure 2.3). Sabo *et al.*, (2005) determined patterns of higher richness in riparian areas were not universal, by region or across a broad range of taxa (plants, lichens, birds). However, our results are consistent with bird studies from other regions (*e.g.*, Larue *et al.*, 1995; McGarigal and McComb 1992) and with other similar studies conducted adjacent to western boreal lakes (Macdonald *et al.*, 2006) and eastern boreal lakes and streams (Larue *et al.*, 1995). Greater availability of food (higher

productivity and more insects) and more habitat niches due to more complex vegetation composition in the ecotone are likely the mechanisms behind these patterns (Macdonald *et al.*, 2006; Pollock *et al.*, 1998; Whitaker and Montevecchi 1997). When the entire ecotone is considered, particularly in areas that encompass several vegetation types across the ecotone, the idea of more habitat niches seems reasonable. However, differences in habitat structure and heterogeneity are more subtle when only the upland portions of transects are considered (MacDonald *et al.*, 2006; Burgess 1997). Our results show that differences in species richness were also reduced when these structurally similar areas were compared, however riparian areas still had higher species richness than either uplands or lowlands.

We found that many species used both upland and shoreline forests and thus were not significant indicators of either the uplands or riparian areas we examined. Most of the species we found to be significant indicators of riparian areas, such as Common Yellowthroat (*Geothlypis trichas*), Song Sparrow (*Melospiza melodia*), and Swamp Sparrow (*Melospiza georgiana*) are described by other authors as riparian and/or wetland-associated species (*e.g.*, Croonquist and Brooks 1991; Macdonald *et al.*, 2006) or are known to be common in other early successional (Hannah 2001; Hobson *et al.*, 2000; Kirk *et al.*, 1996; Schieck and Hobson 2000) and wetland shrub habitats (Erskine 1977; Morissette *et al.*, 2013). Moreover, many other species such as Red-winged Blackbird (*Agelaius phoeniceus*), Bonaparte's Gull (*Chroicocephalus philadelphia*), Wilson's Snipe (*Gallinago delicata*), Lesser Yellowlegs and Solitary Sandpiper have well known facultative or obligate associations with open water (*e.g.*, Erskine 1977). Wetland classification was correlated with assemblages described by our NMS (Figure 2.4) and since wetland classes are representative of changes in nutrients and hydrology reflecting vegetation structure (Harris *et al.*, 1996; Mitsch and Gosselink 2007), their use could

assist in refining our understanding of habitat preferences of boreal species (Chapter 3; Morissette *et al.*, 2013). We also found that significant indicator species of the transition between treed wetlands and uplands (lowland edge) included Yellow-rumped Warbler (*Setophaga coronata*), Hermit Thrush (*Catharus guttatus*) and Western Wood-Pewee (*Catharus guttatus*).

2.4.2 Multivariate dispersion as a measure of beta diversity

Our comparison of variation within communities of each treatment showed that riparian communities had the highest species turnover (multivariate dispersion) when the riparian ecotone was included. However, when only shoreline forest was compared to upland transects the pattern was reversed (Figure 2.5). We consider three possible explanations for this pattern.

First, some species associated with wetlands and riparian areas are considered rare and rare species show greater variability in abundance and occurrence (Helle and Mönkönen 1986 in Niemi *et al.*, 1998). Examples include Yellow Rail (*Coturnicops noveboracensis*), Canada Warbler (*Cardellina Canadensis*), Rusty Blackbird (*Euphagus carolinus*), and Common Yellowthroat (Hannon *et al.*, 2004). Interestingly, species that were indicators of lowland transitions in our study such as Western Wood-Pewee (*Regulus calendula*), White-winged Crossbill (*Loxia leucoptera*) and Red-breasted Nuthatch (*Sitta canadensis*) are also considered rare or irruptive (Hannon *et al.*, 2004). Indeed, we found that many riparian indicators were counted at only few sites. These indicator species could increase species dissimilarity and hence increase multivariate dispersion among riparian transects.

Second, high species turnover in riparian areas relative to upland could also be related to the complexity of ecological systems and subsequently community dynamics at edges (Ries *et al.*, 2004). There are a number of potential responses to edges that would be reflected in relative

species abundances. Factors used to explain species responses to edges include resource mapping (onto vegetation or insects for example), species interactions, ecological flows (nutrients, moisture) and differences in accessibility (Ries *et al.*, 2004). For example, access to resources at an edge decreases for some forest-dependent birds but opportunities to access multiple resources (foraging, nesting) may result in increased suitability for other species. Examples of species in our study for which this scenario is plausible include Ovenbird, Swamp Sparrow, and Alder Flycatcher (*Empidonax alnorum*). Ovenbirds may decrease in abundance near edges due to a reduced availability of soil invertebrates responding to changes in microclimate near edges (*e.g.*, Ball *et al.*, 2009). Likewise, the forest edge may represent a barrier to Swamp Sparrows which often forage on the ground and wade into shallow water for seeds and insects and situate their nests in shoreline vegetation. In contrast, aerial insectivores like Alder Flycatcher may benefit from an increased availability of perches and higher abundance of flying insects in riparian areas (Gray 1993).

A third explanation for increased multivariate dispersion at riparian edges is increased spatial heterogeneity of riparian areas. The riparian edge represents an area of the landscape where a number of “habitat scenarios” occur, potentially resulting in greater variability in species composition. Thus, high levels of species turnover within and among sites might simply suggest that spatial and environmental heterogeneity at multiple scales are important for maintaining a diverse regional species pool (Anderson *et al.*, 2006; Pollock *et al.*, 1998). The ecotonal nature of riparian areas suggests that they may be more heterogeneous and stochastic (less stable) than upland areas (Naiman *et al.*, 2005). However, some researchers have questioned whether boreal forest disturbance regimes in boreal shoreline forests adjacent riparian areas differ substantially from those of upland forested areas (*e.g.*, Burgess 1997; Macdonald *et al.*, 2004). While

experimental studies in other systems have found increased multivariate dispersion in response to disturbances (*e.g.*, Houseman *et al.*, 2008) specific comparisons for riparian areas where natural or anthropogenic disturbances are quantified and related to multivariate dispersion are required.

2.4.3 Specialization

In many regions birds are typically thought to show high habitat specificity (*e.g.*, Becker *et al.*, 2008; Simon *et al.*, 2003), however the dynamic nature of boreal systems (extreme seasonality, natural disturbance) suggests that many species should be relatively plastic (*e.g.*, Mönkönnen and Welsh 1994; Simon *et al.*, 2003) or tolerant of natural habitat and environmental changes (Niemi *et al.*, 1998). The concept of specialization is central to understanding community organization (Gravel *et al.*, 2006; Julliard *et al.*, 2006) and to niche theory (Wiens 1989) because specialization is an expected theoretical response to low stochasticity and spatial heterogeneity in an environment while a generalist strategy reflects the opposite (Julliard *et al.*, 2006; Pandit and Kolasa 2012). Thus, environmental heterogeneity or stochasticity, whatever the cause, is also thought to help predict the composition of generalists and specialists comprising a community (Julliard *et al.*, 2006; Pandit and Kolasa 2012). Thus, environmental heterogeneity or stochasticity in space or in time should favour generalists whereas specialists should benefit from greater consistency in the environment (Julliard *et al.*, 2006; Simon *et al.*, 2003). When only landbirds were included in our analyses, riparian communities were indeed less specialized than upland communities (CSI; Table 2.6) a reasonable result given the heterogeneity of vegetation types and likelihood of more frequent disturbances (*e.g.*, flooding) in riparian areas.

We selected a specialization index that emphasized habitat and measured the breadth and relative abundance of species among habitats (Julliard *et al.*, 2006). However, our measure of

specialization was unable to account for whether or not birds required the juxtaposition of the habitat types concentrated in the riparian ecotone. One example, Lincoln's Sparrow (*Melospiza lincolni*), ranked near the bottom of SSI values in our analysis, but this species is thought to specialize on particular microsites requiring low-lying willow, *Betula sp.* and *Alder sp.* (Ammon, 1996 BNA; Also BAM) associated with fens and swamps. This method also does not account for some unique cases such as "irruptive specialists" (e.g., crossbills) that exploit patches of heavy seeding that are stochastic in abundance and availability through space.

Undoubtedly, classification of a species as either a generalist or specialist is somewhat subjective and individual species have been classified as both generalists and specialists depending on the context (Simon *et al.*, 2003). Thus, one principle advantage of a semi-quantitative approach is that it does not rely on expert knowledge to decide which habitat classes are occupied and establishes a generalist-specialist continuum. Julliard *et al.*, (2006) systematically examined the sensitivity of the SSI to small sample size and breadth of classes sampled within their own and simulated datasets and found the SSI to be robust to small sample sizes.

A number of relatively small habitat patches together in close proximity are expected to result in high numbers of species (Naiman *et al.*, 2005) a pattern expected to lower beta-diversity but increase gamma diversity. We found that many riparian species have wider ecological amplitudes, a pattern that, in contrast to our results, is expected to decrease beta diversity (Magurran 2003; Naiman *et al.*, 2005). An apparent contradiction in our results is that communities dominated by generalists, should be more predictable and thus exhibit less species turnover among sites. One potential explanation for this contradiction is that although many species were more abundant in riparian areas than uplands, other areas on the landscape such as

contiguous wetlands of a particular class could represent less spatially and temporally variable habitat. However, wetlands represent a large proportion of boreal landscapes for which the relative importance to bird assemblages is not as well understood, a knowledge gap that may have important implications for conservation planning.

2.4.5 Implications for conservation and future research

Riparian areas are of conservation concern worldwide (Sabo *et al.*, 2005; Toner and Keddy 1997). Because of their proximity to water, riparian areas can often be degraded by human uses such as urbanization or recreational development, agriculture, forest harvesting and other industrial uses (Naiman *et al.*, 2005). Riparian ecotones contribute substantially to the overall heterogeneity of habitats available to birds, a premise that was supported by our finding of increased multivariate dispersion and species richness in riparian sites. Riparian areas were also a source of unique species and thus increase regional diversity. Areas of high priority for conservation are often assessed based on their ability to support high species richness and diversity locally and regionally (Groves 2003; Margules and Pressey 2000; Sabo *et al.*, 2005). Therefore, our results suggest that a common framework for classifying riparian areas integrated with classes commonly used to categorize upland areas (*e.g.*, forest type) would assist with boreal conservation planning.

Approximately 65 % of species of concern in the boreal and taiga plains are associated with wetlands and populations of many of the species we found to be unique to wetlands and riparian areas or indicators of these habitats are declining (NABCI 2013). Examining a broad suite of habitat classes that includes all types of wetlands will help to broaden recognition of the relative contributions of different types of areas when setting boreal conservation targets. However, more work is needed to improve our understanding of boreal bird assemblages in the full suite of

habitats including a thorough exploration of disturbance effects on riparian and wetland-associated bird communities.

Table 2.1 Description of the three habitat types examined in the Utikuma Lake, Alberta study area in 2002 and 2003.

Code	Description	Sample Size
Riparian	Transects along riparian ecotone	87
Upland	Transects in Upland forest 200 m from water or wetland	38
Lowland	Lowland to Upland interface	13

Table 2.2 Habitat categories used to calculate Species Specialization Index (SSI) values.

Habitat Types	Corresponding Imagery Vegetation Class
Water	Open water
Shoreline	Mudflats
Grass/Sedge (Mineral soil)	Meadow Marsh
Grass Sedge (Peat)	Graminoid Fen
Emergent Vegetation	Emergent Marsh
Low Shrub dry (Upland early successional)	N/A
Low shrub wet (Shrubby wetland)	Shrubby Fen(Rich and Poor)
Deciduous Upland	Upland Deciduous
Coniferous Upland (Jackpine)	Upland Pine
Mixedwood Upland	Upland Mixedwood
Treed Bog	Treed Bog
Treed Fen	Treed Fen
Conifer Swamp	Conifer Swamp
Mixedwood Swamp	Mixedwood Swamp
Deciduous Swamp	Deciduous Swamp
Cutblock	N/A
Agriculture*	N/A

Table 2.3 Indicator values (% of perfect indication) for bird species in riparian compared to upland and lowland transects Utikuma, Alberta.

Maximum				Std.			
Group	AOU	Common Name	IndVal	Mean	Dev	p	SSI*
Riparian	†LISP	Lincoln's Sparrow	59.5	19.4	4.66	0.0002	0.459
	LCSP	Le Conte's Sparrow	35.6	13.2	4.37	0.002	0.878
	LEYE	Lesser Yellowlegs	32.2	12.5	4.41	0.005	1.002
	†ALFL	Alder Flycatcher	28.5	12.7	4.39	0.0088	0.472
	COYE	Common Yellowthroat	24.1	10.2	4.02	0.012	0.473
	SOSA	Solitary Sandpiper	23	9.8	3.88	0.013	0.955
	SWSP	Swamp Sparrow	25.6	11.9	4.27	0.014	0.547
	WISN	Wilson's Snipe	24.5	13.2	4.24	0.0232	0.543
	†CHSP	Chipping Sparrow	39.1	29.8	4.09	0.0334	0.349
	WTSP	White-throated Sparrow	37.8	28.6	4.35	0.0422	0.398
	CCSP	Clay-colored Sparrow	14.9	7.6	3.68	0.0444	0.754
	KILL	Killdeer	13.8	7.4	3.51	0.0454	1.277
	YWAR	Yellow Warbler	27.8	17.9	4.92	0.0462	0.793
	BOGU	Bonaparte's Gull	13.8	7.5	3.57	0.0488	1.116

Maximum			Std.				
Group	AOU	Common Name	IndVal	Mean	Dev	p	SSI*
	RWBL	Red-winged Blackbird	16.2	8.9	4	0.0546	0.358
	SOSP	Song Sparrow	11.5	6.5	3.53	0.0794	0.355
Upland	†OVEN	Ovenbird	53.7	29.9	4.05	0.0002	0.740
	†REVI	Red-eyed Vireo	56	31.7	3.69	0.0002	1.124
	†PHVI	Philadelphia Vireo	34.4	16.5	4.57	0.0076	1.148
	RUGR	Ruffed Grouse	15.1	6.1	3.36	0.0294	1.272
Lowland	†MYWA	Myrtle Warbler	46.8	31.7	3.51	0.0014	0.509
	WWCR	White-winged crossbill	20.1	5.1	3.03	0.0046	1.656
	HETH	Hermit Thrush	40	23.1	4.87	0.0084	0.834
	†WEWP	Western wood Pewee	14	6.2	3.24	0.0314	0.723
	RCKI	Ruby-crowned Kinglet	35.4	25.6	4.57	0.0436	1.038
	RBNU	Red breasted Nuthatch	16.2	10.8	4.25	0.0994	1.038

†Remain significant indicators when only the upland portion of the riparian transect is compared to half the upland transect. See Appendix 1 for complete ISA results.*SSI=Species Specialization Index

Table 2.4 Results of MRPP analysis among habitat types when complete transects (a) and when only the upland/shoreline forest portion of riparian transect is compared to ½ of the upland transect (b).

a)	Habitat type	T	A	<i>p</i>
	Riparian vs. Upland	-26.77	0.127	< 0.0001
	Lowland vs. Upland	-11.64	0.124	< 0.0001
	Lowland vs. Riparian	-11.92	0.078	< 0.0001

b)	Habitat type	T	A	<i>p</i>
	Riparian vs. Upland	-30.415	0.087	< 0.0001
	Lowland vs. Upland	-4.131	0.052	< 0.0001
	Lowland vs. Riparian	-2.325	0.03	0.002

Table 2.5 Post-hoc pairwise comparisons of multivariate dispersions (within group distance from centroid) in PERMDISP2 (Anderson 2006) for (a) whole transects and (b) only the upland/shoreline forest portion of transects in each of riparian, upland and lowland transects (Bray-Curtis distance on untransformed data; Permutation test- 9999 randomizations; Anderson 2006).

a) Habitat type	<i>t</i>	P(tables)	P(perm)
Riparian vs. Upland	4.03	0.0001	0.002
Lowland Edge vs. Upland	0.33	0.742	0.780
Lowland Edge vs. Riparian	3.89	0.0002	0.006

b) Habitat type	<i>t</i>	P(tables)	P(perm)
Riparian vs. Upland	1.7093	0.0905	0.21
Lowland Edge vs. Upland	3.294	0.6670	0.01
Lowland Edge vs. Riparian	0.4327	0.6670	0.66

Table 2.6 Comparison of CSI among habitat types (Oneway Anova; Figure 2.6). Variances were equal (a) and unequal (b-Bartlett's $\text{prob} > \text{chi}^2 = 0.04$), and tests for heteroscedasticity (Levene's) and normality (KS) were not significant.

a)	SS	df	MS	F	Prob > F
Between Groups	0.1850	2	0.0925	19.26	0.0000
Within Groups	0.64852	135	0.00480		
Total	0.8336	137	0.0061		

b)	SS	df	MS	F	Prob > F
Between Groups	0.356	2	0.178	16.04	0.0000
Within Groups	1.49	134	.0110		
Total	1.841	136	.0135		

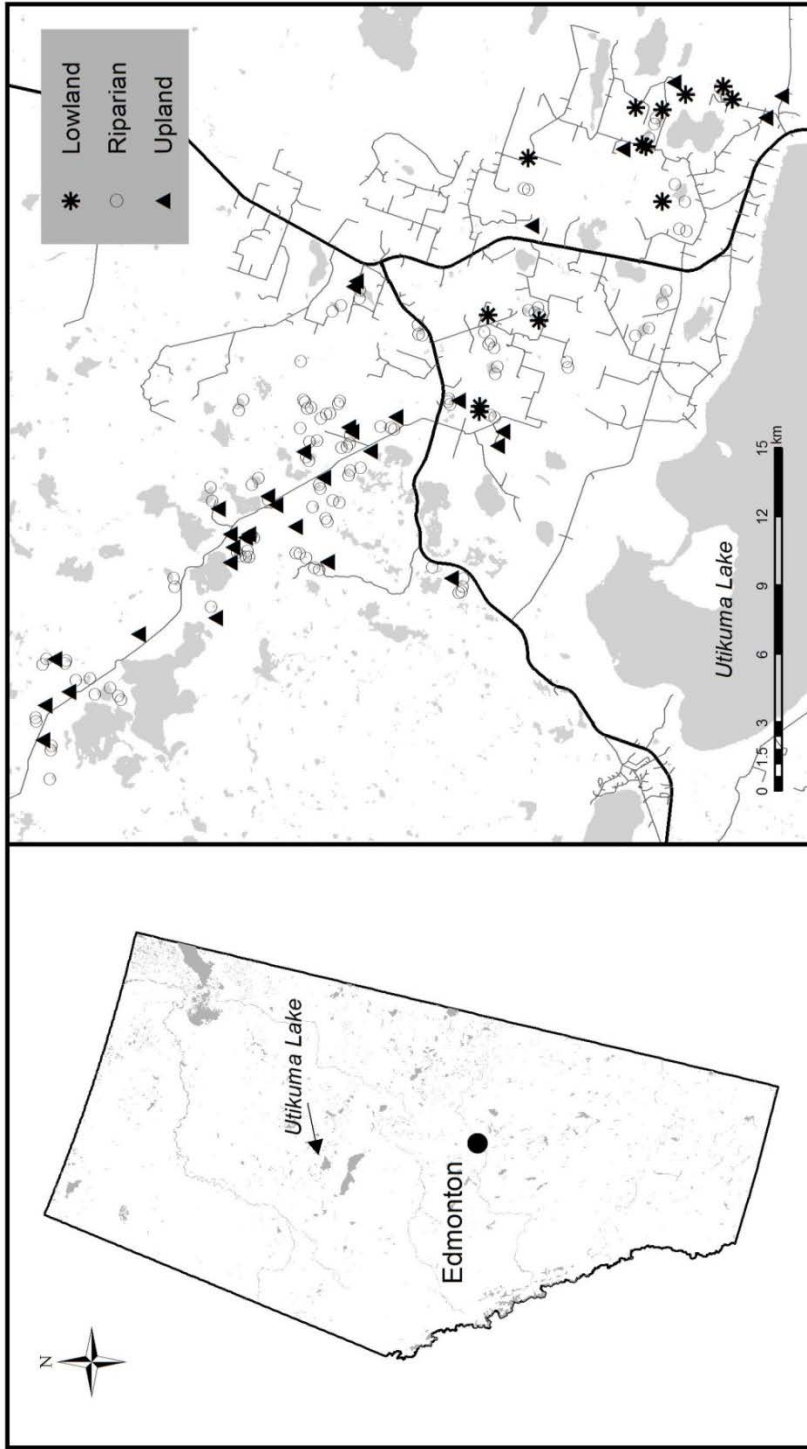


Figure 2.1 Location of riparian, upland and lowland edge transects and the Utikuma Lake (Alberta, Canada) study area.

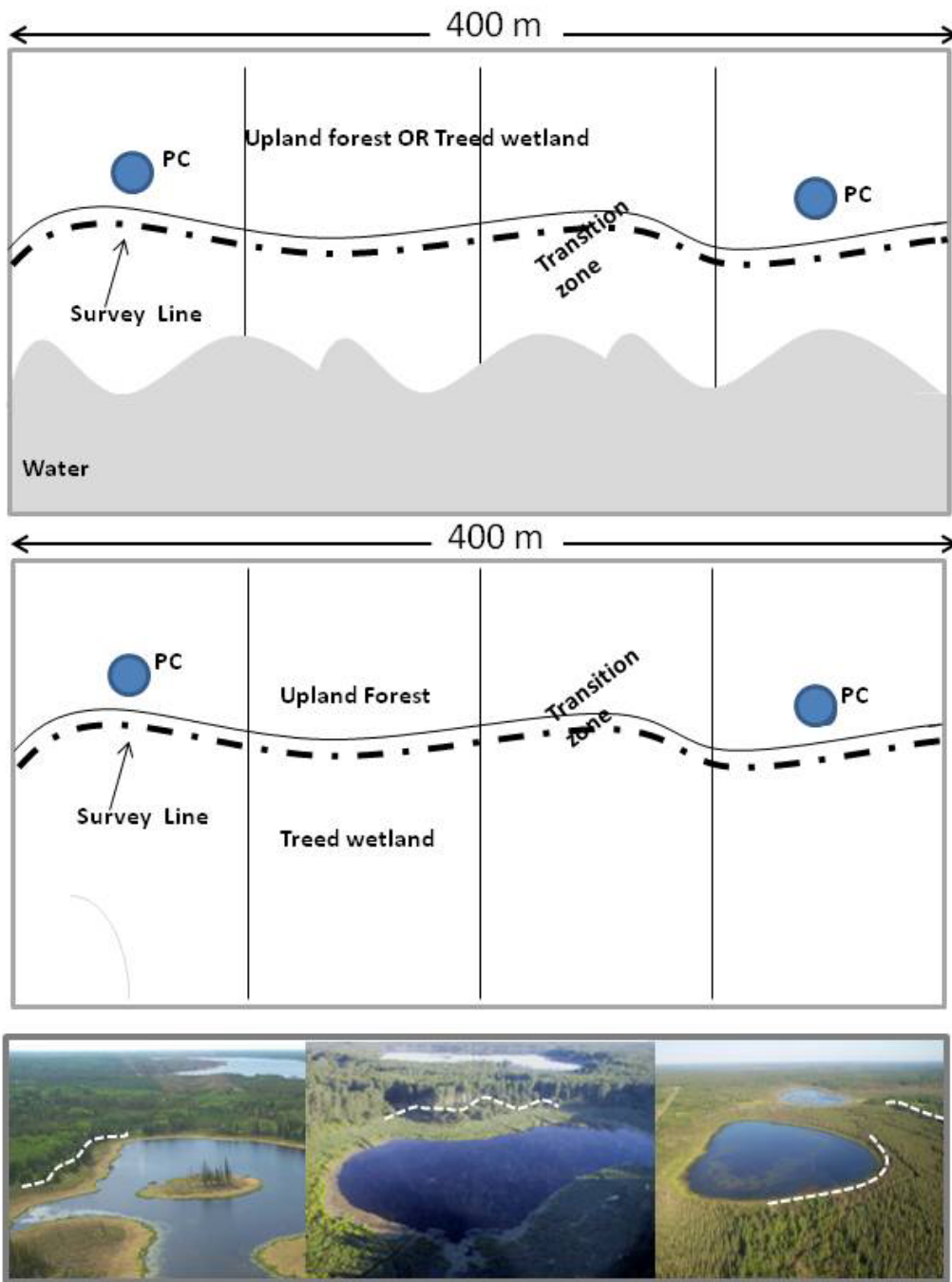


Figure 2.2 Schematic diagram of transect and point count layout along riparian and lowland edge ecotones.

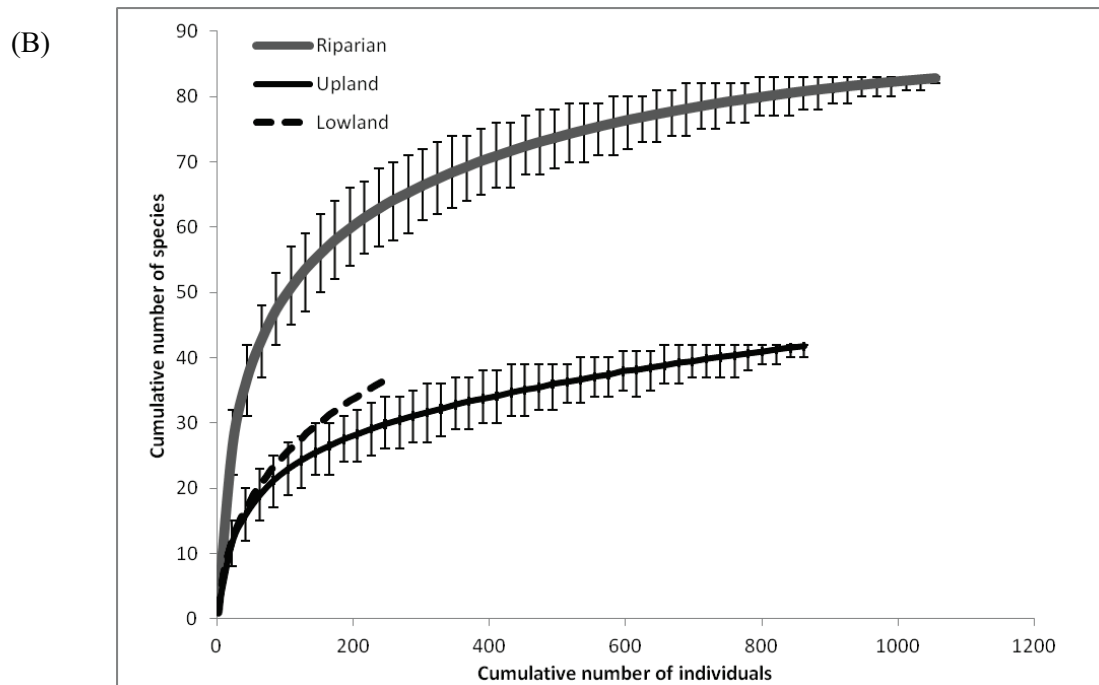
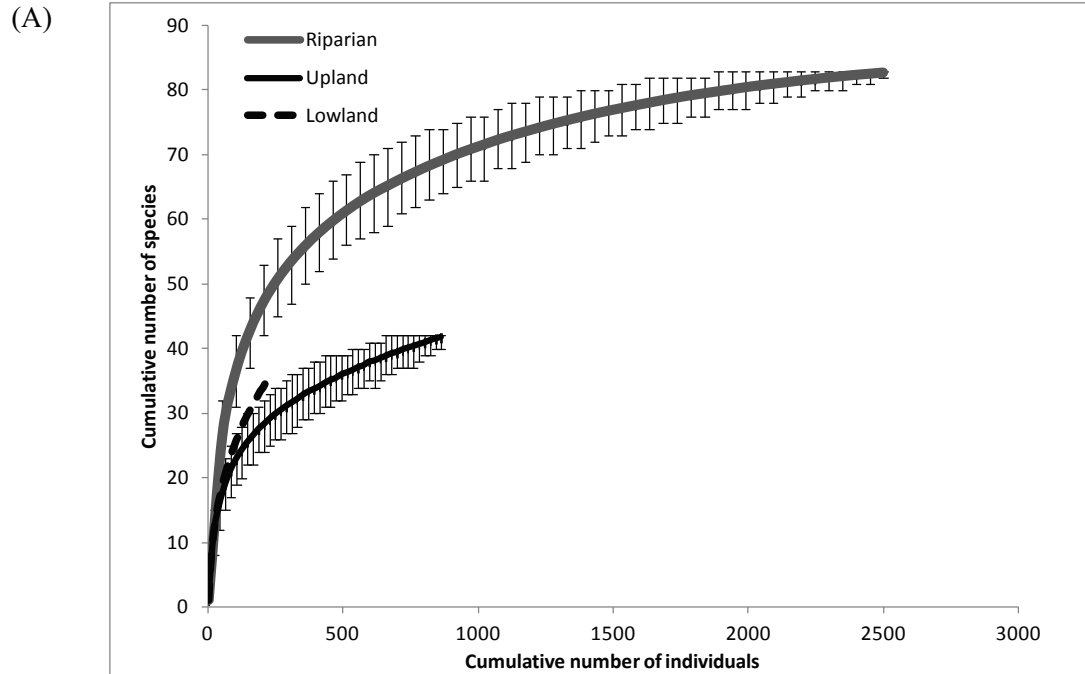


Figure 2.3 Species accumulation curves for birds recorded from both years (2002-2003) in three habitat types: riparian, upland, and lowland edge for whole transects (A) and for only the upland portion of transects (B).

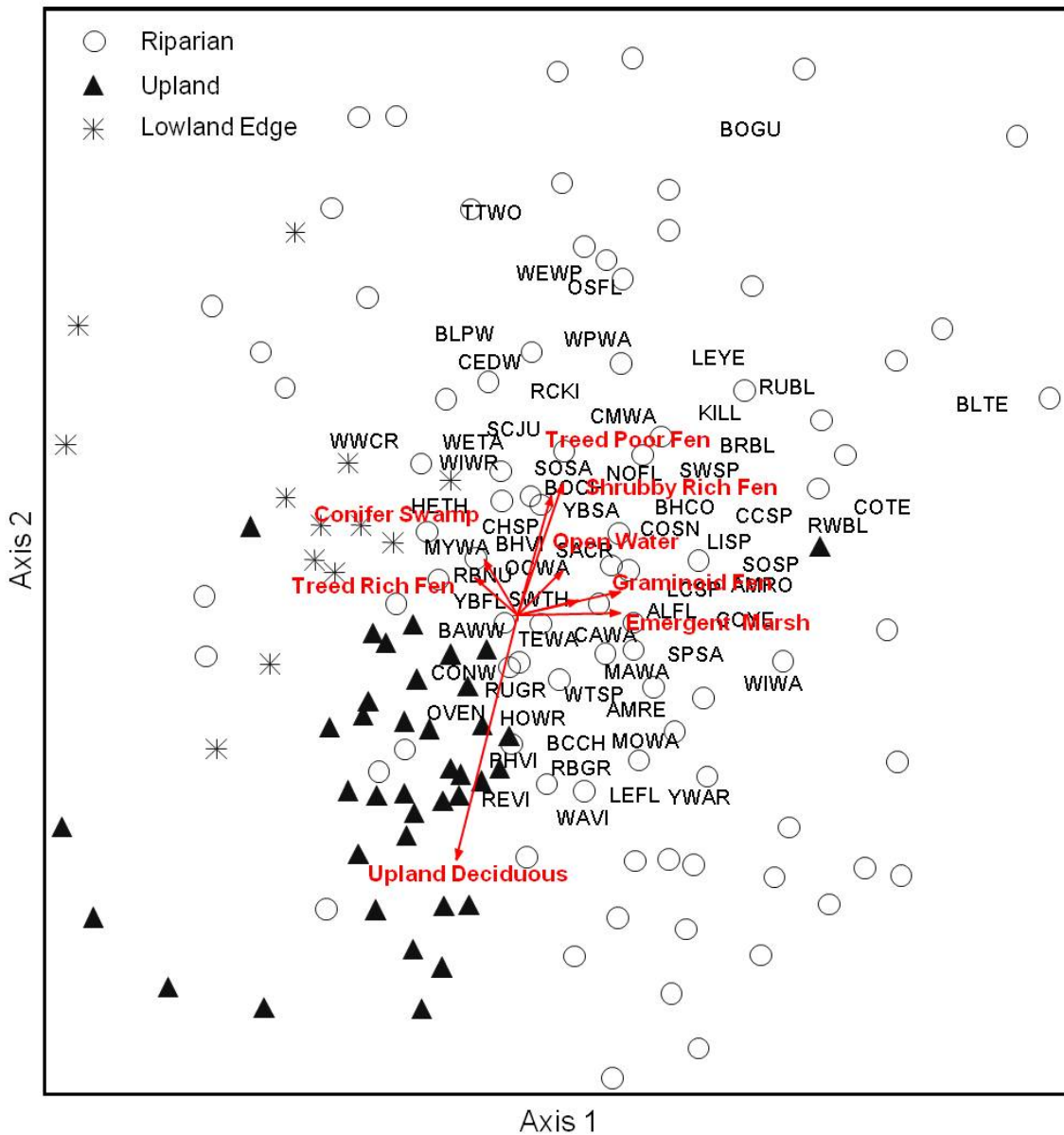


Figure 2.4 NMS (Nonmetric Multidimensional Scaling) ordination of transects from riparian, upland and lowland edge transects. Symbols indicate transects and 4 letter codes indicate bird species (full names associated with four letter codes are located in Appendix 2: Table A2.1).

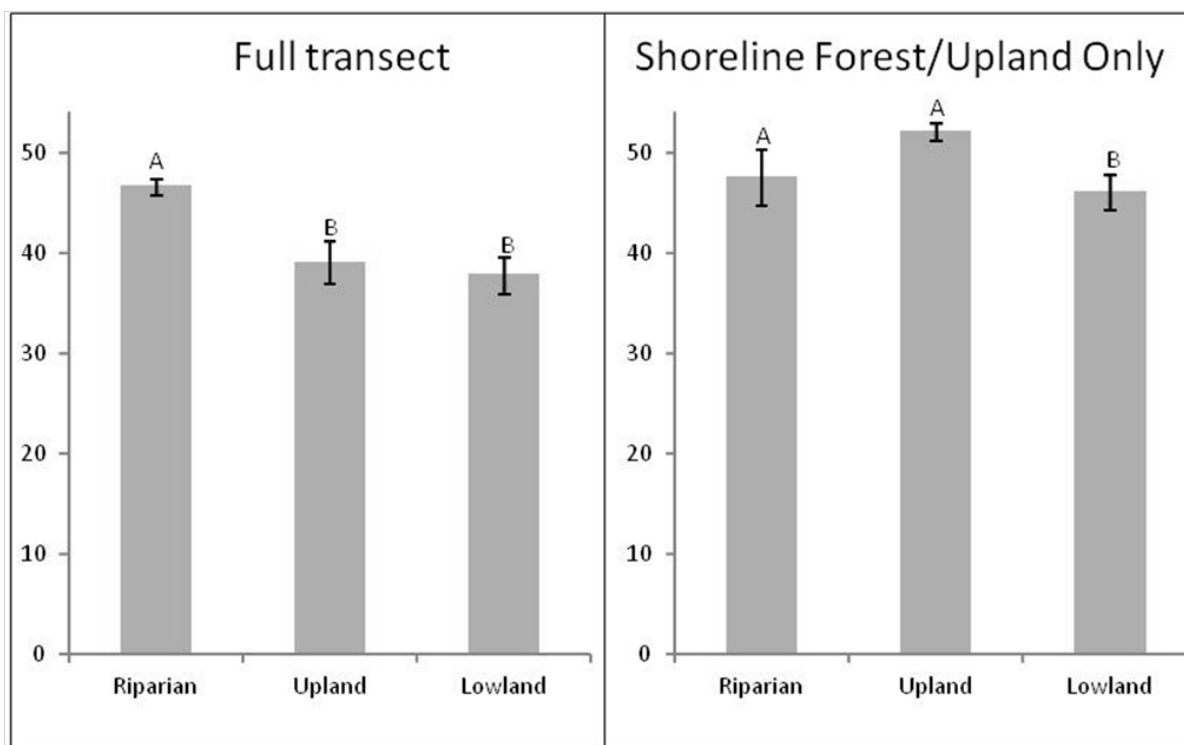


Figure 2.5 Community (multivariate) dispersion among riparian, upland and lowland edge habitat types for complete transect and upland only portion of transect. The panel on the right represents only shoreline forest portion of transect compared to one half of upland transects.

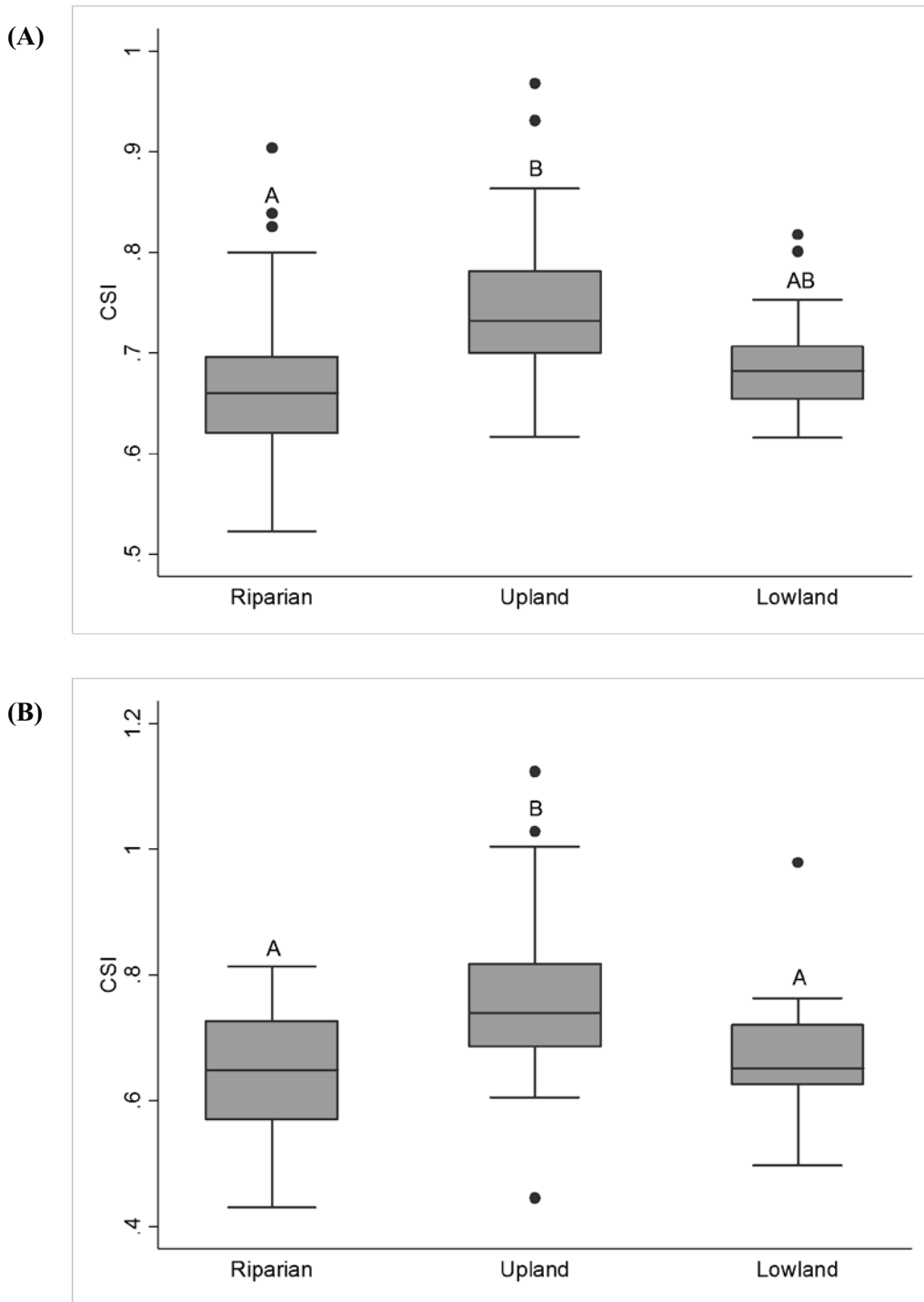


Figure 2.6 Community Specialization Index (landbirds only) by habitat type for Utikuma Lake, AB, comparing entire transects (A) and only the upland portion of transects (B). Different letters represent statistically significant differences (Scheffe test; $p < 0.001$)

2. 5 References

- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19-28.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693.
- Becker, C. D., T. M. Loughin, and T. Santander. 2008. Identifying forest-obligate birds in tropical moist cloud forest of Andean Ecuador. *Journal of Field Ornithology* 79:229-244.
- Boulet, M., M. Darveau, and L. Bélanger. 2003. Nest predation and breeding activity of songbirds in riparian and nonriparian black spruce strips of central Quebec. *Canadian Journal of Forest Research* 33:922-930.
- Burgess, C. J. 1997. Forested landscape patterns in the western boreal mixedwood forest of Alberta: riparian forests, fire history, canopy composition and topography. Department of Biological Sciences, University of Alberta.
- Clarke, K. R. 1999. Nonmetric multivariate analysis in community-level ecotoxicology. *Environmental Toxicology and Chemistry* 18:118-127.
- Conway, C. J. 2002. Standardized North American marsh bird monitoring protocols. 23 pages.
- Croonquist, M. J. and R. P. Brooks. 1991. Use of avian and mammalian guilds as indicators of cumulative impacts in riparian-wetland areas. *Environmental Management* 15:701-714.

- Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail, S. Villeger, and N. Mouquet. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47:15-25.
- Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17:252-261.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: a need for flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Erskine, A. J. 1977. Birds in boreal Canada; communities densities and adptations. Canadian Wildlife Service, Ottawa. Report Series Number 41.
- Ferone, J. M. and K. J. Devito. 2004. Shallow groundwater–surface water interactions in pond–peatland complexes along a Boreal Plains topographic gradient. *Journal of Hydrology* 292:75-95.
- Gotelli, N. J. and G. L. Entsminger. 2000. EcoSim:Null models software for ecology. Acquired Intelligence Inc. & Kesity-Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>.
- Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379-391.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399-409.

- Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *American Midland Naturalist* 129:288-300.
- Groves, C. R. 2003. *Drafting a Conservation Blueprint: A practitioner's guide to planning for biodiversity*. Island Press, Washington.
- Hannah, K. C. 2001. Patterns in habitat quality for the white-throated sparrow (*Zonotrichia albicollis*) in a recently logged landscape. University of Alberta.
- Hannon, S. J., S. E. Cotterill, and F. K. A. Schmiegelow. 2004. Identifying rare species of songbirds in managed forests: application of an ecoregional template to a boreal mixedwood system. *Forest Ecology and Management* 191:157-170.
- Harris, A. G., S. C. McMurray, P. W. C. Uhlig, J. K. Jeglum, R. F. Foster, and G. D. Racey. 1996. *Field guide to the wetland ecosystem classification for northwestern Ontario*. Ontario Ministry of Natural Resources, Northwest Science and Technology, Thunder Bay, Ontario. NWST Field Guide FG-01.
- Hobson, K. A., D. A. Kirk, and A. R. Smith. 2000. A multivariate analysis of breeding bird species of western and central Canadian boreal forests: stand and spatial effects. *Ecoscience* 7:267-280.
- Hobson, K. A. and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecological Applications* 9:849-863.

- Houseman, G. R., G. G. Mittlebach, H. L. Reynolds, and K. L. Gross. 2008. Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology* 89:2172-2180.
- Hunt, L. M. and W. Haider. 2004. Aesthetic impacts of disturbances on selected boreal forested shorelines. *Forest Science* 50:729-738.
- Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters* 9:1237-1244.
- Kardynal, K., K. A. Hobson, S. L. Van Wilgenburg, and J. L. Morissette. 2009. Moving riparian management guidelines towards a natural disturbance model: an example using boreal riparian and shoreline forest bird communities. *Forest Ecology and Management* 257:54-65.
- Kirk, D. A., A. W. Diamond, K. A. Hobson, and A. R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Canadian Journal of Zoology* 74:1749-1770.
- Larue, P., L. Bélanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. *Canadian Journal of Forest Research* 25:555-566.
- Legendre, P. and L. Legendre. 2002. *Numerical Ecology*, 2nd Edition edition. Elsevier, Amsterdam.

- Macdonald, E., C. J. Burgess, G. J. Scrimgeour, S. Boutin, S. Reedyk, and B. Kotak. 2004. Should riparian buffers be part of forest management based on emulation of natural disturbance? *Forest Ecology and Management* 187:185-196.
- Macdonald, S. E., B. Eaton, C. S. Machtans, C. Paszkowski, S. Hannon, and S. Boutin. 2006. Is forest close to lakes ecologically unique? Analysis of vegetation, small mammals, amphibians, and songbirds. *Forest Ecology and Management* 223:1-17.
- Magurran, A. E. 2003. *Measuring Biological Diversity*. Blackwell Science, Malden, MA.
- Margules, C. R. and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.
- McCune, B. and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- McGarigal, K. and W. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. *Journal of Wildlife Management* 56:10-23.
- Mitsch, W. J. and J. G. Gosselink. 2007. *Wetlands*, 2nd edition. Van Nostrand Reinhold, New York.
- Mönkönnen, M. and D. A. Welsh. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. *Annales Zoologici Fennici* 31:61-70.
- Morissette, J. L., K. J. Kardynal, E. M. Bayne, and K. Hobson. 2013. Comparing bird community composition among boreal wetlands: is wetland classification a missing piece of the puzzle? *Wetlands* 33:653-665.

- Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia - ecology, conservation, and management of streamside communities*. Elsevier Academic Press, Burlington, MA.
- National Council for Air Stream Improvement, I. N. 2007. *Synthesis of technical information on forest wetlands in Canada*. National Council for Air and Stream Improvement, Inc., Research Triangle Park, N.C. Technical Bulletin No. 938.
- Niemi, G., J. Hanowski, P. Helle, R. Howe, M. Mönkkönen, L. Vernier, and D. Welsh. 1998. Ecological sustainability of birds in boreal forests. *Conservation Ecology* 2:17.
- Nur, N., G. Ballard, and G. Geupel. 2008. Regional analysis of riparian bird species response to vegetation and local habitat features. *The Wilson Journal of Ornithology* 120:840-855.
- Pandit, S. N. and J. Kolasa. 2012. Opposite effects of environmental variability and species richness on temporal turnover of species in a complex habitat mosaic. *Hydrobiologia* 685:145-154.
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands - a test of biodiversity theory. *Ecology* 79:94-105.
- Ries, L., R. J. Fletcher, Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35:491-522.
- Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* 86:56-62.

- Schieck, J. and K. A. Hobson. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. *Canadian Journal of Forest Research* 30:1281-1295.
- Schmera, D. and J. Podani. 2013. Components of beta diversity in hierarchical sampling designs: a new approach. *Ecological Indicators* 26:126-136.
- Simon, N. P., A. W. Diamond, and F. E. Schwab. 2003. Do northern forest bird communities show more ecological plasticity than southern forest bird communities in eastern Canada? *Ecoscience* 10:289-296.
- Steedman, R. J., R. S. Kushneriuk, and R. L. France. 2001. Littoral water temperature response to experimental shoreline logging around small boreal forest lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1638-1647.
- Toner, M. and P. Keddy. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications* 7:236-246.
- Whitaker, D. M. and W. A. Montevecchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a Balsam fir ecosystem. *Canadian Journal of Forest Research* 27:1159-1167.
- Wiens, J. A. 1989. *Wiens, John A.* University Press, Cambridge.

CHAPTER 3: COMPARING BIRD COMMUNITY COMPOSITION AMONG BOREAL WETLANDS: IS WETLAND CLASSIFICATION A MISSING PIECE OF THE HABITAT PUZZLE?

A version of this chapter has been published. Morissette, JL, KJ Kardynal, EM Bayne, KA Hobson. Wetlands 33(4): 653-665

3.1 Introduction

Wetlands, like many other habitats, are declining in quality and abundance as a result of industrial land use (*e.g.*, agriculture, forestry, peat mining; Foote and Krogman 2006), urban expansion (Mitsch and Gosselink 1993) and climate change (Environment Canada 2004). Most of the world's remaining wetlands are found in boreal and tropical regions (Mitsch and Gosselink 1993) and 24% of the world's wetlands are estimated to be in Canada (National Wetlands Working Group (NWWG) 1997). In the Boreal Plains ecozone of western Canada, 25-60% of the landscape area is classified as being one of five major wetland classes: open water, marsh, swamp, bog or fen (NWWG 1997). These classifications are derived from a range of moisture, nutrient, soil and structural conditions which are important contributing factors to the overall heterogeneity of the boreal region and to our understanding of the diversity of habitats available to birds and other wildlife (*e.g.*, Calmé *et al.*, 2002).

Research on wetland birds in the boreal forest has been limited and focused almost exclusively on factors affecting habitat use, community composition and reproductive success of waterbirds in open water wetlands and lakes (*e.g.*, Brook and Clark 2005; Fast *et al.*, 2004; Paszkowski and Tonn 2000; Rempel *et al.*, 1997). There is a paucity of research examining species composition and abundance of birds among other classes of boreal wetlands, particularly

vegetated wetlands, and for landbirds associated with them. In European boreal regions, studies describing bird community composition in peatlands (Fox and Bell 1994; Virkkala *et al.*, 2005) and marshes (Hågvar *et al.*, 2004), have been conducted but studies describing variation in bird community composition among a suite of wetland classes are currently lacking.

Vegetation structure is well studied as a factor contributing variation in bird communities particularly in a management context (*e.g.*, James, 1971; Swift 1984). Moisture and nutrient gradients have also been utilized to explain patterns in bird community composition in deciduous forested wetlands of the north eastern USA (Swift *et al.*, 1984) and in North American boreal systems (Kirk *et al.*, 1996; Welsh and Loughheed 1996). These gradients are also important components of wetland classification, suggesting that the use of wetland classification schemes may provide greater understanding of the relative importance of different wetland habitats for birds. Insight gained from an increased ability to integrate forest wetlands into models of bird distribution and abundance in this landscape will improve assessments of conservation priorities for individual bird species, communities and habitats.

In forests, such as the boreal, that are dominated by natural disturbance processes, determining whether forest management can emulate fire in its successional trajectories has been a key focus of bird research (*e.g.*, Schieck and Hobson 2000). Early successional harvested areas have been well documented as different from early post-fire habitats (*e.g.*, Schieck and Hobson 2000; Schulte and Niemi 1998). However, some wetland types (*e.g.*, shrub swamps) and early successional forests such as those present in many riparian zones where beaver activity exists may, with respect to structure, be more analogous to harvested areas than habitats created by fire. Thus, some wetland types may be similar enough to post-harvest areas of a certain age to provide habitat for similar species. To fully understand the full suite of wetland habitats used by birds it

is helpful to understand where there might be overlap in community composition between harvested riparian areas and wetlands.

Our objective was to examine differences in wetland-associated bird community composition among eight boreal wetland classes using an established wetland classification scheme, the Canadian Wetland Classification System (NWWG 1997), to evaluate this approach for understanding the composition of wetland-associated bird assemblages in the Boreal Plains ecozone of Western Canada. Given differences in moisture, nutrients, soils and parent materials of wetlands and subsequent variation in vegetation composition and structure, we predicted that each wetland class would support distinct assemblages. To further place our research in the context of forest management activities, we also compared wetland classes to a set of 5-10 year old harvested areas as these are at least superficially similar to some of the shrub-dominated wetland classes. We predicted that for some species, early successional harvested areas and shrub-dominated wetlands may represent similar habitats.

3.2 Methods

3.2.1 Study area

This research was conducted in a 4400 km² area along the Saskatchewan-Manitoba (51°39'N, 100°57'W) border in Duck Mountain (Figure 3.1). Along with the Duck Mountain Provincial Forest, which includes an active forest management license, the study area also incorporated two provincial parks. The landscape contains extensive wetland and peatland complexes, lakes and many shallow ponds which are generally representative of the Boreal Plains ecozone. Duck Mountain reaches a maximum elevation of 832 m above sea level and is located at the southern limits of the Boreal Plain ecozone. Dominant tree species include paper

birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), tamarack (*Larix laricina*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*).

3.2.2 Wetland Classification

Under the Canadian Wetland Classification System (NWWG 1997), boreal wetlands are categorized as either mineral or peatlands (Table 3.1). The composition and structure of the plant community of each wetland class is a reflection of the hydrological regime, nutrient status, connection/isolation from mineral rich water, climate and landscape position (Harris *et al.*, 1996). These categories are further separated into five major wetland classes including shallow open water, marshes, swamps, bogs and fens (NWWG 1997) usually based on vegetation characteristics (Mitsch and Gosselink 1993). Open water wetlands typically have a depth of less than two metres (Mitsch and Gosselink 1993) and are not addressed in this paper because while landbirds may forage or perch there, they do not nest there.

Collectively, bogs and fens are classed as peatlands, while marshes and swamps are characterized by minimal or no peat accumulation (Smith *et al.*, 2007). In some parts of the boreal forest, coniferous treed swamps and peatlands make up a large proportion of the landscape. Treed wetlands generally occur where proximity of the water table to the forest floor results in the formation of hydric soils and growth of water-tolerant vegetation (Cowardin *et al.*, 1979). Some wetlands also blend with the overall canopy rendering them difficult to distinguish based on physiognomy alone (Riffell *et al.*, 2006). Treed swamps are occasionally classified as peatlands, but experience a different rate of peat accumulation and also form a different type of peat. Therefore, we distinguished treed swamps from treed fens and bogs. The classification scheme we used included 13 wetland classes Emergent Marsh, Meadow Marsh, Thicket Swamp,

Conifer Swamp, Hardwood Swamp, Mixedwood Swamp, Tamarack Swamp, Treed Bog, Treed Rich Fen, Treed Poor Fen, Shrubby Rich Fen, Shrubby Poor Fen and Graminoid Fen (Table 3.1). Basic vegetation characteristics of each are described by Smith *et al.*, (2007) and Harris *et al.*, (1996).

3.2.3 Site Selection

We used a remotely sensed wetland classification developed by Ducks Unlimited Canada (DUC 2007, 30 m resolution) to pre-select potential survey sites with at least a 150 m radius (*i.e.*, minimum size 7 ha) and within a homogeneous wetland classification. We randomly selected point-count locations for conducting bird surveys from these sites and we used initial site visits to confirm their classification and accessibility (Harris *et al.*, 1996). Sites were clustered regionally for sampling efficiency; however, we ensured all sites within wetland classes were dispersed throughout the study area to avoid spatial clustering of any one particular class. Sites from any one class were spaced 1500 m- 45 km apart. We established 71 survey locations distributed among 10 wetland classes that occurred in the study area (Table 3.2). During ground-truthing we determined due to their similarities, shrubby rich and shrubby poor fens sites could be pooled. Hardwood and mixedwood sites were also pooled. In addition, we selected ten sites in 5-7 year-old upland harvested areas that had been 80-100 year-old aspen-dominated mixedwood stands prior to harvest as determined by ecosite maps and a detailed forest resource inventory (Louisiana Pacific Forest Industries Swan Valley Division). These sites were selected due to their structural similarity to thicket swamps. All sites classified as treed deciduous and mixedwood swamps were associated with small streams as we were otherwise unable to locate any that met our minimum area requirements. Graminoid fens and emergent marshes were sampled as far into the wetland class as permitted by water depth. Survey points in harvested

areas, bogs, fens and treed swamps were not associated with open water wetlands or riparian areas because these were placed at least 250 m from a lake or open water source.

3.2.4 Bird Surveys

To sample birds, we used a combined marsh bird playback and point-count survey method. Each survey began with a three-minute listening period followed by a playback protocol (Conway *et al.*, 2002) for secretive marsh birds in the order of: Yellow Rail (*Coturnicops noveboracensis*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), American Bittern (*Botaurus lentiginosus*) and Pied-billed Grebe (*Podilymbus podiceps*) to stimulate response calls. Each call was played electronically at 90 decibels for 1 minute followed by a 30-second listening period for a total of 7.5 minutes. Once the playback protocol was completed, we performed a ten-minute limited distance (100 m radius) point count for other species (*e.g.*, songbirds). All survey stations were placed at least 150 m from the edge of other habitat classes and were at least 250 m apart. Only one survey station was placed within each site. Each sampling station was visited once between 30 May and 30 June 30 2006. We initiated our point counts 30 minutes before sunrise and the last count was conducted no later than 4 hours after sunrise. No counts were performed during rain or wind speeds exceeding 25 km/hr (Ralph *et al.*, 1993). Observers were rotated between wetland classes at variable times of the day to reduce potential detectability bias in the dataset. Observers trained together prior to the start of the survey period to ensure taxonomic accuracy and consistency and to calibrate estimates of distance to singing birds.

3.2.5 Data analysis

Differences in Bird Community Composition among Wetland Classes: We used Multiple Response Permutation Procedure (MRPP) to test whether bird community composition was

different among classes of wetlands. MRPP uses pre-existing groups, in our case wetland class, to test the null hypothesis of no difference between two or more groups and provides a measure of the degree of separation among groups (T) as well as a measure of the within-group agreement (A) (McCune and Grace 2002). MRPP has the advantage of not requiring assumptions of the nature of data distributions (e.g., normality). We used a Sørensen distance measure and log $(x+1)$ transformed bird abundance data to control for relative weighting of species prior to analysis. We applied a Bonferroni procedure for multiple comparisons to control for experiment-wide error rate (Quinn and Keough 2002).

Characteristic Bird Communities of Wetland Classes: We used Non-metric Multidimensional Scaling (Clarke 1993; NMS, NMDS) to display the relationship among bird communities in their use of different wetland classes. NMS is one of the most robust ordination techniques because it performs well when beta-diversity is high, when data are non-normal and at a range of scales, and it avoids assumptions of linear relationships among variables. NMS preserves the rank order of among-sample dissimilarities in the rank order of distances (Clarke 1993) which relieves “zero-truncation” issues and any distance measure can be used. We again used Sørensen as the distance metric and all data were log $(x+1)$ transformed. All NMS analyses were performed using PC-Ord 5 (McCune and Grace 2002) using a random starting configuration and 900 runs. Ordination diagrams visually support the results of the MRPP above by displaying the relationship between species and particular wetland classes (McCune and Grace 2002).

Characteristic Species of Wetland Classes: We used Indicator Species Analysis (ISA; Dufrene and Legendre 1997; McCune and Grace 2002) to identify species characteristic of the wetland classes we examined. In ISA, species can be analyzed based on an *a priori* partition of sites. The analysis provides an indicator value (IV) for each species in each wetland class based on its

abundance and frequency of occurrence and is not affected by the abundance of other species. A randomization procedure is used to determine the statistical significance of the association of each species with the selected classes. When the mean number of individuals in each cluster is used the influence of varying sample sizes among clusters is decreased. An indicator value (IV) equals 100% when individuals of a species are found at all sites belonging to a particular class. ISA permits comparisons across taxa that are robust to differences in abundance potentially due to sampling methodology and is robust to the differences in the number of sites among classes (Legendre and Legendre 2002). IVs change based on the number of groups in the analysis. Finally, low numbers of occurrences never result in IVs stronger than expected by chance. We also ran this analysis without the harvested classes to determine if some species were indicators of wetland classes without the influence of harvested sites.

Detection Probability: We were not able to correct for variation in detectability among species and habitat classes because the number of detections was too small for distance sampling (< 10 detections; Nichols *et al.*, 2000) and each site was only visited once. We reduced variation in detectability due to (1) weather by not sampling in inclement weather, (2) temporal differences in singing behavior by making sure each wetland type was visited during different times of the morning and stages of the breeding season, and (3) observer differences by having all point counts conducted by the same three observers that had trained together to standardize ability. Finally, observers were randomly assigned to sites to reduce the potential of any confounding effects of observers.

3.2 Results

For our analyses, we retained a dataset of 851 individual birds representing 75 species from a total of 2270 detections among 81 point counts. Species detected outside of the 100 m radius limit of the point count station were not included.

3.2.1 Differences in Bird Community Composition among Wetland Classes

An initial MRPP indicated that overall, bird communities varied significantly among wetland classes ($T = -17.67$, $A = 0.57$, $p < 0.0001$). Once corrected for multiple tests ($p < 0.002$), pair-wise comparisons from this initial MRPP indicated that some minor and sub-classes (*e.g.*, treed rich fen vs. treed poor fen vs. treed bog, Table 3.1) were not significantly different from one another. These classes were combined for subsequent analyses (See Table 3.3 for final groupings) and the MRPP was repeated (Table 3.2, $T = -23.75$, $A = 0.54$, $p < 0.0001$) for the remaining eight wetland classes and the harvested class. All class comparisons were significantly different except for marsh vs. shrubby fen (Table 3.2). MRPP is vulnerable to data with differing dispersions so we performed an outlier analysis to confirm the efficacy of this analysis for our data. Only one site was considered a moderate outlier ($SD = 2.6$) and this was one of only two sites classified as graminoid fen. The site was not removed from the data set.

3.2.2 Characteristic Bird Communities of Wetland Classes

A two-dimensional solution for NMS (Figure 3.2, stress = 15.5) accounted for 66% of the variation in the dataset. Overall, the NMS indicated that the bird community was stratified at least by physiognomic structure of wetlands and showed separation (*i.e.*, ecological distance) between treed wetland classes (*e.g.*, conifer swamp, treed fens) and shrubby or graminoid classes (*e.g.*, marsh, thicket swamp, shrubby fen). Overall bird community composition of harvested areas, though similar in height and density of shrubs, was distinct from wetlands suggesting that

nutrient and moisture regimes also help structure these bird communities. With the exception of thicket swamps and shrubby fens which were differentiated by vegetation structure, separation among mineral and organic wetlands was not as apparent.

3.2.3 Species Characteristic of Wetland Classes

Indicator Species Analysis results varied depending on the number of groups used in the analysis so we examined both the simplified classification supported by the MRPP and a more complex one reflecting a broader range of wetland classes, but with resulting reduced sample sizes (Table 3.3). Overall, 21 species were significant indicators of either wetland classes or harvested classes (Table 3.3). Each wetland class used in the final MRPP had at least one indicator species (Table 3.3). However, in our analysis, some species considered typical of wetlands in general did not have significant indicator values for any particular class. For example, Sedge Wren (*Cistothorus platensis*) had equivalent occurrence and abundance among meadow marsh, thicket swamp, and shrubby fens. In contrast, we found that several other species were uniquely detected in a particular class (Table 3.3), but that we did not have sufficient detections to attribute a significant indicator for that class. An example is the Yellow-bellied Sapsucker (*Sphyrapicus varius*) which was detected only in harvested areas, but was detected too infrequently to be formally included in the ISA.

When harvested areas were excluded from analysis, American Goldfinch (*Spinus tristis*) and House Wren (*Troglodytes aedon*) became significant indicators of thicket swamps and marshes, respectively, suggesting some species-level overlap between use of harvested areas and these wetland classes for these species. Finally, two species, Common Yellowthroat (*Geothlypis trichas*) and Alder Flycatcher (*Empidonax alnorum*), had reduced indicator values for wetlands when the harvested class was included in the analysis (Table 3.3).

3.3 Discussion

Wetlands represent an important component of the boreal forest landscape for which knowledge of abundance and variation in bird community composition across the diverse wetland types is limited. Our evaluation of bird community composition across different boreal wetland classes highlighted the distinctness of bird assemblages supported by each wetland class. Additionally, we demonstrate that harvested areas are unique relative to any of the wetland types we surveyed despite apparent overlap in general habitat structure (*i.e.*, shrub height, density). Our NMS described 66% of the variation in the bird community despite unmeasured and possible interactions between wetland classes and the influence of the surrounding forest matrix on bird community composition at each site. Further, we were not able to account for the influence of factors such as habitat area and connectivity.

Calmé *et al.*, (2002) demonstrated that in the boreal forest of eastern Canada, several bird species were more common in peatland assemblages than in other habitats of the surrounding upland landscape. Although the wetland classification we used further distinguished bird communities between different types of peatlands (*i.e.*, treed fens and bogs, shrubby and graminoid fens), our species-level findings are consistent with theirs. A similar suite of species, including Yellow Rail and Nelson's Sparrow (*Ammodramus nelsoni*) were detected rarely and only in these classes. In our study, Palm Warbler (*Setophaga palmarum*), Yellow Bellied Flycatcher (*Empidonax flaviventris*), Dark-eyed Junco (*Junco hyemalis*) and Nashville Warbler (*Oreothlypis ruficapilla*) were also significant indicators of the combined class of treed fens and treed bogs, while Yellow-rumped Warbler (*Setophaga coronata*), Ruby-crowned Kinglet (*Regulus calendula*) and Golden-crowned Kinglet (*Regulus satrapa*) were indicative of the conifer (black spruce) swamp class. Previous work either has not directly considered these as a

wetland class (*e.g.*, Kirk *et al.*, 1996) or has combined this class within broader peatland groupings (*e.g.*, Calmé *et al.* 2002). These bird species are characteristic of boreal coniferous forests (Erskine 1977), but not necessarily of peatlands such as bogs and fens. One exception is the Lincoln's Sparrow (*Melospiza linolnii*), which in our study area was not restricted to peatlands and was not an indicator of any particular wetland class. However, concurrent work in Alberta has documented its association with riparian peatland habitats, that is, peatlands associated with open water (Morissette *et al.*, unpub).

Our mixed treed swamp class combined a range of forest types from purely deciduous to mixedwood. In the Boreal Plain, these classes are not always considered wetlands (*e.g.*, in forest inventories), but rather forested stands with higher soil moisture content. We found several species to be indicators of this class (Table 3.3) although most species such as Ovenbird (*Seiurus aurocapilla*) are also found in mesic aspen and mixedwood forest types.

Other authors have noted the importance of wetlands or moisture gradients as determinants of bird community composition (*e.g.*, Swift *et al.*, 1984; Welsh and Loughheed 1996). Swift *et al.*, (1984) found that effects of hydrologic patterns in forested wetlands may have greater influence on the composition of bird assemblages than vegetation structure. Further, Smith (1977) documented the association of several bird species to vegetation characteristics known to respond to moisture gradients within forests. We were unable to test this pattern directly due to our small sample size and the intrinsic linkages between moisture gradients and vegetation structure when exploring a broad range of wetland classes. There was also clear separation between thicket swamps and shrubby fens suggesting that major wetland soil groups and resulting differences in vegetation composition also plays a role in structuring assemblages. Our results show this approach to classifying habitat for birds is useful and further

research should provide additional insight into the variation of bird community composition in according to a recognized wetland classes.

While the NMS suggested limited overlap between harvested areas and wetlands, two species, Common Yellowthroat and Alder Flycatcher, did show reduced indicator values for wetlands when harvested areas were included in the analysis. Additionally, American Goldfinch became a significant indicator of thicket swamp rather than harvested areas once harvested areas were excluded from analysis. Thus, harvested areas and thicket swamps appear to have structural qualities similar enough to at least superficially satisfy habitat requirements of some species. These three species have previously been documented to be abundant in early successional habitats (*e.g.*, Kardynal *et al.*, 2011), with seasonal ponds in harvested areas (*e.g.*, Hanowski *et al.*, 2006) and associated with riparian areas (Darveau *et al.*, 1995; Hanowski *et al.*, 2003; Kardynal *et al.*, 2009).

3.3.1 Management Implications

Our results show that wetland classification schemes are useful tools that should be considered when developing criteria and planning objectives for the conservation of boreal biodiversity in general and avian communities in particular. Conservation value of wetlands by class will vary regionally across the Boreal Plain based on relative availability of habitats and the scale at which conservation priorities are determined. For example, at more northern latitudes of the boreal forest, peatlands are a more dominant habitat feature on the landscape than in southern latitudes. Thus, if conservation priorities are set regionally then more southern peatland areas may warrant higher priority to maintain a regional level of biodiversity (Calmé *et al.* 2002). As such, some wetlands may be regionally scarce or impacted but secure at a larger scale (*i.e.*, provincially). Where conservation efforts or designations for wetland protection do exist they

often emphasize a limited range of classes (marshes) or objectives (*e.g.*, wetlands important to staging waterfowl; NCASI 1997). Although some provinces are beginning to work towards policies to also protect peatlands (*e.g.*, Manitoba Peatland Strategy), most wetland policies in Canada are only in the early stages of development (Clare *et al.*, 2011; Foote and Krogman 2006).

Additional considerations for individual species may also be of value. For example, Palm Warblers are considered peatland specialists (Wilson, Jr. 1996) during the breeding season. We found this species to be most abundant in specific types of peatlands, namely treed fens and bogs. While their population status has shown little change between 1966-2007 (BBS), Calmé and Desrochers (1999) found their presence was also more likely in large peatlands that are part of broader peatland networks suggesting they may be vulnerable to habitat fragmentation. Further research is warranted to also identify or solidify the linkages between other boreal bird species of concern (*e.g.*, Yellow Rail, Rusty Blackbird *Euphagus carolinus*) and particular wetland classes.

Conservation planning will need to also consider regional impacts to wetlands from different types of disturbances. The southern fringe of the boreal plain has been affected by agriculture, mining and urban expansion (Hobson *et al.*, 2002); peatlands in this area may require different conservation measures than in more northerly regions. In the Boreal Plain ecozone, the extent of impacts on wetlands due to oil and gas-related activities and forest vary regionally and provincially. While wetland losses are not well documented for the Boreal Plain, disturbance to and loss of boreal wetlands, is a growing concern as industrial activities and subsequent infrastructure and urban expansion continues and long term effects of these activities become more recognized. Treed wetlands (*e.g.*, conifer swamps) are of particular concern as many are

not well quantified (NCASI 2007), slow regeneration following disturbances is typical (Locky 2005) and in some areas many are also suitable for forest harvesting and peat extraction (Foote and Krogman 2006). More research on the sensitivity of birds to disturbance in boreal wetland classes is needed to confirm potential effects of these activities on wetland associated birds. Our study suggests that using established approaches to classifying wetlands in the boreal plain will be helpful for documenting the full breadth of habitats used by boreal birds and lend support to the conservation of the full spectrum of wetland classes in the boreal landscape.

3.4 References

- Brook, R. W. and R. G. Clark. 2005. Breeding season survival of female lesser scaup in the northern boreal forest. *Arctic* 58:16-20.
- Calmé, S., A. Desrochers, and J.-P. L. Savard. 2002. Regional significance of peatlands for avifaunal diversity in southern Quebec. p. 273-281.
- Clare, S., N. Krogman, L. Foote, and N. Lemphers. 2011. Where is the avoidance in the implementation of wetland law and policy? *Wetlands Ecology and Management* 19:165-182.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D. C.

- Darveau, M., P. Beauchesne, L. Bélanger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. *Journal of Wildlife Management* 59:67-77.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: a need for flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Environment Canada. 2004. Threats to Water Availability in Canada. National Water Research Institute, Burlington, Ontario.
- Fast, P. L. F., R. G. Clark, R. W. Brook, and J. E. Hines. 2004. Patterns of wetland use by brood-rearing Lesser Scaup in northern boreal forest of Canada. *Waterbirds* 27:177-182.
- Foote, L. and N. Krogman. 2006. Wetlands in Canada's western boreal forest: agents of change. *The Forestry Chronicle* 82:825-833.
- Fox, A. D. and M. C. Bell. 1994. Breeding bird communities and environmental variable correlates of Scottish peatland wetlands. *Hydrobiologia* 279/280:297-307.
- Hågvar, S., P. Nygaard, and B. T. Bækken. 2004. Retention of forest strips for bird-life adjacent to water and bogs in Norway: effect of different widths and habitat variables. *Scandinavian Journal of Forest Research* 19:452-465.
- Hanowski, J., N. Danz, and J. Lind. 2006. Response of breeding bird communities to forest harvest around seasonal ponds in northern forests, USA. *Forest Ecology and Management* 229:63-72.
- Hanowski, J., N. Danz, J. Lind, and G. Niemi. 2003. Breeding bird response to riparian forest harvest and harvest equipment. *Forest Ecology and Management* 174:315-328.

Harris, A. G., S. C. McMurray, P. W. C. Uhlig, J. K. Jeglum, R. F. Foster, and G. D. Racey.

1996. Field guide to the wetland ecosystem classification for northwestern Ontario.

Ontario Ministry of Natural Resources, Northwest Science and Technology, Thunder Bay, Ontario. NWST Field Guide FG-01.

Kardynal, K., K. A. Hobson, S. L. Van Wilgenburg, and J. L. Morissette. 2009. Moving riparian

management guidelines towards a natural disturbance model: an example using boreal

riparian and shoreline forest bird communities. *Forest Ecology and Management* 257:54-

65.

Kirk, D. A., A. W. Diamond, K. A. Hobson, and A. R. Smith. 1996. Breeding bird communities

of the western and northern Canadian boreal forest: relationship to forest type. *Canadian*

Journal of Zoology 74:1749-1770.

Legendre, P. and L. Legendre. 2002. *Numerical Ecology*, 2nd Edition edition. Elsevier,

Amsterdam.

Locky, D. A. 2005. *Boreal plains peatlands: characterization, plant diversity, biogeography, and*

impacts from logging. University of Alberta (Canada).

McCune, B. and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design,

Glenden Beach, Oregon.

Mitsch, W. J. and J. G. Gosselink. 1993. *Wetlands*, 2nd edition. Van Nostrand Reinhold, New

York.

- National Wetlands Working Group (NWWG). 1997. The Canadian wetland classification system. Canada Committee on Ecological Land Classification, Environment Canada.
- Paszkowski, C. A. and W. M. Tonn. 2000. Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors. *Freshwater Biology* 43:421-437.
- Quinn, G. P. and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.
- Rempel, R. S., K. F. Abraham, T. R. Gadawski, S. Gabor, and R. K. Ross. 1997. A simple wetland habitat classification for boreal forest waterfowl. *Journal of Wildlife Management* 61:746-757.
- Riffell, S., T. Burton, and M. Murphy. 2006. Birds in depression forested wetlands: area and habitat requirements and model uncertainty. *Wetlands* 26:107-118.
- Schieck, J. and K. A. Hobson. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. *Canadian Journal of Forest Research* 30:1281-1295.
- Schulte, L. A. and G. J. Niemi. 1998. Bird communities of early successional burned and logged forest. *Journal of Wildlife Management* 62:1418-1429.
- Smith, K. B., Smith Christopher E., S. F. Forest, and Richard Alain J. 2007. A field guide to the wetlands of the boreal plains ecozone of Canada. Ducks Unlimited Canada.

Swift, B. L., J. S. Larson, and R. M. DeGraaf. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. *The Wilson Bulletin* 96:48-59.

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

Welsh, D. A. and S. C. Lougheed. 1996. Relationships of bird community structure and species distributions of two environmental gradients in the northern boreal forest. *Ecography* 19:194-208.

Wilson, W. H., Jr. 1996. *The birds of North America: palm warbler (Dendroica palmarum)*. The Academy of Natural Sciences; The American Ornithologist's Union, Philadelphia; Washington D.C.

Table 3.1 Wetland classes as modified from the Canadian Wetland Classification System (CWC) and the classification scheme used by Ducks Unlimited Canada to map wetlands via remote sensing in the Boreal Plains ecozone (Smith *et al.*, 2007). † Moisture and hydrodynamic (vertical or lateral water movement) characteristics are outlined below and modified from Smith *et al.*, (2007).

Major wetland soil group	CWC Major Class	Minor Class <i>(Trees, height % cover.)</i>	Sub-class <i>(Shrubs, height % cover)</i>	Moisture & Hydrodynamic† Characteristics <i>(Moss, forbs, grasses)</i>
Mineral	Marsh	(none)	Emergent/Meadow	Hydric Dynamic
		Swamp	Shrubby	Thicket
		<i>(none)</i>	<i>Alnus spp., Salix spp.</i> <i>(> 2 m)</i>	Moving
	Swamp	Treed	Conifer¹	Subhygric
		<i>Picea mariana</i> ^{1,2} > 10 m	<i>(Alnus spp.</i> <i>Rhododendron groenlandicum)</i>	Moving (vertical)
		Treed	Mixedwood²	Hygric
		<i>(Picea mariana</i> ^{1,2} <i>Larix laricina</i> ^{2,3} > 10 m	<i>Alnus spp., Salix spp.</i>	Moving (vertical/lateral)
	Swamp	Treed	Tamarack³	Hygric
			<i>(Betula glandulosa,</i> <i>Betula pumila, Alnus</i>	Moving

Major wetland soil group	CWC Major Class	Minor Class <i>(Trees, height % cover.)</i>	Sub-class <i>(Shrubs, height % cover)</i>	Moisture & Hydrodynamic† Characteristics <i>(Moss, forbs, grasses)</i>
			spp.	
Peatlands	Bog	Treed <i>(Picea mariana)</i> <i>< 10 m</i>	Rich/poor <i>(Rhododendron groenlandicum, Vaccinium spp. Kalmia spp.)</i>	Subhygric (poor) – hygric Stagnant >20% <i>Sphagnum</i> , ericaceous spp.
	Fen	Treed <i>Picea mariana,</i> <i>Larix laricina</i> <i>25-60% tree cover,</i> <i>< 10 m)</i>	Rich/poor (Ericaceous)	Subhygric (poor) – hygric Slow moving (Buckbean <i>Menyanthes trifoliata,</i> wire sedge <i>Carex lasiocarpa)</i>
	Fen	Shrubby <i>Picea mariana,</i> <i>Larix laricina</i> <i>Tree cover < 25%</i>	Rich/poor <i>(Salix sp. Betula pumila, Myrica gale)</i> <i>< 2 m</i>	Hydric Slow moving (lateral) < 20 % <i>Sphagnum</i>
	Fen	Graminoid	Rich /poor (Buckbean, wire sedge)	Moving < 20 % <i>Sphagnum</i>

Major wetland soil group	CWC Major Class	Minor Class <i>(Trees, height % cover.)</i>	Sub-class <i>(Shrubs, height % cover)</i>	Moisture & Hydrodynamic† Characteristics <i>(Moss, forbs, grasses)</i>
Harvested		Age- 5-7 year old 2-5 m tall	<i>Populus tremuloides,</i> <i>Betula papyrifera)</i>	NA

†*Stagnant*: stable, non-flowing areas with little or no change in hydroperiod. *Slow-moving*: gradual flow-through with minor hydroperiod change. *Moving*: Vertical hydroperiod change common, lateral movement also occurs. *Dynamic*: frequent and strong changes in vertical and lateral movement of water. *Very Dynamic*: high water displacement areas. Hydric soils occur when soils are saturated/ flooded long during entire growing season (Mitsch and Gosselink 1993). Hygric and sub-hygric – soils are wet for most of the growing season with weak gleying possible in hygric soils.

Table 3.2 Multiple Response Permutation Procedures comparing bird community composition among wetland classes. Statistical significance level after Bonferoni correction is $p < 0.002$. Unless otherwise indicated, comparisons were significant $p < 0.0001$ (* indicates $p < 0.002$ and “nss” is non-significant).

Group Compared		<i>T</i>	<i>A</i>
Marsh vs.	Thicket Swamp	-5.3	0.17
	Treed Fen	-13.32	0.34
	Shrubby Fen ^{nss}	-2.14	0.055
	Conifer Swamp	-10	0.42
	Mixed Swamp*	-8.64	0.41
	Harvest	-6.57	0.32
Thicket Swamp vs.	Treed Fen	-14.43	0.38
	Shrub Fen	-5.86	0.13
	Conifer Swamp	-12.45	0.45
	Mixed Swamp*	-8.75	0.33
	Harvest	-6.74	0.24
Treed Fen vs.	Shrubby Fen	-17.7	0.39
	Conifer Swamp	-6.7	0.14
	Harvest	-14.36	0.39
	Mixed Swamp	-6.77	0.15
Shrubby Fen vs.	Conifer swamp	-14.64	0.42
	Mixed Swamp	-10.09	0.38
	Harvest	-11.97	0.28
Conifer Swamp vs.	Harvest	-12.29	0.46
Conifer Swamp vs.	Mixed Swamp*	-5.68	0.18
Harvest vs.	Mixed Swamp	-6.13	0.23

Table 3.3 Significant indicator species ($p < 0.01$) of each wetland class (results apply to the wetland class; sub-classes are presented for reference). **IV** is Indicator Value, **n** is number of sites surveyed. (***IV**) represents the Indicator Value when harvested areas were excluded from the analysis. Scientific names and total number of birds counted are included in Appendix 2: Table A2.1.

Wetland class (n)	Sub-class (n)	Indicator Species (IV)
Marsh (7)	Emergent Marsh (2)	Swamp Sparrow (30)(*47)
		Red-winged Blackbird (58)
	Meadow Marsh (5)	Sora (49)
Treed Fen(19)	Treed Rich Fen (10)	Dark-eyed Junco(42)
	Treed Poor Fen (7)	Palm Warbler (66)
		Yellow-bellied Flycatcher (39)
	Treed Bog (2)	Nashville Warbler (28)
Shrubby and Graminoid Fen (15)	Shrubby Fen (13)	Le Conte's Sparrow (29)
	Graminoid Fen (2)	
Thicket Swamp (10)		Common Yellowthroat (38)(*48)
		Alder Flycatcher (31)(*52)
		American Goldfinch (*30)

Mixed Treed Swamp (9)

Mixed/Hardwood Swamp (5)

Ovenbird **(42)**

Tamarack Swamp (4)

Red-eyed Vireo **(48)**

Black-throated Green Warbler **(33)**

Brown Creeper **(28)**

Conifer Swamp (12)

Yellow-rumped Warbler **(65)**

Ruby-crowned Kinglet **(38)**

Golden-crowned Kinglet **(33)**

Harvest- 5-7 year old (9)

Chestnut-sided Warbler **(66)**

White-throated Sparrow **(52)**

Mourning Warbler **(34.8)**

American Goldfinch **(29)**

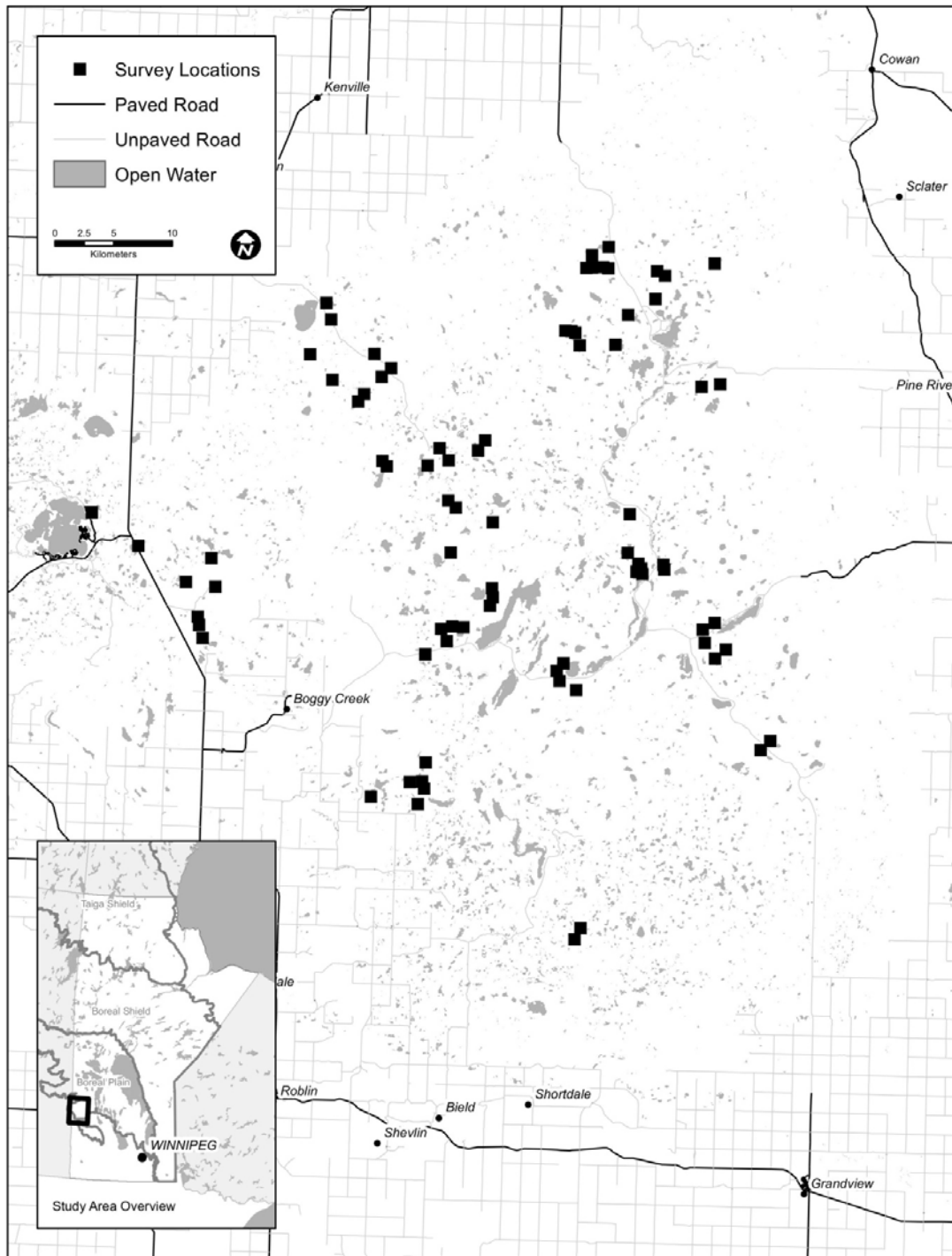


Figure 3.1 Location of Duck Mountain study area in Manitoba and Saskatchewan and locations of wetland classification survey points.

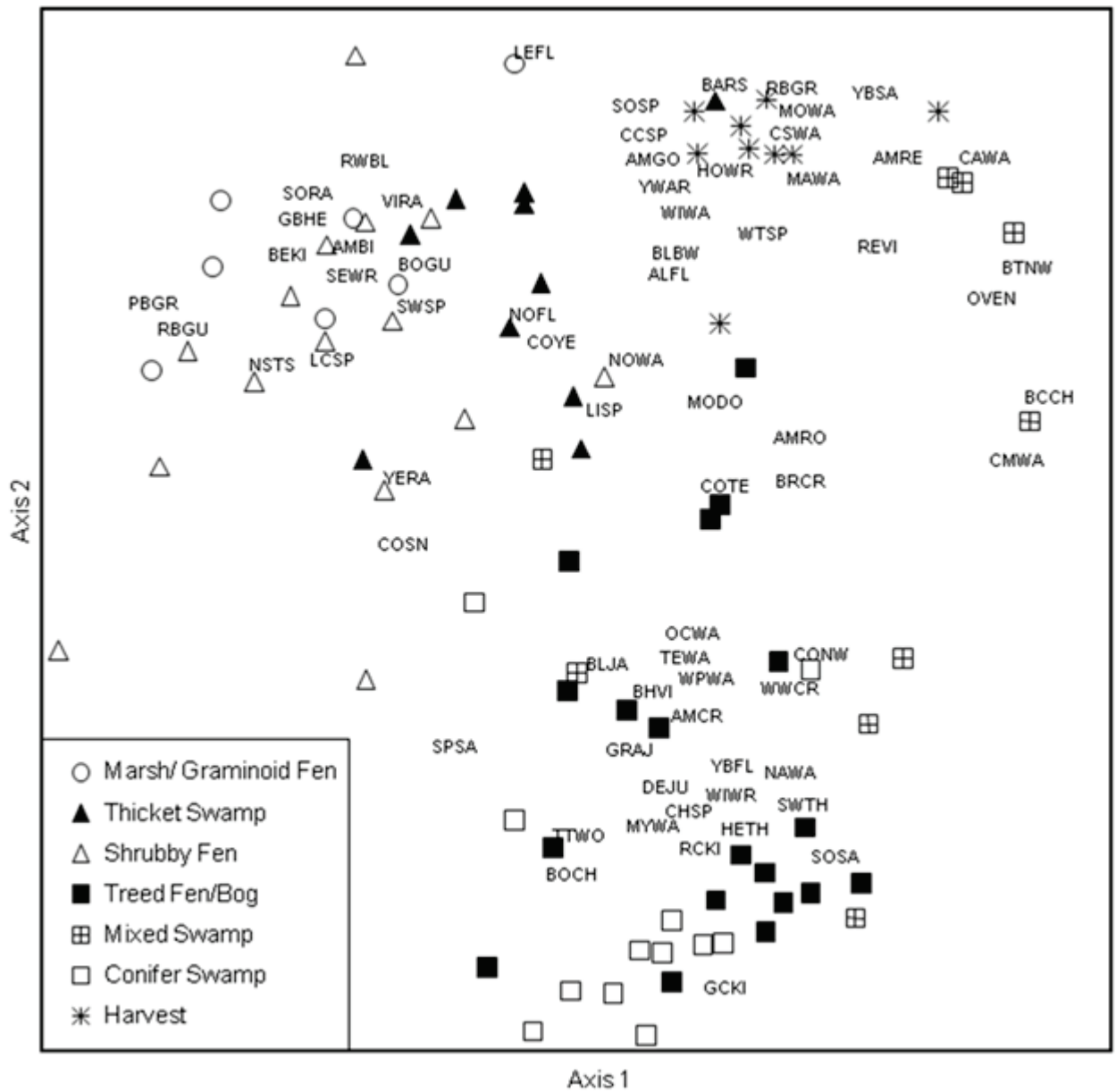


Figure 3.2 Two- dimensional solution for Non-Metric Multidimensional Scaling analysis of bird community composition among pre-assigned wetland classes. Four letter codes and scientific names of bird species are included in Appendix 2: Table A2.1.

CHAPTER 4: ECOLOGICAL CHARACTERISTICS OF BOREAL RIPARIAN BIRD

ASSEMBLAGES: A TRAIT-BASED APPROACH

A version of this chapter is in preparation for publication, Morissette, J.L, E.M. Bayne, T.P. Cobb and K.A. Hobson. In Prep. Ecological Characteristics of boreal riparian bird assemblages a trait-based approach.

4.1 Introduction

The relationship between animal community structure and ecosystem function is an important but poorly understood concept in ecology (see Naeem *et al.*, 1994 for a detailed review; Srivastava and Vellend 2005). Establishing such linkages can also shed light on the relative importance of different habitats within a landscape for conservation and management. For example, riparian areas are often considered unique and dynamic parts of the landscape due to their high spatial and temporal variability (Naiman *et al.*, 1993), which results in a diverse mosaic of habitats relative to adjacent uplands (Naiman *et al.*, 2005). In addition to often having a larger number of species than uplands, riparian areas also tend to contain species not found elsewhere on the landscape (Sabo *et al.*, 2005). Whether or not the higher and unique biodiversity present in riparian areas also translates to unique ecological function remains an important but largely unanswered question. Arguably, an approach which attempts to link directly measures of diversity, such as richness and evenness with specific ecological functions performed by individual species may provide additional insight into how biodiversity influences ecosystem function in riparian areas.

To facilitate greater synthesis between community ecology and ecosystem ecology, McGill *et al.*, (2006) proposed that community ecologists should emphasize functional traits rather than species identities. Functional traits are defined as “measurable aspects of an organism or species affecting its interaction with the environment, its capacity to find and acquire resources and therefore its fitness via effects on growth, reproduction, and survival” (Flynn *et al.*, 2009; McGill *et al.*, 2006). While trait-based approaches have been used for many taxa such as plants (Kyles and Leishman 2009) and arthropods (Lambeets *et al.*, 2008), birds are particularly suitable for this type of comparison because among vertebrates, birds exhibit the most diverse range of ecological functions (Sekercioglu 2006) such as seed dispersal and nutrient transfer, pest control and ecosystem engineering via the creation of burrows and cavities (Sekercioglu 2006). Trait-based approaches have been used to describe avian assemblages and represent species’ functional attributes among different habitats or regions (Petchey *et al.*, 2007), to measure functional changes due to anthropogenic disturbances (*e.g.*, Devictor *et al.*, 2008; Tscharncke *et al.*, 2008) and to evaluate the susceptibility of species to extinction (Sundstrom *et al.*, 2012). Much of the recent work linking functional traits to ecological function of birds has emphasized foraging traits (Karp *et al.*, 2011; Sundstrom *et al.*, 2012; Wardwell *et al.*, 2008)

Similar to trait-based approaches, Allen *et al.*, (2005) recently proposed that the resilience of an ecosystem could be assessed using an extension of the cross-scale resilience model (Peterson *et al.*, 1998). This model proposes that the distribution of functions (represented by traits) within and across scales, structures resilience (Peterson *et al.*, 1998). In this framework, resilience is defined as the capacity of ecosystems to absorb disturbances while maintaining their characteristic functions and feedbacks (Fischer *et al.*, 2007; Holling 1973; Peterson *et al.*, 1998). Thus, greater resilience is exemplified in systems that contain a higher diversity of functions

within scales and greater redundancy of functions across scales such that the loss of a function in one scale may be compensated by the same function at a different scale (Allen *et al.*, 2005; Fischer *et al.*, 2007). In other words, ecosystems that are more resilient contain a broader representation of functions within scales and repetition of functions across scales and should persist despite turnover of specific components (*i.e.*, loss of species) in response to environmental changes.

While the specific functional role that foraging birds play in boreal systems has not been well quantified (Sekercioglu 2006), the relationship between community composition and functional traits provides a useful assessment of whether riparian assemblages are distinct not only in species composition but also in functional composition . We used data from riparian zones associated with shallow boreal-plain ponds to determine whether riparian areas contain different functional traits and combinations of functional traits than upland areas. Given the typically different suite of habitats within the transition between aquatic habitat and shoreline forest relative to upland forests, we hypothesized that riparian areas should also contain a different suite of avian functional traits than upland areas. We expected to find functional traits consistent with an ability to exploit resources of the forest canopy or forest floor to be typical of assemblages in upland forest, while a more diverse suite of functional traits would be associated with transition areas between uplands and boreal wetlands where more feeding niches are available. We hypothesized that because riparian areas are more spatially variable than upland areas, they should contain higher functional diversity and higher measures of resilience than upland areas. We used the cross-scale resilience model (Allen *et al.*, 2005) to explore whether this measure of resilience is reflected in a greater functional richness and redundancy within scales and across scales in riparian areas than in upland areas.

4.2 Methods

4.2.1 Study area

The study area was located in north central Alberta, 400 km north of Edmonton near Utikuma Lake, AB (56°, 52'N, 115° 27' W) in the boreal mixedwood region of the Boreal Plain Ecozone (Figure 4.1). Three geological formations dominate the area, a moraine that runs north-south from Utikuma Lake, an outwash area to the west of the moraine and a lowland lacustrine plain to the east (Kyles and Leishman 2009; Devito *et al.*, unpublished report Whitehouse and Bayley 2005). Shoreline forests and upland forests were dominated by pure or mixed stands of Trembling Aspen (*Populus tremuloides*), Balsam Poplar (*Populus balsamifera*), White Spruce (*Picea glauca*), Balsam Fir (*Abies balsamea*) and Jack Pine (*Pinus banksiana*); the specific combination depended on soil type, disturbance history and topography. Throughout the study area, tree harvest by beavers (*Castor canadensis*) was common adjacent to most wetlands where hardwood tree species were present (Morissette *et al.*, unpubl. data).

Five major wetland classes (marsh, swamp, fen, bog and open water) account for between 30-60% of the total study area (Canadian Wetland Classification System, Chapter 3-table 3.1). The gradient from the water's edge of open-water wetlands and small lakes to the forest was of variable width and composed of aquatic grasses, sedges (*Carex* spp.), rushes (*Juncus* spp.), cattails (*Typha latifolia*), and lowland shrub (*Alnus* spp., *Salix* spp.). In drier sites to more xeric shrub species (e.g., *Cornus canadensis*) and tree species in early stages of succession (< 10 m in height) included Balsam Poplar, Aspen, White Birch (*Betula papyrifera*), Black Spruce (*Picea mariana*), and Tamarack (*Larix laricina*). Lowland edge sites and other sites with treed wetlands were dominated by Black Spruce, Tamarack and *Betula* sp. and *Salix* sp. Thus the transition

zone and shoreline forest of typical boreal ponds or lakes often contained elements of several wetland classes and/or several upland classes resulting in a structurally heterogeneous shoreline.

4.2.2 *Bird surveys*

The bird survey methodology we used combined a 400 m variable-width transect surveyed at a rate of 10 min/100 m with two, 10 min, variable-radius point counts (Hobson and Schieck 1999; Kardynal *et al.*, 2009). We also conducted a 5 min playback for marsh birds using the North American Marsh Bird Monitoring Protocol (Conway 2002). We placed transects parallel to the shoreline at the edge of the shoreline forest. Point count locations were 200 m apart along each transect, typically at the 50 m and 350 m mark and 50 m from the water's edge (Figure 4.2). Individual birds that were detected during both types of surveys were counted only once. Distance to birds was estimated in bands of 0–25 m, 26–50 m, 51–100 m or >100 m from the observer. In 2002, each site was surveyed three times. In 2003, we broadened our study by surveying each site only once and increasing the number of sites sampled. Thus some sites were sampled both years. Observers underwent a period of training prior to conducting surveys and were randomly assigned particular sites to avoid confounding observer and habitat type effects. Surveys took place on days free of rain and wind (< 4 on a Beaufort scale), began 30 minutes before sunrise and ended within 5 hours during 1-30 June 2002 and 2003.

4.2.3 *Site selection and study design*

The first year, we surveyed 24 shallow ponds that were 2.5- 16 ha in size and distributed among three geomorphologic areas typical of the western boreal plain (Kyles and Leishman 2009; Devito *et al.*, unpublished report Whitehouse and Bayley 2005). Each riparian transect was paired with an upland transect at least 200 m away from the riparian transect and from any other pond (Table 4.1). However, in one geomorphologic area (the clay plain), the transition between

upland and aquatic was > 200 m. In these cases, we added another transect to survey the transition between lowland and upland (n = 13). Thus, two types of transitions 1) riparian, representing an aquatic to terrestrial transition and 2) lowland edge, representing a transition between treed wetland and upland were compared to each other and to upland forest (no transition). We used a randomly selected start point and direction of travel for each transect. Ideally we used one single 400 m transect however, in some cases due to inflow channels or unsafe walking conditions, two separate 200 m transects were necessary. We expanded our surveys to a total of 64 ponds the second year.

4.2.4 Functional Diversity and Resilience Measures

Selecting functional traits

To determine functional traits, we used an existing detailed database assembled using an extensive literature review and expert consultation that contained functional traits for bird species (Appendix 3: Table A3.1; Kyles and Leishman 2009; McNicol and Russell 2002). We selected traits reflecting foraging habit and these were further categorized by foraging location, foraging method and food type (Table 4.2; Flynn *et al.*, 2009; Kyles and Leishman 2009; Petchey *et al.*, 2007). Similar to previous authors, we selected traits related to foraging habit that reflect resource use and capture/collection because such traits can drive biodiversity and ecosystem function relationships (Allen *et al.*, 2005; Fischer *et al.*, 2007)

Identifying indicator functional traits

We used Indicator Species Analysis (ISADufrêne and Legendre 1997; Kyles and Leishman 2009) to identify whether some traits could be considered characteristic of bird assemblages in either riparian, lowland transition or upland habitats. Indicator species analysis

combines relative abundance and frequency of occurrence to identify species assemblages characterizing groups of sites (Dufrêne and Legendre 1997). In our analyses we substituted traits for species. We determined the statistical significance of each indicator value using a randomization procedure.

Calculating functional diversity

We calculated several metrics of functional diversity (FD; Table 4.3) each emphasizing a different aspect of diversity (*e.g.*, richness, evenness) or a different metric (*e.g.*, ecological distance such as Sorensen, abundance or occurrence based). Several authors have described methodologies for calculating FD indices, outlining recommendations for their use (*e.g.*, Casanoves *et al.*, 2011; McGill *et al.*, 2006; Poos *et al.*, 2009). This work has illustrated that FD measures are sensitive to both the traits and the methodology used (Petchey and Gaston 2006; Poos *et al.*, 2009). Therefore, to increase the generality of our results, we chose a series of complementary indices of FD measures to ensure consistency of results and used traits for birds selected by many other authors in the literature (Allen *et al.*, 2005; Fischer *et al.*, 2007; Flynn *et al.*, 2009; Petchey *et al.*, 2007).

We first selected basic measures of FD that simply used traditional diversity calculations applied to the trait values; functional richness, effective richness and evenness (Magurran 2003). Functional richness is a measure of how much of the functional niche space is filled by the existing species (Schleuter *et al.*, 2010). A high functional evenness index usually means a very regular distribution, while a low functional evenness index indicates an uneven distribution.

Next, we calculated a series of indices using the method of Petchey and Gaston (2002) and since modified and improved by Petchey and Gaston (2006) and Schleuter *et al.*, (2010).

We describe our calculations briefly here but refer readers to the original papers for more detailed methodological descriptions. One index, FDPG (Petchey and Gaston 2002; Petchey and Gaston 2006), is a continuous measure of FD based on hierarchical classification of the functional traits. We used Gower's distance, to calculate multivariate distances because this metric accommodates continuous, nominal and ordinal data (Flynn *et al.*, 2009). Pair-wise distances were then summarized for the entire species pool, using unweighted pair-group method with an arithmetic mean (UPGMA Flynn *et al.*, 2009; Kyles and Leishman 2009; Legendre and Legendre 2002). FDPG of a community is calculated as the sum of the branch lengths in the classification.

We calculated two other measures of FD based on this approach. FDRao is an index of multivariate divergence based on Simpson's diversity index (Simpson 1949), and is calculated from abundance-weighted variance of the dissimilarities (Euclidean) between all species pairs (Rao's quadratic entropy, Rao 1982; Schleuter *et al.*, 2010). Minimum Spanning Tree (MST) is a measure of evenness that uses abundance weighted distances between all pairs to build a minimum spanning tree and measures the regularity of MST branch lengths (Mason *et al.*, 2003; Mason *et al.*, 2005). We did not transform the original data or rescale the traits in any way (Schleuter *et al.*, 2010) and we performed all FD calculations using the software package CRAN R 10.2.

Combining functional traits and scale to assess resilience

To assess resilience, we used the cross-resilience model based on a theoretical framework first proposed by Holling (1992) and further developed by Peterson *et al.*, (1998) and Allen *et al.*, (2005). This framework proposes that discontinuities in the distribution of body masses in species assemblages can be identified and that such discontinuities represent the different scales

at which organisms function since body size of a species partly governs its interaction with the environment (Allen *et al.*, 2005; Woodward *et al.*, 2005). For example larger birds tend to defend larger territories or have larger home ranges. The same functional groupings (substrate type and food type) as above can also be used, but a smaller number of functional groupings and scales are recommended (Allen *et al.*, 2005).

Body mass groups were derived using hierarchical cluster analysis of log-transformed body masses of all species expected to occur in this region. Following Flynn *et al.*, (2009), we used Ward's linkage, with Euclidean distances and Calinski Stopping rule (Legendre and Legendre 2002). This clustering process allowed for an objective identification of natural discontinuities in the frequency distribution of body masses. While other studies have used 7-9 aggregations (*e.g.*, Fischer *et al.*, 2007), our hierarchical analysis of the log-transformed body mass values suggested that nine groups provided most biologically sensible distribution of groupings (Appendix 3: Table A3.1).

As per Fischer *et al.*, (2007) we adopted substrate type and food type categories to reflect functional groups of resource use (Table 4.2). The number of functional groups (*i.e.*, functional richness) within an aggregation was calculated and then averaged across aggregations to yield average richness (AVRICH). We used the same principle to determine average evenness (AVEVEN) and average diversity (AVDIV). The concept of functional redundancy was integrated via two additional measures 1) within-scale redundancy (WSRED) calculated as the average species richness per functional group within each body mass grouping and cross-scale redundancy (CSRED) or the mean number of body mass groups at which functional groups are represented (Allen *et al.*, 2005).

Statistical comparison of functional diversity

We used analysis of variance (ANOVA) to compare FD indices among habitat types with Type III sums of squares (Biswas and Mallik 2010). Measures of richness, FD and resilience were response variables while habitat type and year were fixed and random factors, respectively. Each model was expressed as:

$$FDindices = Intercept + Habitat + Year + (Habitat*Year),$$

where FD indices included species richness, FD measures, and resilience measures (Table 4.3). In order to meet ANOVA assumptions (*i.e.*, Normality- KS test $P < 0.05$; Homogeneity of variances-Levene's test $P = 0.05$ and autocorrelation of residuals- visual assessment) the following variables were natural log transformed: species richness and MST. We used a Scheffe *post hoc* test, to identify significant differences among the three habitat types, applied a Bonferroni correction procedure (Quinn and Keough 2002) and used a significance value of $P = 0.03$.

4.3 Results

Indicator Traits

Our results are based on a total of 11,868 individuals counted over a period of 2 years across 137 sites. We entered 31 traits (Table 4.3) into the ISA which represented trait assignments for 86 species (Appendix 3: Table A3.2). Assemblages in riparian areas differed in the three classes of foraging traits which were food type, habit and location (Table 4.4). Crustaceavores, omnivores and vermivores were most abundant and frequent in riparian areas while only molluscivores, represented by the Ovenbird (*Seiurus aurocapilla*), were indicators of upland transects. Aerial foraging birds including "hawking" and "sallying" species were indicators of riparian areas while upland sites were more likely to contain species that forage by

"gleaning". Not surprisingly birds with foraging locations more associated with water were indicators of riparian transects. We also counted a greater abundance of birds that forage on the ground associated with riparian transects. No traits were significant indicators of lowland to upland transition sites.

Indices of functional diversity

Every index of FD except was higher in riparian habitats than in either upland or lowland habitats (Table 4.5, Figure 4.3). There was also a significant year effect (Table 4.5), but the interaction between habitat type and year was not significant suggesting this trend was the same regardless of year. *Post-hoc* tests showed that differences between riparian transects and both upland and lowland habitats were significant (Figure 4.3, Scheffe, $p < 0.03$). However, the differences between upland and lowland edge habitat types were not significant (Figure 4.3, Scheffe, $p > 0.03$). Generally, we found more functional groups represented in riparian transects than in upland transects (Figure 4.3; functional group richness panel). Species richness and diversity were higher in riparian than upland and lowland transects (Table 4.5; Figure 4.3).

Applying the cross-resilience model

Cross-scale redundancy (CSRED) and within-scale redundancy (WSRED) also differed between upland and riparian transects (Table 4.6). That is, the average number of species in each function group within a scale (WSRED) and the average number of scales at which functions were represented (CSRED) were both significantly higher in riparian areas than in either upland or lowland areas (Table 4.6). Average richness and average diversity were also higher in riparian habitats than in lowland and upland areas while the average evenness did not differ among habitat types (Table 4.6; Figure 4.4).

4.4 Discussion

Boreal riparian areas were dominated by bird communities with a different suite of traits than either those of the lowland or upland areas we examined. We also found that these differences were consistent across all three of the resource-use categories we selected (foraging location, substrate, food type). For example, foraging locations associated with water and with aerial foraging habits were indicators of riparian assemblages while upland sites were more likely to contain gleaners. Together with previous work carried out at a guild level (*e.g.*, Croonquist and Brooks 1991) and with our species-level understanding of distributions of boreal birds among riparian and upland landscapes (*e.g.*, Chapter 2, MacDonald *et al.*, 2006; Kardynal *et al.*, 2009), these patterns suggest that riparian areas provide a suite of foraging opportunities that are distinct from those of other vegetation classes. Interestingly Bub *et al.*, (2004) found foliage- gleaners were more abundant in riparian forests. Thus different results are possible by combining foraging substrate and style into one guild suggesting methods that quantify variability in trait combinations are beneficial.

According to the various FD metrics we examined, functional richness and diversity were greater in riparian areas than in either upland or lowland areas. These results were consistent across a variety of different methods (Table 4.3), whether ecological distance, abundance or occurrence values of traits were used. This provides confidence in this pattern independent of the specific methods used to calculate functional diversity. There was a significant year effect in our results with a lower FD for all indices in 2003 than in 2002 which may simply reflect the change in our sampling effort across years. However, we found this change in sampling effort did not affect patterns of FD associated with riparian and upland habitats.

Many approaches have been used to compare biodiversity in riparian and upland areas. Most approaches are aimed at species- (Macdonald *et al.*, 2006; Whitaker and Montevercchi 1997) or guild-level (Croonquist and Brooks 1991; Larue *et al.*, 1995) characterization of communities and establishing the conservation value of riparian areas in a wide variety of landscapes (*e.g.*, Saab 1999; Sabo *et al.*, 2005). These studies also generally include some measure of species diversity (*e.g.*, H') without paying additional attention to specific functional traits or their diversity. However, a principle advantage of trait-based approaches is that multiple functions can be taken together to assess resulting patterns of functional diversity, distribution among spatial scales and provide a quantitative approach to assessing functions while generating community-level hypotheses related to environmental conditions or gradients (Biswas and Mallik 2011; McGill *et al.*, 2006; Schleuter *et al.*, 2010).

Debate regarding the best methods for trait-based analyses is ongoing (*e.g.*, Laliberté and Legendre 2010; Mouchet *et al.*, 2008) and metrics include various categorical and continuous indices of single or combined ecological traits of species in an assemblage (see Schleuter *et al.*, 2010 for a detailed review). While more research to prioritize traits most indicative of ecological function is required, authors have generally selected traits reflecting resource acquisition and use. Foraging and body size (*i.e.*, mass) are examples of traits clearly linked to growth, reproduction and survival of individuals and frequently used in other trait- based approaches for birds because of presumed or known linkages to ecological functions of birds in ecosystems (*e.g.*, Flynn *et al.*, 2009). The number of traits selected can, but does not necessarily, affect the level of observed redundancy (Petchey and Gaston 2002; Schleuter *et al.*, 2010). For this reason we used types and numbers of traits widely recognized to indicate resource use among bird species and that have been used in previous studies of functional diversity in avian assemblages (*e.g.*, Fischer *et*

al., 2007; Flynn *et al.*, 2009; Sundstrom *et al.*, 2012). Other traits such as nesting ecology might also eventually be beneficial to consider as some species (*e.g.*, primary cavity excavators) may play a pivotal functional role in maintaining species composition in bird communities by providing nesting sites.

Increases in functional diversity can be correlated with increases in species richness (*e.g.*, Petchey *et al.*, 2007). We used a range of FD metrics including those metrics (*e.g.*, MST and FDRao) that have been demonstrated to be less correlated with species richness (Schleuter *et al.*, 2010). However, research considered to be foundational in the field of “biodiversity and ecosystem function” have shown not only that high species diversity also often results in high functional diversity (Hooper *et al.*, 2005; Tilman *et al.*, 2001) but that assemblages generally exhibit less functional redundancy than expected by chance (Petchey *et al.*, 2007). Thus, also considering not only the number and diversity of functions relative to random assemblages (Petchey *et al.*, 2007) but also the degree that traits are repeated within and among scales (Allen *et al.*, 2005) refines our understanding of resilience in real bird communities.

When we applied the cross-resilience model, our results suggested that riparian bird communities were more resilient than either upland or lowland bird communities. Riparian areas represent a unique spatial organization as a mosaic of habitats and substantial small-scale heterogeneity in response to changes in water availability, topography, and soils. Some authors consider ecotones like riparian areas unstable, highly dynamic (vanderMaarel 1990 in Yarrow and Marín 2007) and fragile (Biswas and Mallik 2010), while others contend that riparian areas support vegetation and organisms necessarily well adapted to disturbance (*e.g.*, Kardynal *et al.*, 2011; Reeves *et al.*, 2006). Methods for quantifying resilience have been termed a “research frontier” particularly when applied to land management questions (Fischer *et al.*, 2007). The

assumption that the distribution of foraging guilds across body mass groups represents a meaningful index for the distribution of ecological functions across scales is central to the interpretation of the comparison we provide between boreal upland and riparian areas (Fischer *et al.*, 2007; Allen *et al.*, 2005). Furthermore, relationships between biodiversity and ecosystem function are complex and a mechanistic understanding of consequences of biodiversity losses is lacking. Regardless of these uncertainties, our findings highlight differences in functional composition of upland and riparian bird communities supporting calls by previous work for a greater understanding of the dynamics of these systems.

Conclusions and future research

Boreal forests are under increasing pressure from human disturbances. Therefore, an understanding of the ecological complexity comprising bird communities among different habitat types that consider both species identities and functional traits will assist in the development of successful conservation strategies. Our study examined only a subset of the species present in the area (86 of > 150 possible species), and a subset of functional roles of birds which likely oversimplifies the scope and complexity of ecological interactions (Paszkowski and Tonn 2006). Nevertheless, our results indicate riparian bird assemblages possess a different suite of functional traits, higher functional diversity, and greater resilience than other areas of the landscape we examined. Undoubtedly further debate regarding the best approaches to measuring functional diversity and assessing the resilience of ecosystems will continue to advance this approach to assessing biodiversity. In the meantime, many are beginning to apply these measures with interesting results within and among trophic levels (Biswas and Mallik 2010; Duffy *et al.*, 2007; Laliberté and Legendre 2010) including birds (Karp *et al.*, 2011; Sundstrom *et al.*, 2012).

From a conservation perspective, maintaining functional diversity is only one of several process- and pattern-oriented strategies (*e.g.*, maintaining natural disturbance regimes, conserving native vegetation) that have been suggested for managing the working landscape (Fischer *et al.*, 2007). However, we agree with others that suggest a greater consideration of ecological traits of species will assist in building the complementarity of species-level and ecosystem-based approaches (Lindenmayer *et al.*, 2007) and in developing effective conservation and sustainable land use strategies. Data from long term studies of boreal forest bird communities that strategically consider both species- and ecosystem-level changes in boreal bird assemblages in response to environmental change over time and across gradients (*e.g.*, land use intensity) will be critical to this effort.

Table 4.1 Sample sizes and descriptions of transect placement for each of the three habitat types sampled.

Abbreviation	Site type description	Sample Size
Riparian	Transects along transition between aquatic and upland forest (Figure 4.2)	87
Upland	Transects in upland forest at least 200 m from water	38
Lowland	Transects situated along the transition between treed wetlands and upland forest (Figure 4.2)	13

Table 4.2 Functional traits used for calculating indices of functional diversity and resilience (as per sources in table 4.3).

Functional Trait	Type
Body Mass	NA
Food Type	Carnivore, herbivore, insectivore, omnivore, molluscivore, granivore, crustaceavore, vermivore, piscivore
Foraging Habit	Ambusher, diver, dabbler, excavator, foot-plunger, forager, grazer, gleaner, hawkler, hover- gleaner, strangler, plunger, screener, scavenger, scaler, prober, sallier
Foraging Location	Aerial, bark, floral, water, water bottom, water -marsh, water-shoreline, water-surface, ground, lower canopy shrub, muddy, upper canopy

Table 4.3 Selected measures of functional diversity and resilience used to distinguish functional attributes and contributions of riparian areas (Modified from: Petchey and Gaston 2006; Schleuter *et al.*, 2010).

Measure	Description	Calculated from	Abundance	Categorical	Source
Functional					
FDPG ^a	Sum of branch length of classification; richness measure	Hierarchical Classification	No	Yes	Petchey and Gaston 2002; 2006
FDRao ^b	Branch lengths between species; divergence measure ^c	Hierarchical Classification	Yes	Yes	Rao 1982
MST	Abundance –weighted distances between all pairs to build a minimum spanning tree; measure of regularity of branch lengths; evenness measure	Distance Matrix	Yes	Yes	Villéger <i>et al.</i> , 2008
Evenness	Evenness of trait values (one-dimensional)	Trait values	Yes	Yes	Mouillot <i>et al.</i> , 2005
Richness ^a	Number of functional groups	Trait values	No	Yes	NA
Effective Richness ^a	Exp(H)	Trait values	Yes	Yes	Magurran <i>et al.</i> , 2004

Cross-scale resilience^a

WSRED	Average number of species within each functional group / aggregation ^d as a measure of redundancy;	Trait values	No	Yes	Allen <i>et al.</i> , 2005;
CSRED	Average number of aggregation at which each function is represented	Trait values	No	Yes	As above
AVRICH	Number of functional groups within aggregations averaged across aggregations	Trait values	No	Yes	As above
AVEVEN	Same as above except evenness	Trait values	No	Yes	As above
AVDIV	Same as above except diversity	Trait values	No	Yes	As above

^a Correlated with species richness

^b Also called quadratic entropy; FD_Q ; Rao 1982

^c Divergence is low when the most abundant species have traits close to the center of the range, high when the most abundant species have extreme functional trait values (Schleuter *et al.*, 2010).

^d Aggregations refer to groups represented by results of cluster analysis of body mass and represent scale

Table 4.4 Results of foraging trait–level indicator species analysis (ISA) among the three habitat types described in Table 4.1.

Habitat Type	Food Type	<i>Habit</i>	<i>Location</i>
Riparian	Crustaceavore, omnivore,vermivore	Aerial, forager, hawker, prober, sallier	Ground , muddy, water surface, water
Upland	Molluscivore	Gleaner	Upper canopy
Lowland	N/A	N/A	N/A

Table 4.5 Results of ANOVAs comparing FD indices among three habitat types. FD indices were dependent variables; habitat type was entered as a fixed factor and year as a random factor.

Response variable & Effects	df	MS	<i>F</i>	<i>P</i>
FDPG				
Habitat type	2	2074109.0207	608.042	0.002
Year	1	2497553.647	141.986	< 0.0001
Habitat X Year	2	3411.129	0.055	0.947
Error	132	62383.245		
FDRAO				
Habitat type	2	79.815	50.928	0.019
Year	1	17.824	6.574	0.028
Habitat X Year	2	1.567	0.248	0.781
Error	132	6.325		
FUNVEVE (MST)				
Habitat type	2	1579870.789	439.79	0.002
Year	1	1862459.024	136.779	< 0.0001
Habitat X Year	2	3592.329	0.079	0.924
Error	132	45284.22		

Response variable & Effects	df	MS	<i>F</i>	<i>P</i>
EFFRICH				
Habitat type	2	227.031	60.923	0.016
Year	1	386.111	83.479	< 0.001
Habitat X Year	2	3.72	0.499	0.608
Error	132	7.464		
Evenness				
Habitat type	2	0.005	12.105	0.076
Year	1	0.017	10.941	0.002
Habitat X Year	2	0.000	0.74	0.929
Error	132	0.005		
Species Richness				
Habitat type	2	313.42	93.646	0.011
Year	1	440.409	90.225	< 0.0001
Habitat X Year	2	4.881	0.344	0.710
Error	132	9.729		

Response variable & Effects	df	MS	<i>F</i>	<i>P</i>
Functional Richness				
Habitat type	2	132.547	77.582	0.013
Year	1	39.571	13.869	0.004
Habitat X Year	2	1.708	0.264	0.768
Error	132	6.49		

Table 4.6 Results of ANOVAs for resilience measures as dependent variables; habitat type was entered as a fixed factor and year as a random factor.

Response variable & Effects	df	MS	<i>F</i>	<i>P</i>
WSRED				
Habitat type	2	0.967	46.292	0.021
Year	1	0.610	26.548	0.006
Habitat X Year	2	0.021	0.706	0.496
Error	132	0.030		
CSRED				
Habitat type	2	0.773	406.67	0.002
Year	1	0.220	30.92	0.002
Habitat X Year	2	0.002	0.81	0.922
Error	132	0.024		
AVEVEN				
Habitat type	2	0.004	13.457	0.069
Year	1	0.000	0.957	0.385
Habitat X Year	2	0.000	0.807	0.448
Error	132	0.024		

Response variable & Effects	df	MS	<i>F</i>	<i>P</i>
AVRICH				
Habitat type	2	17.65	406.659	0.002
Year	1	5.018	30.923	<0.0001
Habitat X Year	2	0.162	0.081	0.922
Error	132	0.538	0.967	
AVDIV				
Habitat type	2	0.945	620.769	0.002
Year	1	0.049	5.905	0.018
Habitat X Year	2	0.002	0.051	0.95
Error	132	0.030		

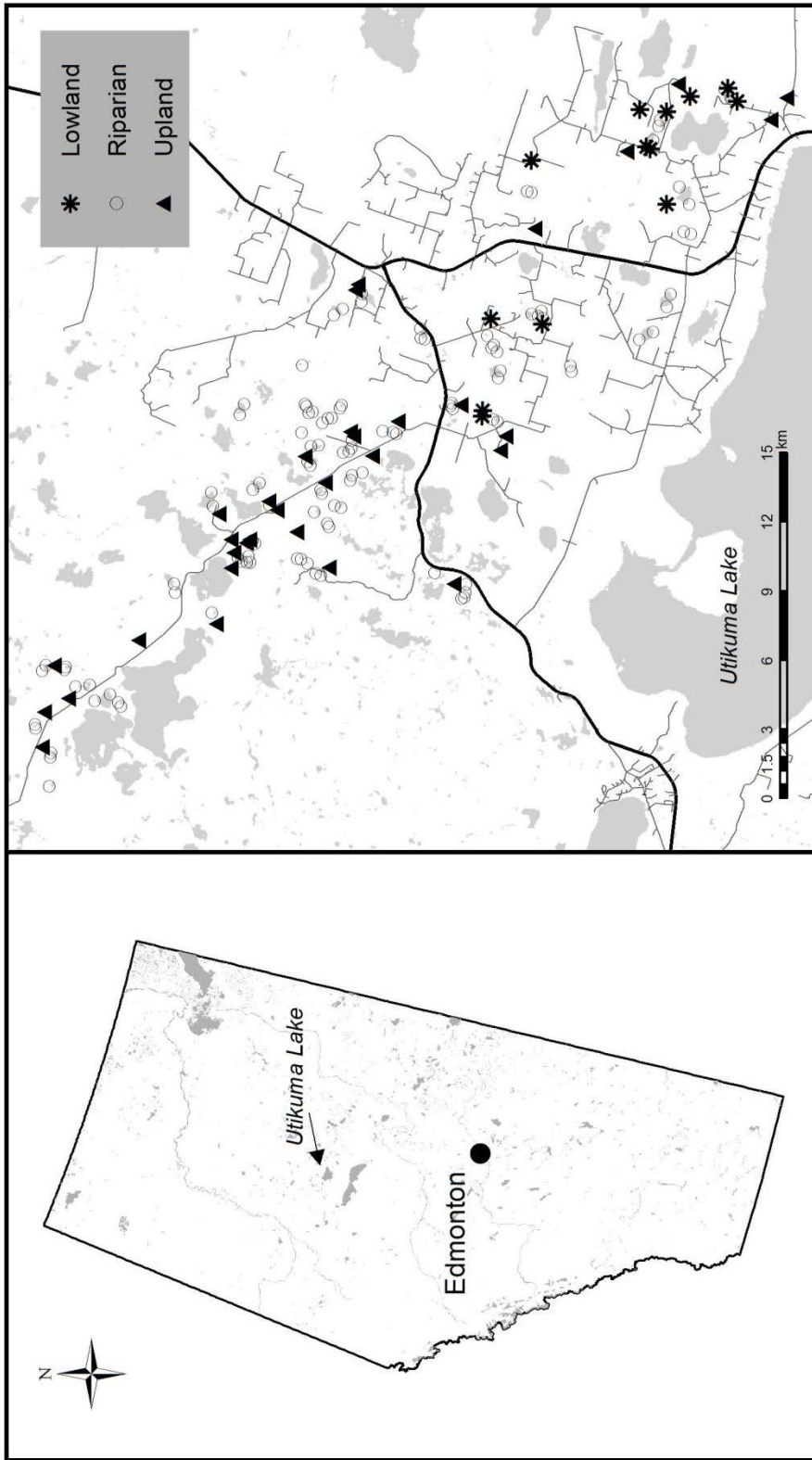


Figure 4.1 Distribution of transect locations in the Utikuma study area.

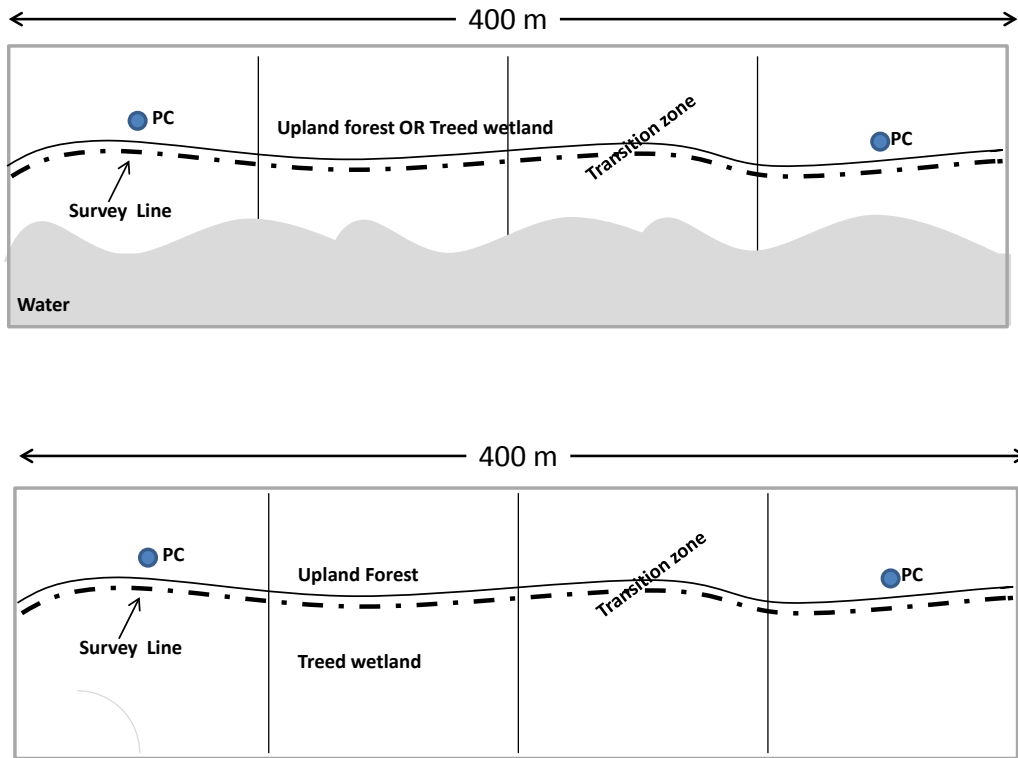


Figure 4.2 Diagram representing placement of transect survey line in transition zone between habitat types.

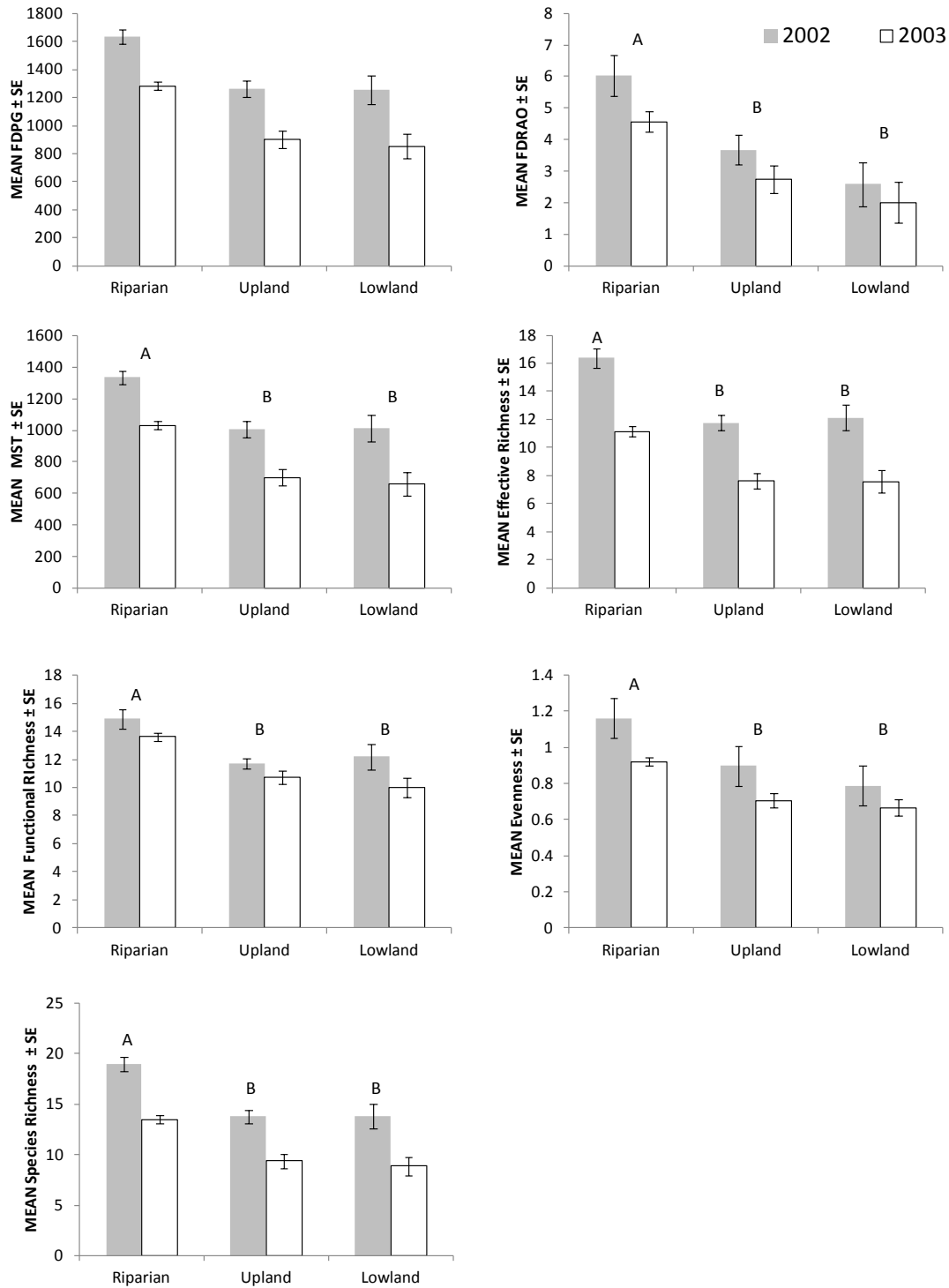


Figure 4.3 Comparison of mean FD measures among the three habitat types. Error bars represent \pm SE. Based on Tukey's post hoc test bars marked with the same letter are not significantly different at $\alpha < 0.03$.

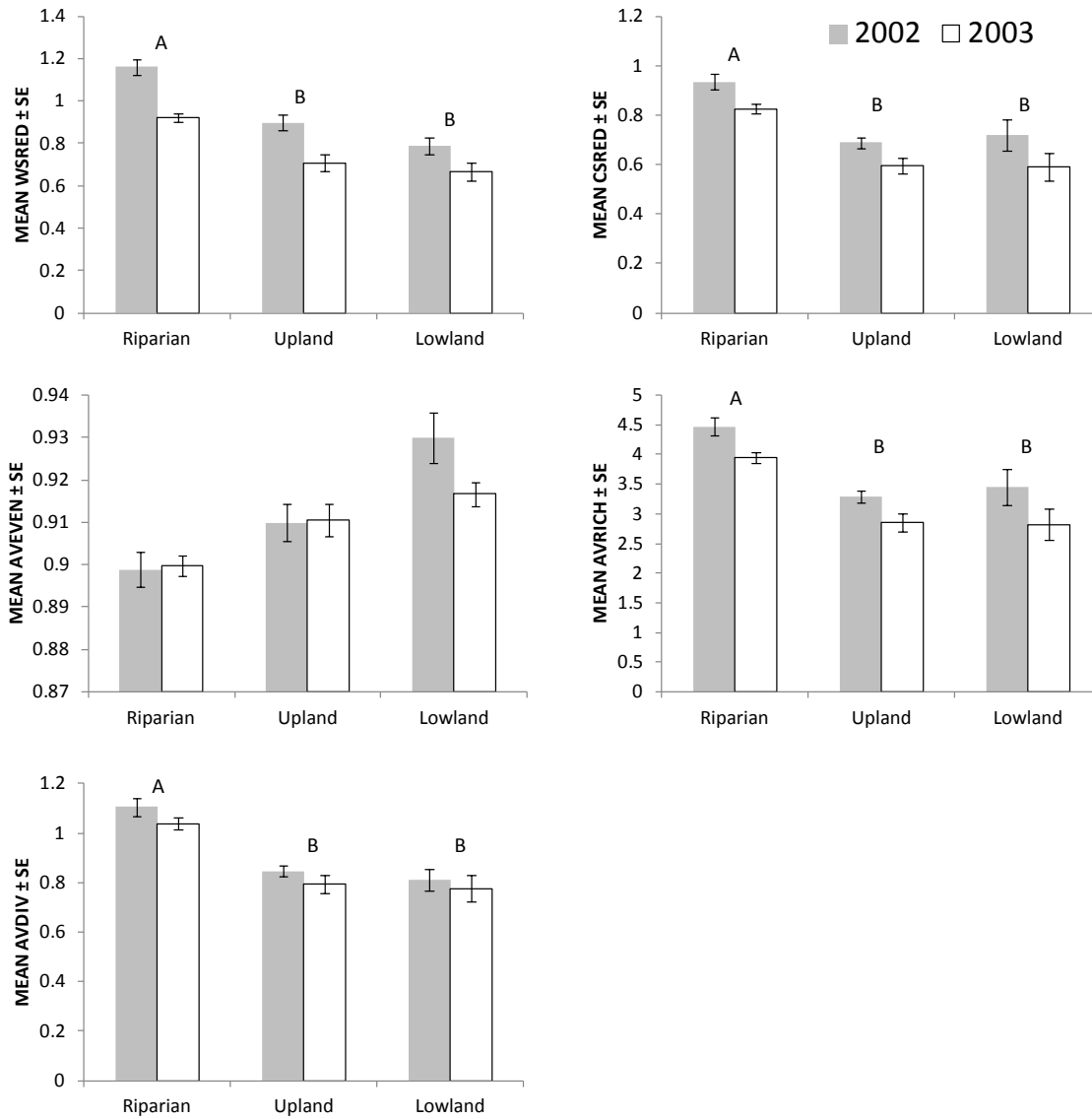


Figure 4.4 Comparison of mean resilience measures among the three habitat types. Error bars represent \pm SE. Based on Tukey's post hoc test, bars marked with the same letter are not significantly different at $\alpha < 0.03$.

4.5 References

- Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958-966.
- Biswas, S. R. and A. U. Mallik. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology* 9:28-35.
- Biswas, S. R. and A. U. Mallik. 2011. Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere* 2:1-10.
- Bub, B. R., D. J. Flaspohler, and C. J. F. Huckins. 2004. Riparian and upland breeding-bird assemblages along headwater streams in Michigan's upper peninsula. *Journal of Wildlife Management* 68:383-392.
- Casanoves, F., L. E. Pla, and J. A. Di Rienzo. 2011. FDiversity: an Integrated Tool to Estimate and Analyze Functional Diversity. *Bulletin of the Ecological Society of America* 92:147-152.
- Conway, C. J. 2002. Standardized North American marsh bird monitoring protocols. 1-23.
- Croonquist, M. J. and R. P. Brooks. 1991. Use of avian and mammalian guilds as indicators of cumulative impacts in riparian-wetland areas. *Environmental Management* 15:701-714.
- Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17:252-261.

- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522-538.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: a need for flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. A. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- Flynn, D. F., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. Trautman Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and D. L. DeGiusti. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12:22-33.
- Hobson, K. A. and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecological Applications* 9:849-863.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-23.
- Hooper, D. U., F. S. Chapin, III, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, and A. J. Symstad. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3-35.

- Kardynal, K. J., J. L. Morissette, S. L. VanWilgenburg, E. M. Bayne, and K. A. Hobson. 2011. Avian response to experimental harvest in southern boreal mixedwood shoreline forests: implications for riparian buffer management. *Canadian Journal of Forest Research* 41:2375-2388.
- Kardynal, K., K. A. Hobson, S. L. Van Wilgenburg, and J. L. Morissette. 2009. Moving riparian management guidelines towards a natural disturbance model: an example using boreal riparian and shoreline forest bird communities. *Forest Ecology and Management* 257:54-65.
- Karp, D. S., G. Ziv, J. Zook, P. R. Ehrlich, and G. C. Daily. 2011. Resilience and stability in bird guilds across a tropical countryside. *Proceedings of the National Academy of Sciences* 108:21134-21139.
- Kyles, G. A. R. R. and M. R. Leishman. 2009. Plant functional trait variation in relation to riparian geomorphology: The importance of disturbance. *Austral Ecology* 34:793-804.
- Laliberté, E. and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305.
- Lambeets, K., M. L. Vandegehuchte, J. P. Maelfait, and D. Bonte. 2008. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology* 77:1162-1174.
- Larue, P., L. Bélanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. *Canadian Journal of Forest Research* 25:555-566.

- Legendre, P. and L. Legendre. 2002. Numerical Ecology, 2nd Edition edition. Elsevier, Amsterdam.
- Lindenmayer, D. B., J. Fischer, A. Felton, R. Montague-Drake, A. D. Manning, D. Simberloff, K. Youngentob, D. Saunders, D. Wilson, A. M. Felton, C. Blackmore, A. Lowe, S. Bond, N. Munro, and C. P. Elliott. 2007. The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos* 116:1220-1226.
- Macdonald, S. E., B. Eaton, C. S. Machtans, C. Paszkowski, S. Hannon, and S. Boutin. 2006. Is forest close to lakes ecologically unique? Analysis of vegetation, small mammals, amphibians, and songbirds. *Forest Ecology and Management* 223:1-17.
- Magurran, A. E. 2003. Measuring Biological Diversity. Blackwell Science, Malden, MA.
- Mason, N. W. H., K. MacGillivray, J. B. Steel, and J. B. Wilson. 2003. An index of functional diversity. *Journal of Vegetation Science* 14:571-578.
- Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112-118.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution* 21:178-185.
- McNicol, D. K. and R. Russell. 2002. Project WILDSPACETM: Avian Lifehistory Database. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario Canada.

- Mouchet, M., F. Guilhaumon, S. Villeger, N. W. H. Mason, J.-A. Tomasini, and D. Mouillot. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117:794-800.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734-737.
- Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia - ecology, conservation, and management of streamside communities*. Elsevier Academic Press, Burlington, MA.
- Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209-212.
- Paszkowski, C. A. and W. M. Tonn. 2006. Foraging guilds of aquatic birds on productive boreal lakes: environmental relations and concordance patterns. *Hydrobiologia* 567:19-30.
- Petchey, O. L., K. L. Evans, I. S. Fishburn, and K. J. Gaston. 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology* 76:977-985.
- Petchey, O. L. and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402-411.
- Petchey, O. L. and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741-758.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.

- Poos, M. S., S. C. Walker, and D. A. Jackson. 2009. Functional-diversity indices can be driven by methodological choices and species richness. *Ecology* 90:341-347.
- Quinn, G. P. and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, United Kingdom.
- Rao, C. R. 1982. Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* 21:24-43.
- Reeves, G. H., P. A. Bisson, B. E. Rieman, and L. E. Benda. 2006. Postfire logging in riparian areas. *Conservation Biology* 20:994-1004.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9:135-151.
- Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* 86:56-62.
- Schleuter, D., M. Daufresne, F. Massol, and C. Argiller. 2010. A user's guide to functional diversity indices. *Ecological Monographs* 80:469-484.
- Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. *Trends in Ecology & Evolution* 21:464-471.
- Srivastava, D. S. and M. Vellend. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution and Systematics* 36:267-294.

- Sundstrom, S. M., C. R. Allen, and C. Barichievy. 2012. Species, Functional Groups, and Thresholds in Ecological Resilience. *Conservation Biology* 26:305-314.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843-808.
- Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89:944-951.
- Wardwell, D. A., C. R. Allen, G. D. Peterson, and A. J. Tyre. 2008. A test of the cross-scale resilience model: Functional richness in Mediterranean-climate ecosystems. *Ecological Complexity* 5:165-182.
- Whitaker, D. M. and W. A. Montevecchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a Balsam fir ecosystem. *Canadian Journal of Forest Research* 27:1159-1167.
- Whitehouse, H. E. and S. E. Bayley. 2005. Vegetation patterns and biodiversity of peatland plant communities surrounding mid-boreal wetland ponds in Alberta, Canada. *Canadian Journal of Botany* 83:621-637.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *TRENDS in Ecology and Evolution*.

Yarrow, M. M. and V. H. Marín. 2007. Toward conceptual cohesiveness: a historical analysis of the theory and utility of ecological boundaries and transition zones. *Ecosystems* 10:462-476.

CHAPTER 5: REGIONAL VARIATION IN THRESHOLD RESPONSES OF WETLAND- ASSOCIATED BIRD COMMUNITIES TO CONVERSION OF BOREAL FOREST TO AGRICULTURE

A version of this chapter has been submitted for publication. Morissette, J.L., E.M. Bayne, K.A. Hobson.

In Review. Regional variation in threshold responses of wetland- associated bird communities to conversion of boreal forest to agriculture. *Biological Conservation.*

5.1 Introduction

Worldwide, loss and fragmentation of forest due to agricultural conversion is one of the largest causes of biodiversity loss (but see Gaston *et al.*, 2003). Agriculture has also resulted in loss and degradation of wetlands and riparian areas in forested areas because of drainage, eutrophication, pesticide use and use as water sources for cattle (Houlahan and Findlay 2004; Tilman *et al.*, 2001). More recently, many regions are developing or have adopted wetland policies, regulations and financial incentives that try to conserve remaining wetlands. However, depending on regulatory context, these practices typically consider a limited range of wetland types and protect only the wetland itself and occasionally small amounts of adjoining riparian areas and shoreline forests (Bauer *et al.*, 2010; Foote and Krogman 2006). This type of protection and management does not consider landscape- level effects that may also be influencing biodiversity in these areas.

Although local conditions are no doubt important for biodiversity (Bauer *et al.*, 2010; Saab 1999), there is increasing evidence to suggest that the loss of forest around wetlands and riparian areas has significant negative effects on wetland biodiversity (Lougheed *et al.*, 2008;

Radford *et al.*, 2005; Saab 1999). These effects are expected to be greatest where species may track temporally variable resources (*e.g.*, insect emergences), or concurrently use different parts of the landscape (*e.g.*, bufflehead, *Bucephala albeola* which forage in water and nest in tree cavities). Relative to the amount of research conducted in upland forests that has documented how forest loss and fragmentation influence birds, the extent to which changes in the landscape matrix influence wetland- and riparian-associated birds, where core habitat (shoreline forests, riparian areas and the wetland itself) is intact has not been well documented (but see Houlihan *et al.*, 2006).

Between 1951 and 1999, the boreal forest of western Canada experienced annual rates of deforestation on privately-owned lands from 0.87 % to 1.76 % annually (Hobson *et al.*, 2002). Moreover, in Alberta, Saskatchewan and Manitoba as much as 25 %, 31 % and 48 % of the boreal plains is considered at risk of being converted to agriculture (*e.g.*, annual crops and pasture; Hobson *et al.*, 2002). To date, relative to other biomes, the boreal region is the least affected by agricultural conversion. However climate change is anticipated to increase the suitability of some boreal areas for agriculture, suggesting that the risk of deforestation due to agricultural conversion will continue to increase (Mills 1994). Combined with drier conditions expected due to climate change (Foote and Krogman 2006) and other impacts of agriculture, loss and degradation of boreal forest wetlands seems inevitable under these scenarios. A better understanding of responses of wetland and riparian biodiversity to these changes will be crucial to evaluating the success of wetland conservation initiatives in forested landscapes undergoing conversion to agriculture.

One approach to quantifying changes in both terrestrial and aquatic ecosystems is the determination of ecological thresholds, defined as zones or points where an abrupt change in an

ecosystem property occurs in response to an environmental driver (Groffman *et al.*, 2006). In general, evidence for density or population thresholds has been equivocal with results being metric-, scale- and species-dependent (Swift and Hannon 2010). Further, when community-level metrics such as diversity and species richness are used to determine thresholds, their application in an environmental management context becomes problematic. These metrics obscure species-level changes (*i.e.*, species identity) and do not distinguish between positively responding and negatively responding species. Either of positive or negative species responses to land use changes are potentially important management tools. For example, positively-responding species often contribute to species richness in areas of intermediate disturbance (Lepczyk *et al.*, 2008; Shea *et al.*, 2004). However examining species identity confirms species that respond positively to novel gradients such as human disturbances are frequently non-native (Ervin *et al.*, 2006) or species generalists (Devictor and Robert 2009). Increases in species richness may also mask declines in the occurrence and abundance of native species and specialists.

In cases where thresholds in species richness and diversity have been identified, ecological interpretation often also includes caveats that a rapid decrease in species richness represents the “endpoint of extinction processes for multiple species” (Radford *et al.*, 2005), a point at which management intervention is less likely to be successful. Methods that detect contributions of individual taxa to community change along a novel environmental gradient (*e.g.*, Baker and King 2010) and thus provide an index of whether community-level thresholds have occurred are more informative and allow managers to assess both species-level tradeoffs as well as broader community level implications of land-use change.

Indeed there are several definitions of and approaches to determining thresholds (Swift and Hannon 2010). Recently, Hilderbrand *et al.*, (2010) suggested the use of an “initiation of

impact” threshold (minimum detectable response). This type of threshold is defined as a zone or point at which disturbances or stressors (here agricultural conversion of boreal forest) begin to affect organisms negatively (e.g. measured as relative abundance and frequency of occurrence). This approach is potentially useful in predictive models and environmental management as determining an “initiation of impact” could provide managers an estimate of when a particular land-use practice may be approaching a critical threshold and potentially non-reversible change (Groffman *et al.*, 2006).

Recognizing whether species-level and community composition thresholds exist relative to the amount of forest cover around wetlands will help to inform managers about which wetlands should be conserved if the objective is to maintain avian wetland communities consistent with those in forested ecosystems. However, for these types of thresholds to be practically applied, they also must be generalizable and applicable at scales suitable for management.

To examine probable drivers influencing distribution and abundances of species, many authors have used a multi-scaled approach to assess the relative importance of local habitat features affecting communities and influences of the broader landscape context on the distribution abundance and dynamics of birds (Kennedy *et al.*, 2011; Saab 1999). In the context of identifying thresholds in abundance or frequency of occurrence at the scale of the patch (local habitat), changes may appear abrupt due to the sudden loss of a key species (Chapin, III *et al.*, 2004); at a landscape scale, transitions may appear more gradual due to changes being distributed over longer scales of space and time (Radford *et al.*, 2005). As many bird species are ecologically linked, directly or indirectly, to both terrestrial and aquatic ecosystems in some way

via riparian areas and wetlands we consider avian assemblages in shoreline forests and riparian areas as “trophic links” between terrestrial and aquatic systems (Larsen *et al.*, 2010).

Here, we studied avian assemblages using boreal wetlands, riparian areas and shoreline forests along a gradient of agricultural conversion at two nested scales; individual wetlands and 5 x5 km landscapes. We set out to (1) characterize species-level changes in response to increasing levels of conversion of forest to agriculture; (2) determine whether these change points resulted in community-level composition thresholds; (3) determine whether these thresholds were consistent when habitat loss was measured at local- and landscape scales; and (4) compare these responses in two different regions of the Boreal Plain ecozone western Canada –one a small region of contiguous forest completely surrounded by agricultural land uses (*i.e.*, an “island” of forest in a “sea” of agriculture), the other adjacent to and embedded within relatively contiguous forest. As birds typically occurring in late seral-stages are more sensitive to agricultural conversion than early successional species and edge species (Hobson and Bayne 2000), we expected species typically associated with riparian areas and wetlands to be more tolerant of changes in the surrounding habitat matrix than those typically associated with areas of intact forest. This tolerance would be exhibited by species-level change points later along the disturbance gradient.

5.2. Methods

5.2.1 Description of Study areas

Fieldwork took place in two different study areas within the Boreal Plains Ecozone (Environment Canada 2005), Figure 5.1a). The first study area was located in northeastern Alberta (NEAB; 56°52’N, 115°27’W; Figure 5.1b) and the second, referred to as the Duck

Mountain (DMMB; 51°39'N, 100°57'W; Figure 5.1c) was largely in west central Manitoba but also extended across the Saskatchewan-Manitoba border. Both study areas were along the southern fringe of the Boreal Plain and encompassed the Boreal Transition Ecoregion that marks the transition between the Prairie and the Boreal Plains Ecozones (Ecological Stratification Working Group 1996). In most years, climate is relatively dry with evapotranspiration rates slightly exceeding precipitation (Petronne *et al.*, 2007). The landscape ranges from extensively cleared to more intact mosaics of mixedwood and deciduous forests (Hobson *et al.*, 2002). In uncultivated areas, grasslands have been reduced with the suppression of the natural fires which once controlled the margins of the forest. Agricultural activities in both study areas date back to the late 1800s and now include practices such as converting forest to pasture to graze livestock and growing annual crops like legumes, canola, barley and alfalfa. Other human land-use activities in these areas include sparse urban and municipal developments, exploration and extraction of oil and natural gas (AB only), forest harvesting, hunting and other recreational activities.

Five major wetland classes (marsh, swamp, fen, bog and open water < 2 m) account for between 20-60% of the total study area. Transitions between open water and upland habitats often comprise one or more of these wetland classes (Locky *et al.*, 2005; Whitehouse and Bayley 2005). Upland forests, depending on soil characteristics, disturbance history and topography, occur as pure or mixed stands of any combination of trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and jack pine (*Pinus banksiana*). Dominant tree species in forested wetlands (lowland) sites include balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*).

5.2.2 Landscape selection, quantifying total human disturbance and conversion to agriculture

Using Geographic Information Systems and roving window analysis with a fixed size of 25 km², we generated a set of all possible 5X5 km ‘landscapes’ in each study area. This landscape size was selected because it reflected the mean catchment size for DMMB, could easily contain 5 wetlands at least 500 m apart and encompassed a broad range of landscape features. We assessed each landscape for forest composition, wetland composition, and amount of agricultural conversion. Individual landscapes were selected for further study on the basis of the following characteristics: a) located within 2 km of a road to facilitate ground access; b) presence of at least 5 discrete open-water ponds (wetlands) that were 2-16 ha in size and 500 m apart; c) forest-stand composition prior to human disturbance of > 50 % aspen and aspen-mixed wood forests (*i.e.*, not dominated by peatlands); and d) distance of > 500 m from any another study landscape. Landscapes known to contain recent fires (< 30 years) were excluded. Since we used remotely sensed habitat maps to quantify agricultural disturbance, we grouped all types of crops and pastures into one agricultural disturbance class. Landscapes were then randomly selected from the potential pool of suitable landscapes, but stratified according to a gradient of increasing conversion to agriculture.

5.2.3 Wetland selection

In each landscape, we randomly selected five ponds (shallow-open water wetlands National Wetlands Working Group 1997) that were two-25 ha and ≥ 500 m apart. We visited each site prior to the bird survey period to determine appropriate access routes and to determine an approach to the wetland at a central location that was best suited for obtaining an inventory of as much of the bird community as possible. When necessary, pre-selected wetlands that were inaccessible by land were replaced with alternate accessible wetlands. In some pre-selected

landscapes (*e.g.*, those with high amounts of agricultural conversion) we were unable to find five wetlands meeting our size requirements or a suitable alternate landscape. In these instances, we selected suitable wetlands within 3 km of a landscape boundary to be used only in wetland scale analyses (below). Landowner permission was obtained prior to all surveys on private land.

5.2.4 Wetland-scale disturbance calculations

Using the same list of disturbance variables described in section 2.2, we calculated area of habitat and disturbance variables within 500 m of the perimeter of the wetland. We then converted area calculations to proportional values to account for difference in total area due to wetland shape.

5.2.5 Bird Surveys

During 2003 and 2004 in NEAB and 2005 in DMMB, we conducted surveys of bird communities between 1 June - 5 July. To maximize the number of sites surveyed along the agricultural gradient, we sampled many wetlands once rather than conducting repeated visits at fewer sites (Carlson and Schmiegelow 2002). Bird surveys, beginning no sooner than 30 minutes before sunrise and ending no later than 5 hours after sunrise, were conducted only on days with little or no wind and no rain (Schieck and Hobson 2000). Because the productivity and diversity of riparian areas can generally be attributed to biotic and nutrient exchanges between terrestrial and aquatic areas, we treated aquatic, wetland and upland bird assemblages as a single community (Croonquist and Brooks 1991).

At each wetland, we used a range of survey techniques to maximize bird detections in upland, riparian and aquatic habitats. First, we conducted a 20-minute waterfowl point count, followed by a 10-minute, fixed-radius point count (Dettmers *et al.*, 1999) for land birds and

concluded the survey with a 5-minute playback protocol (Conway 2002) for 5 non-passerine wetland bird species common in the area Sora (*Porzana carolina*), Virginia rail (*Rallus limicola*), pied-billed grebe (*Podilymbus podiceps*), American bittern (*Botaurus lentiginosus*), yellow rail (*Coturnicops noveboracensis*). Birds in flight were not counted unless they landed within the survey area during the appropriate survey period. All observers received annual audio census training and we compared counts across individual observers to improve consistency. For safety, two observers worked simultaneously in a given landscape and each surveyed between two and four wetlands per day. Timing of surveys (early or late morning and day within the breeding season) for each landscape was randomized across the disturbance gradient to avoid temporal biases (Bibby *et al.*, 2000).

5.2.6 Statistical Analysis

We used TITAN (Threshold Indicator Taxa Analysis; (Baker and King 2010) to identify abrupt changes in both frequency of occurrence and relative abundance of birds along a gradient of agricultural conversion. TITAN, described in detail in Baker and King (2010) and King *et al.*, (2010), permits an examination of the relative synchrony and uncertainty of any species-level changes as a nonparametric estimator of a community threshold. In addition, this technique distinguishes between positive and negative species-level responses to an environmental gradient which in our study was conversion to agriculture.

In TITAN, potential change-points (a point along a distribution of population index values where the characteristics before and after the point were different) for a single species are identified using indicator value scores. Midpoints between observed values along an environmental gradient are identified as candidate change points. TITAN uses each change point to divide observations into two candidate groups, those showing a positive response with respect

to the environmental gradient and those showing a negative response. In this analysis, larger differences between values on each side of a candidate change point receive greater indicator value scores. TITAN retains the largest of these two indicator value scores for comparison with values at other candidate change points.

Indicator values are calculated using Indicator Species Analysis (ISA). ISA uses a permutation procedure (in this case, 250 permutations) to estimate the probability of obtaining an equal or greater indicator value score from random data (Dufrene and Legendre 1997). Taxa with a total of < 5 and occurrences of < 3 in either study area were excluded (Baker and King 2010; De'ath and Fabricius 2000) and Bray-Curtis dissimilarity was used as the metric for all distance-based calculations (McCune and Grace 2002).

TITAN initiates a bootstrap procedure (500 iterations) which estimates confidence intervals around change points (percentiles) as well as consistency of the response direction (positive or negative) of each species (purity) (Baker and King, 2010). A high purity level (approaching 1) means species are consistently assigned the same response direction expressed as the proportion of change point directions among bootstrap replicates that agree with the observed response. Confidence limits for species with low occurrence frequencies were interpreted with caution because these may be unreliable (Manly 1997) regardless of the method used (Baker and King, 2010). We also used TITAN to estimate community thresholds as zones along an environmental gradient that showed synchronous changes by either positively or negatively responding taxa. We calculated and plotted these thresholds as the sum of the standardized indicator values (sum z^+ or z^-). We then repeated TITAN at each scale for each study area. All analyses were performed with a modified version of TITAN package in R.10.2.1 (Baker and King, 2010).

5.3. Results

In the NEAB study area (2003-2004), we surveyed 25 landscapes and 140 wetlands resulting in approximately 5231 bird records. We obtained data for 114 species, however only 75 species were sufficiently abundant to be retained in detailed analyses. In 2005, we repeated our survey in the DMMB study area recording 4720 detections representing 103 species at 36 landscapes and 179 wetlands. Here, 82 species were sufficiently abundant to be retained for analysis.

5.3.1 Landscape-level community thresholds and species change points

We found substantial differences between regions for landscape-level community thresholds in response to a total disturbance gradient dominated by conversion to agriculture (Table 5.1; Figures 5.2 and 5.3). In NEAB, TITAN identified an overall community threshold of 51 % for negative taxa and 70 % for positive taxa while in DMMB these values were 14 % and 40 %, respectively (Table 5.1). However, confidence intervals around all community-level thresholds were quite large (\pm 39-53 %) and once plotted, sum (z) values indicated more than one point where synchronous changes (measured as peaks in sum (z) values) occurred (Figure 2, Figure 5.3).

At the landscape-level in NEAB, synchronous changes in sum (z-) occurred at 30 % and at 50 % agricultural conversion. Peaks in sum (z+) were apparent at each of 25 %, 50 % and 70 % with an overall community threshold calculated at 70 %. At the landscape scale, TITAN identified seven significant declining indicators (negative response to gradient). Buffleheads (*Bucephala albeola*) showed a maximum change point at 20 % with confidence intervals spanning most of the gradient, whereas the remaining six species reached their maximum change

points between 45-54 % agricultural conversion (Figure 5.2). Nine increasing species (Figure 5.2) showed positive changes with five of these occurring in the 25-29 % range, three between 51-55 % and the last species at 60 %. Bootstrapped percentile values for all significant indicator species are listed in Appendix 4: Table A4.1 and Table A4.2.

In DMMB, landscape-level community responses for declining taxa peaked at 20% with relatively high sum (z-) values up to 40 % (Figure 5.3). This was likely due to species showing maximal change point values throughout the agricultural conversion gradient. Three species showed maximum change points at 8-15 % agriculture, another at 20 %, two more at 30 %, three at 40 % and the final two at 50-60 % (Figure 5.3). In this study area, 17 species also responded positively to total disturbance (Figure 5.3). Twelve of these had change points in the highest range where agricultural conversion was between 40 and 60 %, but four species had change points prior to 20 % total disturbance (Figure 5.3). With the entire community considered, TITAN identified a peak change point at 40% total disturbance for positively responding species (Table 5.1; Appendix 4: Tables A4.1 and A4.2).

5.3.2 Wetland- level community thresholds and species change points

In general, many of the species found to be significant indicators at the landscape scale were also significant at the wetland scale, but there were also several new negatively responding species (Figure 5.2 and 5.3; Appendix 5.1). In the NEAB study area with total conversion to agriculture measured within 500 m of wetlands, TITAN identified 13 species that responded negatively between 10-64 % total conversion to agriculture and 19 that responded positively between 8-70 % (Figure 5.2). Sum (z-) values increased at low levels of agricultural conversion, but occurred regularly along the gradient resulting in a cumulative threshold frequency reached at 40 %. Sum (z+) values peaked quickly before 20 % and showed further peaks at 30 % and 40

% and 50 % (cumulative threshold frequency peaks at 60 %) suggesting continued gradual species introductions throughout the gradient.

In the DMMB study area at 500 m, peaks in both sum (z+) and sum (z-) values occurred early along the total disturbance gradient, at just 10 %. Subsequent species declines and species introductions occurred gradually throughout the entire disturbance gradient. Cumulative threshold frequencies peaked at 40 % for negatively responding species and not until 80 % for positively responding species. We also found that five species, red-breasted nuthatch (*Sitta Canadensis*), ruby-crowned kinglet (*Regulus calendula*), common loon (*Gavia immer*), myrtle warbler (*Dendroica coronata*), and swainson's thrush (*Catharus ustulatus*) showed negative thresholds prior to wetlands being impacted by 10 % conversion to agriculture within 500 m. Negative thresholds for five other species mourning warbler (*Oporornis philadelphia*), ovenbird (*Seiurus aurocapillus*), chipping sparrow (*Spizella passerina*) and swamp sparrow (*Melospiza georgiana*) were calculated between 10-40 %. At this scale, 18 species showed positive thresholds as conversion to agriculture increased and these occurred gradually along the entire conversion gradient, a pattern that was therefore also reflected in the community-level results (Figure 5.3).

5.4. Discussion

Many areas of the world have experienced declines in avian biodiversity attributed to loss of habitat resulting from deforestation and various other land-use practices (Fischer *et al.*, 2007; Kirk *et al.*, 2011). Under less intense agricultural systems or in areas where the landscape matrix contains both forested and agricultural areas increases in species richness also occur. In Canada's Boreal Plain Ecozone rapid rates of deforestation have also occurred as a consequence of agricultural conversion particularly along its southern fringe, the Boreal Transition Zone

(Hobson *et al.*, 2002). We present the first examination of threshold responses of wetland- and riparian-associated birds to habitat loss in the landscape matrix. The TITAN methodology allowed us to differentiate species with positive responses to agricultural conversion from those with negative responses. TITAN then allows the user to examine combined species-level responses, either positive or negative, and assess whether community-level thresholds are occurring along a gradient of agricultural conversion in the landscape matrix.

5.4.1 Community-level effects

Our results showed that riparian- and wetland-associated bird communities did not typically exhibit a single threshold to agricultural conversion but rather that changes tended to occur throughout the disturbance gradient. So whereas TITAN identified community-level thresholds, confidence intervals around these tended to be large (Table 1). However, several species exhibited synchronous change points along the agricultural conversion gradient particularly at the landscape level in NEAB (Figure 5.2a). Baker and King (2010) noted that when anthropogenic disturbances result in positive responses within species assemblages, these may not represent well-organized communities but rather, either of two types of potential community dynamics. First, they may be composed of native taxa that either directly or indirectly (benefit from resulting habitat changes (*e.g.*, American coot, *Fulica americana*) related to resource subsidies or realized niche expansion or reduced competition or predation, respectively. Second these responses may also be indicative of invasions of species not historically present (*e.g.*, brown-headed cowbird- *Molothrus ater*) but now able to cross ecosystem boundaries because of habitat changes brought about by the anthropogenic disturbances (Baker and King 2010).

5.4.2 Species-level effects

In our study, several species met TITAN requirements for significance, reliability and purity and thus exhibited change points with increasing amounts of agricultural conversion at both a landscape- and local (500 m) scales. For example, common loon (*Gravia immer*) and Swainson's thrush (*Catharus ustulatus*) showed change points at both scales in both regions. Many species also showed uncertainty around identified change points. For example, in DMMB, the blue jay (*Cyanocitta cristata*) showed a weak change point at nearly the end of the disturbance gradient with confidence intervals spanning nearly its entire length and reliability levels at the lowest required by TITAN. This type of response may be indicative of a unimodal response to a disturbance gradient consistent with those seen under intermediate disturbance levels and not well measured by TITAN (Baker and King 2010). Variable species responses like this are not unexpected given that most species generally have a range of different habitat requirements and tolerances to habitat loss, introduction of competitive species, and isolation (Huggett 2005).

Similarly, one could argue that response to changes in the surrounding landscape should be variable because different bird species use the landscape at varying scales and are sensitive to different kinds of changes. For example, birds typically occurring in late seral stages are more sensitive to agricultural conversion than early successional species and edge species (Hobson and Bayne, 2000). Consistent with other studies, we found that most landbirds typical of contiguous forests such Swainson's thrush, red-breasted nuthatch (*Sitta canadensis*) and Blackburnian warbler (*Dendroica fusca*) responded negatively to increasing amounts of agriculture in the surrounding landscape (Hobson and Bayne, 2000). For these species, agricultural conversion resulted in habitat loss due to permanent conversion of forest to another land use.

In contrast, most waterbird species responded positively to increasing levels of agricultural conversion. Studies have shown breeding waterfowl densities are greatest in shallow, productive nutrient rich lakes and that densities increase even along a more limited productivity gradient (*i.e.*, eutrophic to hypereutrophic; Epner *et al.*, 2010). Thus, waterbirds may have been responding to increased food availability resulting from increased total dissolved phosphorous and subsequent productivity (Epner *et al.*, 2010), as the amount of area converted to agriculture increases (Hobson *et al.*, unpublished data). Further study is needed to establish whether these increases in abundance in fact represent an increase in habitat quality or whether they reflect a “crowding” response (increase in density) resulting from the loss of suitable wetlands elsewhere on the landscape. Also, predators such as corvids, coyotes and skunks are also typically more abundant in agricultural areas and could potentially result in less nest success and increased mortality (Bayne and Hobson 1997; Hobson and Bayne 2000; Sargeant and Raveling 1992). Exceptions in our study were ring-necked duck (*Aythya collaris*) and common loon (*Gavia immer*), which declined in response to agricultural conversion. These species could also be responding to changes in prey base since highly eutrophic wetlands are less likely to contain fish, other wetland characteristics (amount of open water) associated with eutrophication, or they may be responding to changes in competitive interactions among other duck species. In essence, clearing and fragmenting boreal forest results in a superficial transition to more of a Prairie Pothole landscape that results in a range expansion of more open-country waterfowl into previously forested regions.

Riparian species showed variable responses to agricultural conversion. For example, swamp sparrow (*Melospiza georgiana*) declined across scales in both study areas, but only showed a significant change-point in NEAB at 500 m scale. White-throated sparrow

(*Zonotrichia albicollis*), an early successional species typical of boreal riparian zones, showed consistent declines in both regions although at the landscape level in NEAB, there was no evidence of a change point. Bonaparte's gull (*Larus philadelphia*) a colonial nesting species typical of boreal wetlands also decreased early in the agricultural gradient. Despite evidence from other studies of population declines attributed to wetland loss resulting from agricultural development (Guzy and Ritchison 1999), common yellowthroat (*Geothlypis trichas*) seemed neutral to agricultural changes in the landscape matrix. Song sparrow (*Melospiza melodia*), sora (*Pozana carolina*) and red-winged blackbirds (*Agelaius phoeniceus*) all showed increases in response to agriculture. Red-winged blackbird are among species thought to have benefited from agriculture (Kirk et al 2011) and in both study areas did in fact respond positively to an increase in agriculture at both landscape and wetland levels.

5.4.3 Landscape-level vs. wetland-level effects

While most studies select research sites with the goal of assessing the landscape context, we selected specific landscape contexts to assess effects of an increasing amount of agricultural conversion on bird communities. The advantage of this design is variation between sites associated with habitat differences among wetlands is dampened (Radford *et al.*, 2005). For example, changes appeared more gradual at the landscape scale than at the wetland scale (as exemplified by typically wider confidence intervals and fewer significant indicators (Figure 5.2) illustrating direct impacts that may not be apparent at the landscape scale. Ecological variability can also create uncertainty around change-point estimates and could obscure other threshold relationships in our data (*e.g.*, Lindenmayer *et al.*, 2005). We did not set out to test the effects of varying habitat configuration (see Lindenmayer *et al.*, 2008) because we were explicitly testing changes in the landscape matrix around small open-water wetlands.

At the scale of an individual patch, transitions may appear abrupt due to the sudden loss of a key species (Chapin, III *et al.*, 2004) while at a landscape scale changes may appear more gradual due to changes being distributed over space and time (Radford *et al.*, 2005). For many species that exhibited negative responses to gradients in total disturbance in our study, thresholds were identified at relatively low levels of agricultural conversion (*e.g.*, red-breasted nuthatch, common loon, mourning warbler), still others did not show negative effects until more agricultural conversion had occurred. Variability in our landscapes related to “permeability” of the landscape to different species (Machtans *et al.*, 1996) could account for the variability in thresholds across scales and regions. For some bird species, the more traditional view of a landscape as a matrix of available and non-available habitat suggested by island biogeography (MacArthur and Wilson 1967) is not supported by the results of studies that have investigated their interaction with the landscape (Fischer *et al.*, 2006; Fahrig *et al.*, 2011) or of those with evidence for “habitat compensation” where species shift to less preferred habitat in response to habitat loss (Norton *et al.*, 2000).

5.4.4 Regional responses to agricultural conversion

Patterns in the occurrence of thresholds were different between our two study regions particularly at the landscape level. For species that were common to both regions, direction of response was generally consistent, but change points differed among regions. However, there were some exceptions to these patterns. For example, buffleheads (*Bucephala albeola*) showed opposite responses in each region, increasing in DMMB and declining in NEAB. Interestingly, these patterns are consistent with those we found for their primary cavity excavators the northern flicker (*Colaptes auratus*) and the yellow-bellied sapsucker (*Sphyrapicus varius*- NEAB only). On the other hand, mourning warbler (*Oporornis philadelphia*) exhibited a decrease in DMMB

but not in NEAB. Finally, in NEAB thresholds generally occurred at higher levels of agricultural conversion than in DMMB.

There are a number of possible explanations for these differences between the two study areas. The DMMB is an insular forest completely surrounded by agriculture and earlier change points could reflect greater sensitivity to habitat loss due to greater distances to contiguous forest (Hobson and Bayne 2000) than in NEAB. Habitat loss can also lead to interactions between factors such as fragmentation and vegetation cover resulting in a range of thresholds (Huggett 2005). Smaller population sizes are also predicted to show lower tolerances habitat loss (Swift and Hannon 2010) and regional populations in the DMMB are potentially smaller than areas more connected to relatively large expanses of forest (Brown 1984; Swift and Hannon 2010).

Long-term persistence depends on maintaining breeding populations and our study addresses frequency of occurrence and relative abundances of species. Whether change points are related to differing population trends in these two areas is potentially important and warrants more study. We did not explicitly test whether certain types of agriculture would result in earlier thresholds than others, however in DMMB most farmland was planted to annual crops whereas in NEAB a mixture of areas cleared for grazing (tame pasture) and annual crops was present and these cover types may represent different levels of permeability for some species (Fahrig *et al.*, 2011, Kirk *et al.*, 2011).

5.5 Conclusions and management implications

Our study is the first to identify and compare thresholds in community composition of birds at wetlands along a gradient of agricultural conversion in two geographic regions of Canada's boreal transition zone (Ecological Stratification Working Group 1996). We offer evidence for

lower thresholds for several species than those typically predicted by theoretical population models of *extinction* thresholds. Theory developed using simulation models, generally predicts *extinction* thresholds at 10-30 % of habitat remaining (70-90 % conversion) on the landscape (Andren 1994; Fahrig 2001). This difference can potentially be explained by our analytical approach which examines *initiation of impact* thresholds rather than *extinction* thresholds. Using this approach we found most species that responded negatively did so prior to 50 % agricultural conversion.

Some conservation groups have suggested a conservation target of 50 % intactness in order to conserve the boreal forest in perpetuity (*e.g.*, Boreal Conservation Framework, 2013). Taking into consideration that this suggested target is intended to be applied at much broader scales than the scale of our study and in combination with sustainable development objectives on the rest of the boreal landbase our results suggest this target may be sufficient to prevent overall community level changes in NEAB but not in DMMB. These differences underscore the need to consider regional context (*e.g.*, area effects, isolation effects, configuration *etc.*) in setting goals for conservation planning (Fischer *et al.*, 2006).

Initiation of impact thresholds highlight the point at which a stressor begins to negatively affect species (*i.e.*, the minimum detectable response) and could be used to highlight the need for implementing management plans before population-level changes occur (Hilderbrand *et al.*, 2010). Therefore, these thresholds can be used to guide development in cases where growth is inevitable (Hilderbrand *et al.*, 2010) and the use of methodologies such as TITAN highlights species-level trade-offs of landscape-level management decisions.

Concrete applications of thresholds in habitat management can be problematic if the threshold is used by decision makers as a target (Huggett 2005). Given large confidence

intervals associated with the community level change points we found, we suggest these values be interpreted with caution with careful consideration to both species and community level changes that may be occurring. Our results also lend weight to concerns shared by others that thresholds are species, scale and region dependent (Hugget *et al.*, 2005; Swift and Hannon 2010) and thus limited in potential for broad management application throughout the Boreal Plain Ecozone.

Our understanding of thresholds and their complicated underlying factors is still in its infancy in this region and elsewhere, particularly when the variability among regions and a backdrop of uncertainties surrounding global change are considered. Knowing when thresholds are likely to occur is important, but their values often represents the bare minimum of the habitat requirements of a species and generally cannot completely account for interactions of multiple factors (*e.g.*, breeding success, mortality during migration, fluctuations in prey availability). Therefore, the use of thresholds based on frequency and abundance as targets in management and conservation planning is risky without additional detailed complementary work that outlines these interactions.

The next 50 years are predicted to be the final expansion phase of modern agriculture (Tilman *et al.*, 2001) and particularly in the southern boreal plain, the landscape is at risk of rapid conversion to agriculture (Hobson *et al.*, 2002). Conversion to agriculture not only leads to permanent conversion of forested habitat but also to wetland loss (Slattery *et al.*, 2010). Our results support the results of other studies in upland boreal forest (Bayne and Hobson 1997; Hobson *et al.*, 2002) that suggest that to preserve boreal bird communities, policy changes that ensure forest cover is maintained and wetland loss eliminated in the southern boreal mixedwood forest should be implemented.

Table 5.1 Community change-point (cp) results for TITAN at landscape, 500 m and 100 m scales along an agricultural gradient in NEAB and DMMB. Values for 5 %, 10 %, 50 %, 90 % and 95 % quantiles are included. For comparison, results of typical change- point analyses that examine ecological distances without considering direction of the species responses are also included.

	Cp	0.05	0.10	0.50	0.90	0.95
NEAB-Landscape						
sumz-	0.51	0.16	0.19	0.29	0.51	0.56
sumz+	0.70	0.25	0.26	0.53	0.70	0.72
ncpa.bc	0.51	0.23	0.26	0.46	0.56	0.60
ncpa.euc	0.51	0.23	0.25	0.36	0.60	0.66
NEAB-500 m						
sumz-	0.34	0.18	0.21	0.34	0.42	0.44
sumz+	0.49	0.33	0.35	0.51	0.57	0.57
ncpa.bc	0.35	0.17	0.21	0.33	0.42	0.46
ncpa.euc	0.35	0.15	0.17	0.33	0.52	0.55

	Cp	0.05	0.10	0.50	0.90	0.95
DMMB-LANDSCAPE						
sumz-	0.14	0.01	0.01	0.08	0.32	0.40
sumz+	0.40	0.14	0.30	0.56	0.67	0.68
ncpa.bc	0.14	0.03	0.03	0.21	0.56	0.56
ncpa.euc	0.40	0.03	0.07	0.40	0.60	0.60
DMMB-500 m						
sumz-	0.17	0.01	0.02	0.17	0.33	0.40
sumz+	0.43	0.38	0.42	0.50	0.77	0.79
ncpa.bc	0.24	0.02	0.06	0.32	0.44	0.50
ncpa.euc	0.42	0.17	0.28	0.35	0.50	0.56

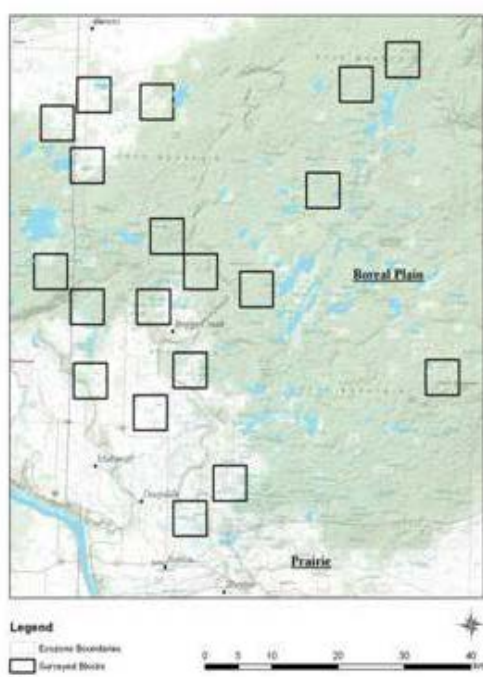
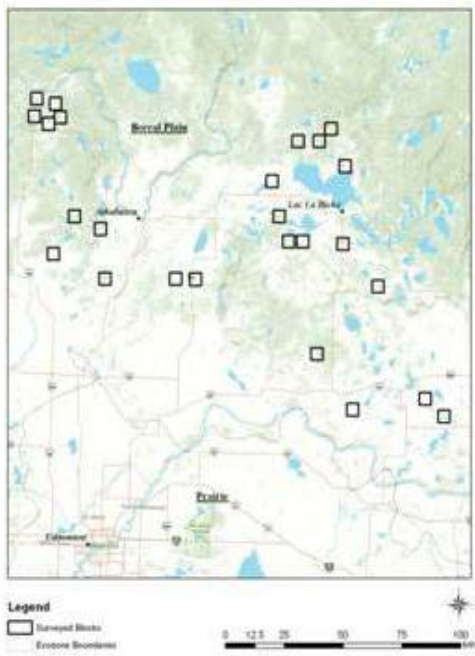
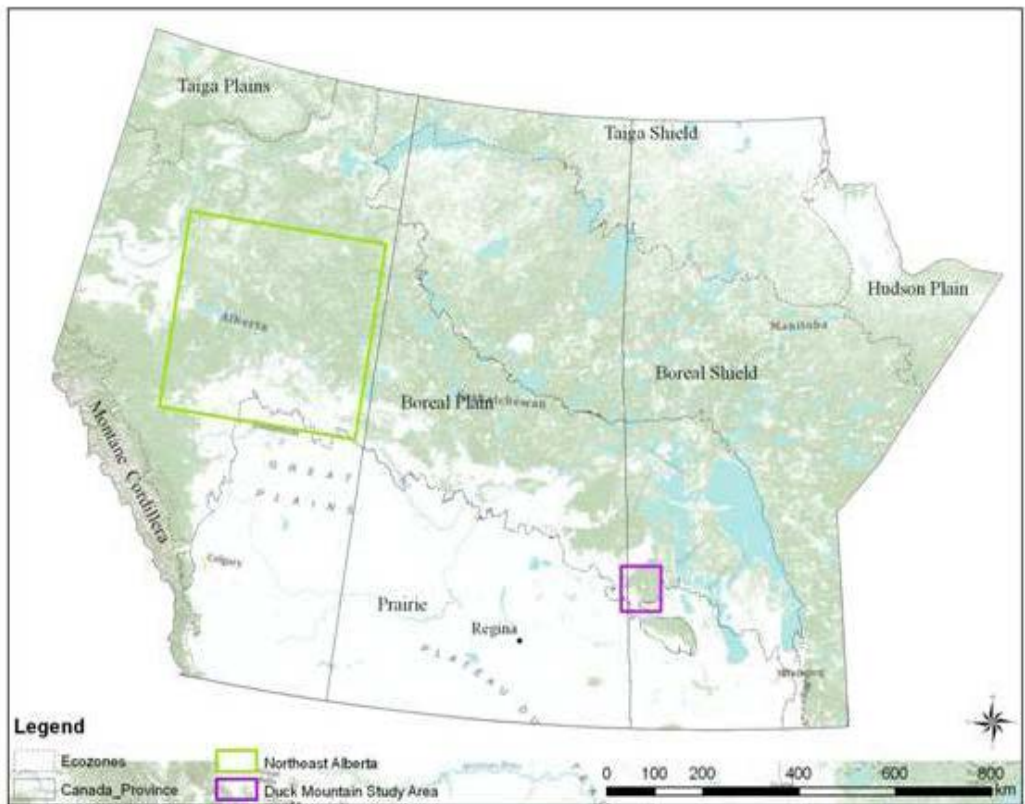


Figure 5.1 a) Overview map of study areas relative to one another, b) North Eastern Alberta (NEAB) study area and c) Duck Mountain study area in west central Manitoba (DMMB).

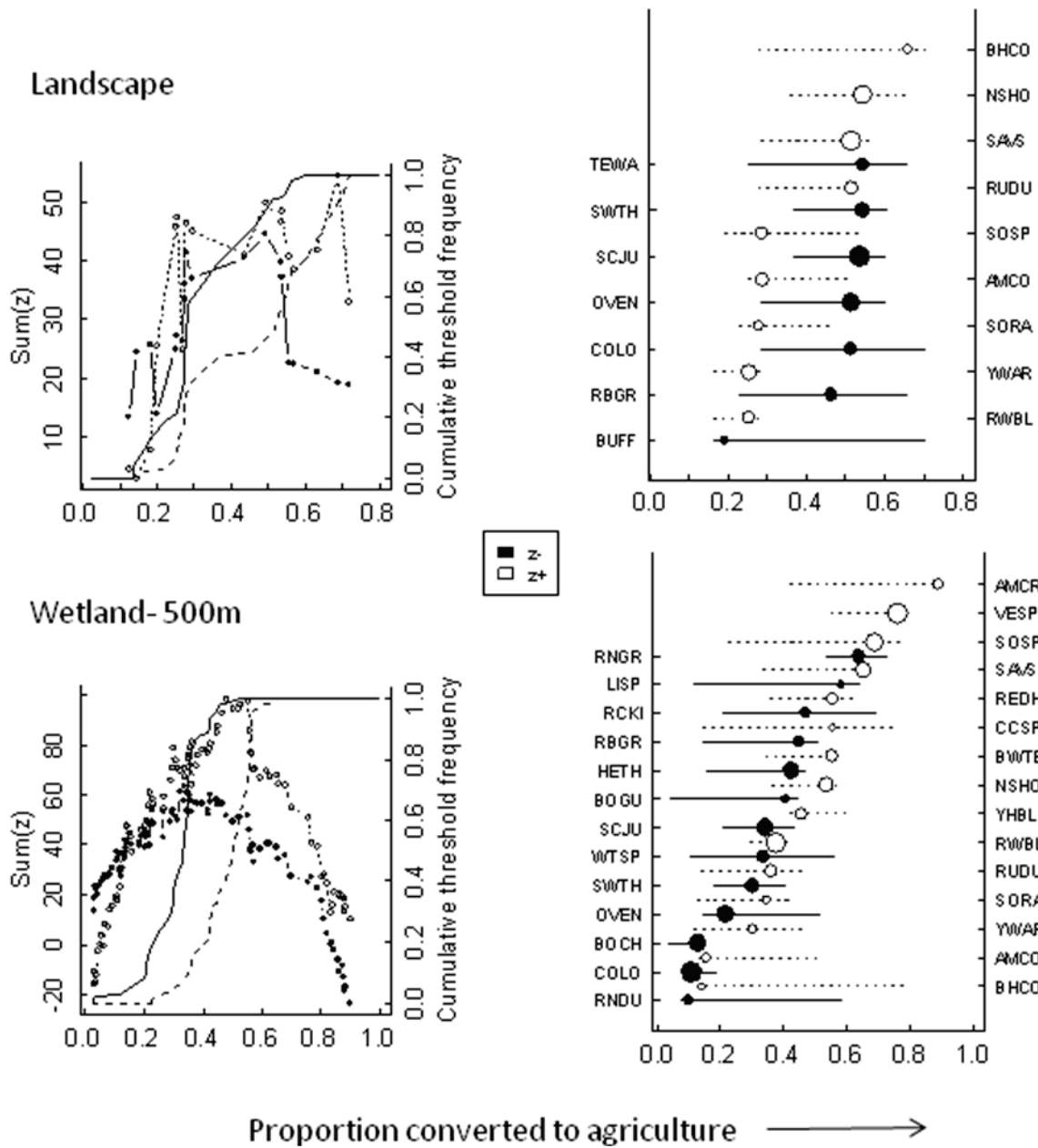


Figure 5.2 Thresholds Indicator Taxa Analysis(TITAN; Baker and King 2010) of bird community responses to proportion total human disturbance (conversion of forest to agriculture, roads) for NEAB study site the landscape scale (5 wetlands in 5 by 5 km area), and within 500m of a wetland respectively. Figures in the first column represent community-level thresholds. Peaks in sum (z) values represent points at which synchronous species increases (z+) or declines

(z^-) are occurring. Solid and dashed lines represent cumulative frequency distribution of change points (x_{cp} thresholds among 100 bootstrap replicates). Figures in the second column represent species-level thresholds to total disturbance gradient. Species are plotted in increasing order of change point and solid symbols correspond to negative indicator species (z^-) while open symbols correspond to positive indicator species (z^+). Symbols are sized in proportion to the magnitude of the response (higher the z -value the bigger the symbol). Lines through the symbols represent the extent of the 5th and 95th percentiles. See Appendix 4: Table A4.1 for species names, and numerical values associated with this figure. Scatter plots of the abundance of each species against a gradient of agricultural conversion are found in Appendix 4 Figure A4.1 (negative) and Figure A4.2 (positive).

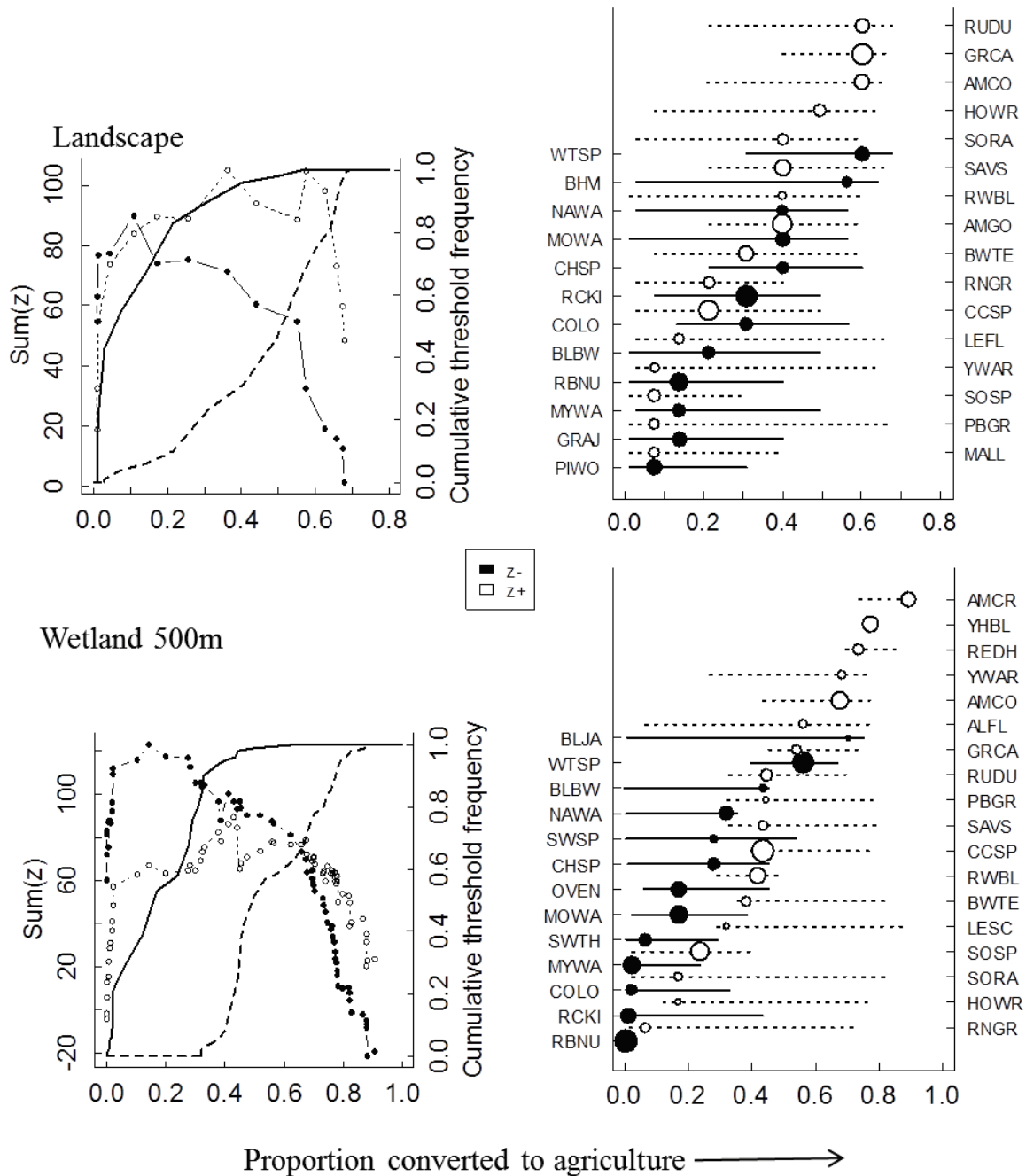


Figure 5.3 Thresholds Indicator Taxa Analysis (TITAN; Baker and King 2010) of bird community response to proportion total disturbance (conversion of forest to agriculture, roads) for DMMB study site at 2 scales: Block scale (5 wetlands in 5 by 5 km area), and within 500 (m) of a wetland respectively. See Figure 5.2 for additional interpretive details.

5.6 References

- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355-366.
- Baker, M. E., and R. S. King. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* 1:25-37.
- Bauer, D. M., P. W. Paton, and S. K. Swallow. 2010. Are wetland regulations cost effective for species protection? A case study of amphibian metapopulations. *Ecological Applications* 20:798-815.
- Bayne, E. M., and K. A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418-1429.
- Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe. 2000. *Bird Census Techniques*. Academic Press, London.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255-279.
- Carlson, M., and F. Schmiegelow. 2002. Cost-effective sampling design applied to large-scale monitoring of boreal birds. *Conservation Ecology* 6:1-11.
- Chapin, F. S., III, T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio* 33:361-365.

- Conway, C. J. 2002. Standardized North American marsh bird monitoring protocols.1-23.
- Croonquist, M. J., and R. P. Brooks. 1991. Use of avian and mammalian guilds as indicators of cumulative impacts in riparian-wetland areas. *Environmental Management* 15:701-714.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178-392.
- Dettmers, R., D. A. Buehler, J. G. Bartlett, and N. A. Klaus. 1999. Influence of point count length ad repeated visits on habitat model performance. *Journal of Wildlife Management* 63:815-823.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: a need for flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Ecological Stratification Working Group.1996. A national ecological framework for Canada. Environment Canada. [online]. 2005. Narrative descriptions of terrestrial ecozones and ecoregions of Canada. <http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/default.cfm>.
- Epner, C. A., S. E. Bayley, J. E. Thompson, and W. M. Tonn. 2010. Influence of fish assemblage and shallow lake productivity on waterfowl communities in the Boreal Transition Zone of western Canada. *Freshwater Biology* 55:2265-2280.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100:65-74.

- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J. L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14:101-112.
- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. A. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4:80-86.
- Foote, L., and N. Krogman. 2006. Wetlands in Canada's western boreal forest: agents of change. *The Forestry Chronicle* 82:825-833.
- Gaston, K. J., T. M. Blackburn, and K. K. Goldewijk. 2003. Habitat Conversion and Global Avian Biodiversity Loss. *Proceedings: Biological Sciences* 270:1293-1300.
- Groffman, P. M., J. S. Baron, T. Blett, A. J. Gold, I. Goodman, L. H. Gunderson, B. M. Levinson, M. A. Palmer, H. W. Paerl, G. D. Peterson, N. L. Poff, D. W. Rejeski, J. F. Reynolds, M. G. Turner, K. C. Weathers, and J. Wiens. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1-13.
- Guzy, M. J., and G. Ritchison. 1999. Common Yellowthroat (*Geothlypis trichas*), In A. Poole, and F. Gill [eds.], *The Birds of North America*, Inc. Philadelphia, PA.

- Hilderbrand, R. H., R. M. Utz, S. A. Stranko, and R. L. Raesly. 2010. Applying thresholds to forecast potential biodiversity loss from human development. *Journal of the North American Benthological Society* 29:1009-1016.
- Hobson, K. A., and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixedwoods of western Canada. *Wilson Bulletin* 112:373-387.
- Hobson, K. A., E. M. Bayne, and S. L. Van Wilgenburg. 2002. Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. *Conservation Biology* 16:1530-1541.
- Houlahan, J. E., and C. S. Findlay. 2004. Estimating the 'critical' distance at which adjacent land-use degrades wetland water and sediment quality. *Landscape Ecology* 19:677-690.
- Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124:301-310.
- Kennedy, C. M., E. H. C. Grant, M. C. Neel, W. F. Fagan, and P. P. Marra. 2011. Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores. *Ecological Applications* 21:1837-1850.
- King, R. S., M. E. Baker, P. F. Kazyak, and D. E. Weller. 2010. How novel is too novel? Stream community thresholds at exceptionally low levels of catchment urbanization. *Ecological Applications* 21:1659-1678.
- Kirk, D. A., K. E. Lindsay, and R. W. Brook. 2011. Risk of Agricultural Practices and Habitat Change to Farmland Birds. *Avian Conservation and Ecology* 6:

- Lindenmayer, D. B., J. Fischer, and R. B. Cunningham. 2005. Native vegetation cover thresholds associated with species responses. *Biological Conservation* 124:311-316.
- Locky, D. A., S. E. Bayley, and D. H. Vitt. 2005. The vegetational ecology of black spruce swamps, fens, and bogs in southern boreal Manitoba, Canada. *Wetlands* 25:564-582.
- Lougheed, V. L., M. D. McIntosh, C. A. Parker, and R. J. Stevenson. 2008. Wetland degradation leads to homogenization of the biota at local and landscape scales. *Freshwater Biology* 53:2402-2413.
- Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* 10:1366-1379.
- Manly, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. 2nd Edition ed. Chapman and Hall, London.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- Mills, P. F. 1994. The agricultural potential of northwestern Canada and Alaska and the impact of climatic change. *Arctic* 47:115-123.
- Norton, M. R., S. J. Hannon, and F. K. A. Schmiegelow. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. *Ecography* 23:209-223.

- Petrone, R. M., U. Silins, and K. J. Devito. 2007. Potential impacts of catchment microclimatic variability on pond evaporation in the western boreal plain, Alberta, Canada. *Hydrological Processes* 21:1391-1401.
- Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124:317-337.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9:135-151.
- Sargeant, A. B., and D. G. Raveling. 1992. Mortality during the breeding season, p. 396-422. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, USA.
- Schieck, J., and K. A. Hobson. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. *Canadian Journal of Forest Research* 30:1281-1295.
- Swift, T. L., and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. *Biological Reviews* 85:35-53.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. P. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281-284.

Whitehouse, H. E., and S. E. Bayley. 2005. Vegetation patterns and biodiversity of peatland plant communities surrounding mid-boreal wetland ponds in Alberta, Canada. *Canadian Journal of Botany* 83:621-637.

CHAPTER 6: SYNTHESIS

The objectives of this dissertation were to advance understanding of boreal riparian and wetland-associated bird communities and to evaluate emerging community-level metrics for comparing different habitats and measuring effects of human disturbance. Below, I discuss my findings in the context of their implications for gaining insight into habitat associations of boreal birds and for the application of community ecology in conservation and management.

6.1 Habitat associations of boreal birds

The work presented here augments a growing body of work regarding habitat associations of boreal birds and the commonly held view that shoreline forests and riparian areas are “ecologically unique” (*sensu* Macdonald *et al.*, 2006). I characterized species composition and ecological characteristics of boreal riparian areas associated with open water wetlands and representing a broad spectrum of habitats available to boreal birds. I found that riparian zones associated with boreal plain wetlands (shallow lakes and ponds) act as a source of unique bird species and that community dynamics of these ecotones were different from that of upland bird communities (Chapter 2). My results showed that riparian bird communities were more variable in species composition than upland sites and supported assemblages of land birds that on average were less specialized in their habitat preferences than those in upland communities. These results were consistent with those of many other studies which have reported riparian areas act as a source of unique species, often have higher richness and beta diversity and therefore increase regional diversity (reviewed in Sabo *et al.*, 2005). Insight into habitat associations of boreal birds is emerging in conjunction with a growing body of work aimed at directly or indirectly describing these associations (*e.g.*, Cumming *et al.*, 2010). Within this research, several frameworks are used to describe habitat associations of birds including references to age class

(*e.g.*, early successional, old growth), forest type (*e.g.*, deciduous, coniferous), structure (*e.g.*, short shrub, tall shrub, open) or any combination of these (Imbeau *et al.*, 2003; Song 2002). Although conceptually simple, pre-classified guilds such as these are not always mutually exclusive (Imbeau *et al.*, 2003) and some classifications may also yield misleading results when predictions based on an *a priori* classification (*e.g.*, edge avoidance) are compared to observed responses (Villard *et al.*, 2007).

For predictive models, vegetation classes are often determined by and limited to the availability of spatial information (*e.g.*, forest inventories, classified satellite imagery) corresponding to the scale of the study (Betts *et al.*, 2006; Virkkala *et al.*, 2005). However, even within similar geographic areas, a universally accepted riparian classification scheme does not exist (Naiman *et al.*, 2005) and most maps are either incomplete or at a resolution that is not conducive to studying finer scale processes. Remotely sensed inventories of wetlands are becoming more common (*e.g.*, Ducks Unlimited Canada- Smith *et al.*, 2007) and I have shown (Chapter 2) that wetland classification, even when remotely sensed, is a tool that could assist in developing a classification scheme for habitat associations and riparian areas. In boreal systems, this avenue for improving our understanding of avian ecology has not yet been sufficiently tested (Rempel *et al.*, 1997). I also examined whether applying an accepted wetland classification scheme would refine current understanding of habitat associations for birds (Chapter 3). My analysis showed that bird communities were structured differently among a suite of wetland classes with some overlap in community composition among wetlands of roughly similar habitat structure (*i.e.*, shrubby wetlands). In addition, this work also showed that wetland communities were distinct from upland communities of similar structure created by forest harvesting.

While my results indicated strong correlation between vegetation classes and bird species abundance, there remain many questions beyond the scope of my study about whether increased abundance in riparian areas reflects adaptive choices resulting in increased fitness for riparian species. In addition, I did not evaluate other criteria that may be influencing birds such as availability of nest sites, abundance of food items (MacNally and Timewell 2005; Whitaker *et al.*, 2000), competition (Holmes *et al.*, 1986) or intraspecific attraction. As such there is no assurance that increased abundance of some species in riparian areas also reflects increased habitat quality (Van Horne 1983). Therefore, further study that confirms whether riparian areas are more attractive to birds for reasons that translate to high reproductive success is needed.

6.2 Community-level metrics complement species-level work

Despite, and perhaps in response to, recommendations from Wiens (1989) and others (Lawton 1999) suggesting that macro-parameters such as diversity contribute little to the advancement of community ecology, discussions of diversity, its measurement and role in the functioning of ecosystems remain some of the most active topics of community ecology research (Hillebrand and Matthiessen 2009; McGill *et al.*, 2006; Pasari *et al.*, 2013). Recently, there has been a renewed effort to reframe some fundamental concepts of community ecology to achieve consensus amongst disparate or unclear definitions but also better align with the current needs of natural resource management and biodiversity conservation (Srivastava and Vellend 2005). This effort has included such things as redefining of community interactions via traits rather than species (Schmera and Podani 2013; Violle *et al.*, 2007), a revival of the concept of species specialization (Devictor *et al.*, 2010; Hughes 2000; Pandit and Kolasa 2012), and a refinement of methods for measuring diversity components (Anderson *et al.*, 2011; Anderson *et al.*, 2006; Legendre *et al.*, 2005; Loreau 2000; Pélissier *et al.*, 2008). Although progress has been made

regarding many aspects of community-level metrics, ecological interpretations of identified patterns and agreement on specific methodologies and definitions continue to generate debate. These three lines of inquiry have resulted in not only greater discussion of the theoretical framework into which these concept fit (*e.g.*, metacommunity theory; Leibold *et al.*, 2004), but have also led to testing the sensitivity of these methods for conservation applications (*e.g.*, Srivastava and Vellend 2005).

My dissertation is centered on how common interpretations of some of the more commonly used metrics could apply to riparian areas. Acceptance of the idea that variability may have ecological meaning beyond “statistical noise” is growing along with the usefulness of community methods that assist with its interpretation. I found that riparian bird communities were more variable in species composition than upland sites and also supported assemblages of landbirds that were less specialized in their habitat preferences than those in upland communities (Chapter 2). If moderate levels of variability in space and/or time are considered to be natural components of biological communities, extreme fluctuations (either positive or negative) in community composition likely have important implications for biodiversity conservation and warrant further study (Anderson *et al.*, 2011). In the case of riparian areas investigated here, variability in species composition could simply reflect habitat heterogeneity, but it may also yield insight into temporal dynamics of species composition if measured over time. For instance, some authors have described dramatic increases in compositional variability with disturbance (*e.g.*, marine benthic communities, (Warwick and Clarke 2001), while others have predicted or described a homogenizing effect (Harris 1988). Low severity or infrequent disturbances may increase variability in community composition, but homogenization may result from high severity or frequent disturbances (Shea *et al.*, 2004). This homogenizing effect has also been

applied to the metrics of habitat specialization I used (Chapter 2) where community specialization was reduced at higher levels of anthropogenic disturbance (Devictor *et al.*, 2008; Devictor and Robert 2009).

I also examined indices of functional diversity and resilience based on ecological traits of the bird community. Functional diversity represents the spectrum of ecological roles performed by different species in an ecosystem (Fischer *et al.*, 2006). I found that riparian bird assemblages possessed a different suite of functional traits, higher functional diversity, and greater resilience than the other areas of the landscape I examined (Chapter 4). Resilience of boreal bird communities has been inferred by several authors based on understanding of how boreal bird communities have evolved and their apparent adaptability to natural and human disturbances (Mönkönnen and Welsh 1994; Villard *et al.*, 2007). However, traits-based approaches and indices of resilience presented here have not previously been assessed in boreal assemblages and when tested more broadly may further support or refute these ideas. I followed the examples of other authors (Flynn *et al.*, 2009; Petchey *et al.*, 2007; Schleuter *et al.*, 2010) using similar statistical methods and selecting a similar suite of avian functional traits (*i.e.*, emphasizing foraging). Functional diversity metrics are sensitive to the number and types of traits selected, suggesting that a thorough exploration of ecological traits of boreal birds is warranted to more fully assess relative importance in overall ecosystem functioning. For example, traits related to nesting ecology were beyond the scope of my analysis, but "ecosystem engineers" like cavity nesting bird species may exert a stronger influence on ecosystem function via their nesting habit than foraging habits (Blanc and Walters 2007).

Riparian areas had higher indices of resilience than upland areas suggesting that riparian bird communities may be more resilient to disturbance than upland communities. This finding is

at least partially supported by other related work which showed that the effects of forest harvesting on “riparian species” were less than the effects on forest dependent species (Kardynal *et al.*, 2009, 2011). However, variation of disturbance and hydrologic dynamics among different types of boreal riparian areas including wetlands and relative to uplands are poorly understood. An understanding of any differences in upland vs. riparian/wetland systems would refine any predictions made regarding community dynamics and allow these to be tested in a natural setting, for different taxa and a range of disturbance types.

As a first step to understanding changes in community composition along disturbance gradients, I examined the response of boreal wetland and riparian associated bird communities to increasing amounts of agricultural conversion in the surrounding landscape matrix (Chapter 5). I used Threshold Indicator Taxa Analysis (TITAN), a technique developed specifically for identifying community-level thresholds (Baker and King 2010), to explore species- and community-level changes along this gradient. I compared two spatial scales (local and landscape level) and two geographic regions one with extensive relatively intact boreal forest immediately to the north and another forested landscape embedded in a matrix of agricultural conversion (Chapter 5). I found that evidence for community level thresholds using this technique was equivocal particularly at the landscape scale. Community- level changes also occurred at different points along the agricultural gradient in each of the two regions sampled. Finally, species level change-points along the disturbance gradient were different between regions and among scales; however the list of “winners and losers” (McKinney and Lockwood 1999) was similar in both regions. Taken together, these findings lend support to concerns that thresholds may depend on species, scale and landscape context (Huggett 2005; Swift and Hannon 2010). However, for many species, evidence of changes in abundance and frequency of occurrence,

whether positive or negative, began at low levels of agricultural conversion (< 25%). An extension of the traits-based approach presented in Chapter 4, may help to further elucidate implications of these species changes for functional composition and response diversity of bird assemblages along disturbance gradients (Morissette *et al.*, *in prep*). Response diversity represents the diversity of responses to an external change (*i.e.*, do all species within a functional group decline in abundance?) and is an increasingly fundamental component of traits-based approaches (Devictor and Robert 2009; Sundstrom *et al.*, 2012).

The results of work using these integrated measures of diversity and function has highlighted interesting patterns of functional diversity. For example, using a long-term dataset for British avian assemblages, Petchey *et al.*, (2007) found that that co-occurring species were more similar in functional traits than a random set of species of identical number and concluded that real assemblages may have too few species to have any real redundancy. The idea that species may be considered functionally equivalent (or redundant) is a hotly debated topic (Fischer *et al.*, 2007). In addition to philosophical concerns around the idea of redundancy, empirical concerns arise from grouping species thereby limiting our understanding of the consequences of varying species compositions (Chalcraft and Resetarits 2003).

While the hypothesis that biodiversity contributes to the function of ecosystems is generally supported (Elmqvist *et al.*, 2003; Gamfeldt *et al.*, 2008), exact mechanisms have been elusive. However, studies examining broadly defined communities which incorporate more than one ecosystem type remain at the forefront of community ecological research because many are identifying previously unknown or unmeasured interactions. For example, Knight *et al.*, (2005) demonstrated that presence and absence of fish that are predators of dragonfly larvae influenced the plant species composition adjacent to waterbodies due to trophic cascades that altered the

community of insect pollinators. Studies that consider food-webs across terrestrial and aquatic ecosystem boundaries and that also consider birds are not common (*e.g.*, Murakami and Nakano 2002).

6.2.1 Detectability

I did not account for differences in species detectability which could be considered a limiting factor in my analysis. Vocalizations of some bird species are less detectable than others. Thus, knowledge of species composition is less than perfect without properly accounting for this systematic error (Keith 2010). However, the survey methods I used violate the assumption of closure and the costs and logistics of double-observer methods which are required for proper detectability analyses made such an approach infeasible. Current hierarchical approaches to modeling detection only allow for univariate analyses and are not adaptable to community level analyses. However, while it is possible that the precision of my data may have been improved by adjusting for species-specific detectability, it is doubtful that such an adjustment would significantly alter patterns I described or my conclusions. Additionally, I chose to increase sample size both within years and among years instead of conducting repeated surveys of the same sites (Carlson and Schmiegelow 2002). Previous studies have found that although species richness may not vary greatly across years, underlying species composition can change substantially (Rice *et al.*, 1983) which, although partially confounded by visiting different sites, may help to explain the strong year effect I reported in Chapters 2 and 3 and further supports the need for long-term studies.

6.3 Conclusions & Further research

Overall, my results indicate that boreal birds are effective indicators of ecological function and that community-level metrics may be useful for differentiating boreal avian

assemblages and for measuring effects of land-use change. A clear description of patterns is a necessary first step to further inquiry (McGill *et al.*, 2006; Underwood *et al.*, 2000) thus the community-level metrics I have tested point to the need for identifying mechanisms behind these patterns and for experimental work that assesses how species interactions may be altered under different land-use change or management scenarios (Chalcraft and Resetarits, Jr. 2003). Community-level approaches should assist in setting conservation priorities grounded in improved understanding of the implications of altered species assemblages and species interactions (Fischer *et al.*, 2006). Although many authors in other regions are making use of long term datasets collected by monitoring programs to test ideas of community dynamics as well as examine the impacts of changes in land use (*e.g.*, Karanth *et al.*, 2006; MacNally 1995; Meynard and Quinn 2008) a considerable limitation to studying these metrics in boreal systems is that such datasets for boreal birds remain uncommon.

Boreal ecosystems continue to face unprecedented rates of land-use change (Schneider 2002) and some authors contend that aquatic ecosystems and wetlands will be disproportionately affected by climate change (Schindler 2001) because of sensitivity to changes in the relationship between precipitation and actual evapotranspiration (Petroni *et al.*, 2007). While shoreline forests and wetlands clearly play a supporting role as habitat for birds, the specific roles these species play in supporting ecosystem function at the interface of these two systems is less clear. Understanding the role of community composition (biodiversity) in the functioning of ecosystems (*e.g.*, invasions, water quality through food web structure) will undoubtedly complement species-level research in building our understanding of the potential consequences of large-scale changes (Lindenmayer *et al.*, 2007).

6.4 References

- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of α diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19-28.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693.
- Baker, M. E. and R. S. King. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* 1:25-37.
- Betts, M. G., A. W. Diamond, G. J. Forbes, M.-A. Villard, and J. S. Gunn. 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling* 191:197-224.
- Blanc, L. A. and J. R. Walters. 2007. Cavity-nesting community webs as predictive tools: where do we go from here? *Journal of Ornithology* 148:S417-S423.
- Carlson, M. and F. Schmiegelow. 2002. Cost-effective sampling design applied to large-scale monitoring of boreal birds. *Conservation Ecology* 6:1-11.
- Chalcraft, D. R. and W. Resetarits, Jr. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology* 84:2407-2418.
- Cumming, S. G., K. L. Lefever, E. M. Bayne, T. Fontaine, F. K. A. Schmiegelow, and S. J. Song. 2010. Toward conservation of Canada's boreal forest avifauna: design and

- application of ecological models at continental extents. *Avian Conservation and Ecology* 5:-8.
- Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail, S. Villeger, and N. Mouquet. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47:15-25.
- Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17:252-261.
- Devictor, V. and A. Robert. 2009. Measuring community responses to large-scale disturbance in conservation biogeography. *Diversity and Distributions* 15:122-130.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488-494.
- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. A. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4:80-86.

- Flynn, D. F., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. Trautman Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and D. L. DeGiusti. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12:22-33.
- Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89:1223-1231.
- Hillebrand, H. and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12:1405-1419.
- Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. *Ecological Monographs* 56:201-220.
- Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124:301-310.
- Hughes, J. B. 2000. The Scale of Resource Specialization and the Distribution and Abundance of Lycaenid Butterflies. *Oecologia* 123:375-383.
- Imbeau, L., P. Drapeau, and M. Mönkönnen. 2003. Are forest birds categorised as “edge species” strictly associated with edges? *Ecography* 26:514-520.
- Karant, K. K., J. D. Nichols, J. R. Sauer, and J. E. Hines. 2006. Comparative dynamics of avian communities across edges and interiors of North American ecoregions. *Journal of Biogeography* 33:674-682.

- Kardynal, K., K. A. Hobson, S. L. Van Wilgenburg, and J. L. Morissette. 2009. Moving riparian management guidelines towards a natural disturbance model: an example using boreal riparian and shoreline forest bird communities. *Forest Ecology and Management* 257:54-65.
- Kardynal, K. J., J. L. Morissette, S. L. VanWilgenburg, E. M. Bayne, and K. A. Hobson. 2011. Avian response to experimental harvest in southern boreal mixedwood shoreline forests: implications for riparian buffer management. *Canadian Journal of Forest Research* 41:2375-2388.
- Keith, D. A. 2010. The interpretation, assessment and conservation of ecological communities. *Ecological Management and restoration* 10:S3-S15.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880-883.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177-192.
- Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435-450.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.

- Lindenmayer, D. B., J. Fischer, A. Felton, R. Montague-Drake, A. D. Manning, D. Simberloff, K. Youngentob, D. Saunders, D. Wilson, A. M. Felton, C. Blackmore, A. Lowe, S. Bond, N. Munro, and C. P. Elliott. 2007. The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos* 116:1220-1226.
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters* 3:73-76.
- Macdonald, S. E., B. Eaton, C. S. Machtans, C. Paszkowski, S. Hannon, and S. Boutin. 2006. Is forest close to lakes ecologically unique? Analysis of vegetation, small mammals, amphibians, and songbirds. *Forest Ecology and Management* 223:1-17.
- MacNally, R. and C. A. R. Timewell. 2005. Resource availability controls bird-assemblage composition through interspecific aggression. *The Auk* 122:1097-1111.
- MacNally, R. C. 1995. On large-scale dynamics and community structure in forest birds: lessons from some eucalypt forests of southeastern Australia. *Philosophical Transactions of the Royal Society of London* 350:369-379.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution* 21:178-185.
- McKinney, M. L. and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *TRENDS in Ecology and Evolution* 14:450-453.
- Meynard, C. N. and J. F. Quinn. 2008. Bird metacommunities in temperate south american forest: vegetation structure, area and climate effects. *Ecology* 89:981-990.

- Mönkönnen, M. and D. A. Welsh. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. *Annales Zoologici Fennici* 31:61-70.
- Murakami, M. and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through predation by birds. *Ecology Letters* 5: 333-337.
- Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia - ecology, conservation, and management of streamside communities*. Elsevier Academic Press, Burlington, MA.
- Pandit, S. N. and J. Kolasa. 2012. Opposite effects of environmental variability and species richness on temporal turnover of species in a complex habitat mosaic. *Hydrobiologia* 685:145-154.
- Pasari, J. R., T. Levi, E. S. Zavaleta, and D. Tilman. 2013. Several scales of biodiversity affect ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* 110:10219-10222.
- Pélissier, R., P. Couteron, and S. Dray. 2008. Analyzing or explaining beta diversity? comment. *Ecology* 89:3227-3232.
- Petchey, O. L., K. L. Evans, I. S. Fishburn, and K. J. Gaston. 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology* 76:977-985.
- Petrone, R.M., U. Silins, and K.J. Devito. 2007. Dynamics of evapotranspiration from a riparian pond complex in the Western Boreal Forest, Alberta Canada. *Hydrological Processes* 21:1391-1401

- Rempel, R. S., K. F. Abraham, T. R. Gadawski, S. Gabor, and R. K. Ross. 1997. A simple wetland habitat classification for boreal forest waterfowl. *Journal of Wildlife Management* 61:746-757.
- Rice, J., R. D. Ohmart, and B. W. Anderson. 1983. Turnovers in species composition of avian communities in contiguous riparian habitats. *Ecology* 64:1444-1455.
- Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* 86:56-62.
- Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millenium. *Canadian Journal of Fish and Aquatic Science* 58:18-29.
- Schleuter, D., M. Daufresne, F. Massol, and C. Argiller. 2010. A user's guide to functional diversity indices. *Ecological Monographs* 80:469-484.
- Schmera, D. and J. Podani. 2013. Components of beta diversity in hierarchical sampling designs: a new approach. *Ecological Indicators* 26:126-136.
- Schneider, R. R. 2002. *Alternative futures: Alberta's boreal forest at the crossroads*. The Federation of Alberta Naturalists; The Alberta Center for Boreal Research, Edmonton, Alberta.

- Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7:491-508.
- Smith, K. B., C.E. Smith, S. F. Forest, and A.J. Richard. 2007. A field guide to the wetlands of the boreal plains ecozone of Canada. Ducks Unlimited Canada.
- Song, S. 2002. The ecological basis for stand management: a summary and synthesis of ecological responses to wildfire and harvesting in boreal forests. Alberta Research Council, Vegreville, Alberta.
- Srivastava, D. S. and M. Vellend. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution and Systematics* 36:267-294.
- Sundstrom, S. M., C. R. Allen, and C. Barichievy. 2012. Species, Functional Groups, and Thresholds in Ecological Resilience. *Conservation Biology* 26:305-314.
- Swift, T. L. and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. *Biological Reviews* 85:35-53.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding patterns. *Journal of Experimental Marine Biology and Ecology* 250:97-115.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.

- Villard, M.-A., F. K. A. Schmiegelow, and M. K. Trzcinski. 2007. Short-term response of forest birds to experimental clearcut edges. *The Auk* 124:828-840.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116:882-892.
- Virkkala, R., M. Luoto, R. K. Heikkinen, and N. Leikola. 2005. Distribution patterns of boreal marshland birds: modelling the relationships to land cover and climate. *Journal of Biogeography* 32:1957-1970.
- Whitaker, D. M., A. L. Carroll, and W. A. Montevecchi. 2000. Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. *Canadian Journal of Zoology* 78:740-747.
- Wiens, J. A. 1989. *The ecology of bird communities. Volume 1. Foundations and patterns.* University Press, Cambridge.

BIBLIOGRAPHY

- Allen, C. R., G. S. Cumming, A. S. Garmestani, P. D. Taylor, and B. H. Walker. 2011. Managing for resilience. *Wildlife Biology* 17:337-349.
- Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958-966.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of α diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19-28.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355-366.
- Bacaro, G., C. Ricotta, and S. Mazzoleni. 2007. Measuring beta-diversity from taxonomic similarity. *Journal of Vegetation Science* 18:793-798.
- Baker, M. E. and R. S. King. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* 1:25-37.
- Bakermans, M. H. 2003. Hierarchical habitat selection by the Acadian flycatcher: implications for conservation of riparian forests. The Ohio State University.

- Bauer, D. M., P. W. Paton, and S. K. Swallow. 2010. Are wetland regulations cost effective for species protection? A case study of amphibian metapopulations. *Ecological Applications* 20:798-815.
- Bayne, E. M., and K. A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418-1429.
- Becker, C. D., T. M. Loughin, and T. Santander. 2008. Identifying forest-obligate birds in tropical moist cloud forest of Andean Ecuador. *Journal of Field Ornithology* 79:229-244.
- Betts, M. G., A. W. Diamond, G. J. Forbes, M.-A. Villard, and J. S. Gunn. 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling* 191:197-224.
- Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe. 2000. *Bird Census Techniques*. Academic Press, London.
- Biswas, S. R. and A. U. Mallik. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology* 9:28-35.
- Biswas, S. R. and A. U. Mallik. 2011. Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere* 2:1-10.
- Blanc, L. A. and J. R. Walters. 2007. Cavity-nesting community webs as predictive tools: where do we go from here? *Journal of Ornithology* 148:S417-S423.

- Boulet, M., M. Darveau, and L. Bélanger. 2003. Nest predation and breeding activity of songbirds in riparian and nonriparian black spruce strips of central Quebec. *Canadian Journal of Forest Research* 33:922-930.
- Brook, R. W. and R. G. Clark. 2005. Breeding season survival of female lesser scaup in the northern boreal forest. *Arctic* 58:16-20.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255-279.
- Bub, B. R., D. J. Flaspohler, and C. J. F. Huckins. 2004. Riparian and upland breeding-bird assemblages along headwater streams in Michigan's upper peninsula. *Journal of Wildlife Management* 68:383-392.
- Bureau of Land Management. 2013. Birds as indicators of riparian vegetation condition in the western U.S. Bureau of Land Management, Partners in Flight, Boise, Idaho.
- Burgess, C. J. 1997. Forested landscape patterns in the western boreal mixedwood forest of Alberta: riparian forests, fire history, canopy composition and topography. Department of Biological Sciences, University of Alberta.
- Calmé, S., A. Desrochers, and J.-P. L. Savard. 2002. Regional significance of peatlands for avifaunal diversity in southern Quebec. p. 273-281.
- Carlson, M., and F. Schmiegelow. 2002. Cost-effective sampling design applied to large-scale monitoring of boreal birds. *Conservation Ecology* 6:1-11.

- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4:765-781.
- Casanoves, F., L. E. Pla, and J. A. Di Rienzo. 2011. FDiversity: an Integrated Tool to Estimate and Analyze Functional Diversity. *Bulletin of the Ecological Society of America* 92:147-152.
- Chapin, F. S., III, T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio* 33:361-365.
- Chalcraft, D. R. and W. Reserits, Jr. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology* 84:2407-2418.
- Clarke, K. R. 1999. Nonmetric multivariate analysis in community-level ecotoxicology. *Environmental Toxicology and Chemistry* 18:118-127.
- Clare, S., N. Krogman, L. Foote, and N. Lemphers. 2011. Where is the avoidance in the implementation of wetland law and policy? *Wetlands Ecology and Management* 19:165-182.
- Conway, C. J. 2002. Standardized North American marsh bird monitoring protocols. 23 pages.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D. C.

- Crist, T. O. and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species-area relationships: unifying alpha-, beta- and gamma-diversity with sample size and habitat area. *Ecology Letters* 9:923-932.
- Croonquist, M. J. and R. P. Brooks. 1991. Use of avian and mammalian guilds as indicators of cumulative impacts in riparian-wetland areas. *Environmental Management* 15:701-714.
- Cumming, S. G., K. L. Lefever, E. M. Bayne, T. Fontaine, F. K. A. Schmiegelow, and S. J. Song. 2010. Toward conservation of Canada's boreal forest avifauna: design and application of ecological models at continental extents. *Avian Conservation and Ecology* 5:-8.
- Darveau, M., P. Beauchesne, L. Bélanger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. *Journal of Wildlife Management* 59:67-77.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178-392.
- Desrochers, A. and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11:1204-1210.
- Dettmers, R., D. A. Buehler, J. G. Bartlett, and N. A. Klaus. 1999. Influence of point count length ad repeated visits on habitat model performance. *Journal of Wildlife Management* 63:815-823.

- Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail, S. Villeger, and N. Mouquet. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47:15-25.
- Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17:252-261.
- Devictor, V. and A. Robert. 2009. Measuring community responses to large-scale disturbance in conservation biogeography. *Diversity and Distributions* 15:122-130.
- Dickson, J. G., R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll. 1979. The role of insectivorous birds in forest ecosystems. Academic Press, New York.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: a need for flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522-538.
- Ecological Stratification Working Group. 1996. A national ecological framework for Canada. Environment Canada. [online]. 2005. Narrative descriptions of terrestrial ecozones and ecoregions of Canada. <http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/default.cfm>.

- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488-494.
- Environment Canada. 2013. Bird Conservation Strategy for Bird Conservation Region 6: Boreal Taiga Plains. Canadian Wildlife Service, Environment Canada, Edmonton, Alberta.
- Epner, C. A., S. E. Bayley, J. E. Thompson, and W. M. Tonn. 2010. Influence of fish assemblage and shallow lake productivity on waterfowl communities in the Boreal Transition Zone of western Canada. *Freshwater Biology* 55:2265-2280.
- Erskine, A. J. 1977. Birds in boreal Canada; communities densities and adptations. Canadian Wildlife Service, Ottawa. Report Series Number 41.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100:65-74.
- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J. L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14:101-112.
- Fast, P. L. F., R. G. Clark, R. W. Brook, and J. E. Hines. 2004. Patterns of wetland use by brood-rearing Lesser Scaup in northern boreal forest of Canada. *Waterbirds* 27:177-182.
- Ferone, J. M. and K. J. Devito. 2004. Shallow groundwater–surface water interactions in pond–peatland complexes along a Boreal Plains topographic gradient. *Journal of Hydrology* 292:75-95.

- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. A. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4:80-86.
- Flohre, A., C. Fischer, T. Aavik, J. Bengtsson, F. Berendse, R. Bommarco, P. Ceryngier, L. W. Clement, C. Dennis, S. +. Eggers, M. Emmerson, F. Geiger, I. Guerrero, V. Hawro, P. Inchausti, J. Liira, M. B. Morales, J. J. O+late, T. P+ñrt, W. W. Weisser, C. Winqvist, C. Thies, and T. Tscharntke. 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications* 21:1772-1781.
- Flynn, D. F., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. Trautman Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and D. L. DeGiusti. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12:22-33.
- Foote, L. and N. Krogman. 2006. Wetlands in Canada's western boreal forest: agents of change. *The Forestry Chronicle* 82:825-833.
- Fox, A. D. and M. C. Bell. 1994. Breeding bird communities and environmental variable correlates of Scottish peatland wetlands. *Hydrobiologia* 279/280:297-307.
- Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89:1223-1231.

- Gaston, K. J., T. M. Blackburn, and K. K. Goldewijk. 2003. Habitat Conversion and Global Avian Biodiversity Loss. *Proceedings: Biological Sciences* 270:1293-1300.
- Gotelli, N. J. and G. L. Entsminger. 2000. EcoSim:Null models software for ecology. Acquired Intelligence Inc. & Kesy-Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>.
- Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379-391.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399-409.
- Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *American Midland Naturalist* 129:288-300.
- Groffman, P. M., J. S. Baron, T. Blett, A. J. Gold, I. Goodman, L. H. Gunderson, B. M. Levinson, M. A. Palmer, H. W. Paerl, G. D. Peterson, N. L. Poff, D. W. Rejeski, J. F. Reynolds, M. G. Turner, K. C. Weathers, and J. Wiens. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1-13.
- Groom, J. D. and T. C. Grubb. 2002. Bird Species Associated with Riparian Woodland in Fragmented, Temperate-Deciduous Forest. *Conservation Biology* 16:832-836.
- Groves, C. R. 2003. *Drafting a Conservation Blueprint: A practitioner's guide to planning for biodiversity*. Island Press, Washington.

- Guzy, M. J., and G. Ritchison. 1999. Common Yellowthroat (*Geothlypis trichas*), In A. Poole, and F. Gill [eds.], The Birds of North America, Inc. Philadelphia, PA.
- Hågvar, S., P. Nygaard, and B. T. Bækken. 2004. Retention of forest strips for bird-life adjacent to water and bogs in Norway: effect of different widths and habitat variables. Scandinavian Journal of Forest Research 19:452-465.
- Hahn, S. S., S. S. Bauer, and M. Klaassen. 2008. Quantification of allochthonous nutrient input into freshwater bodies by herbivorous waterbirds. Freshwater Biology 53:181-193.
- Hannah, K. C. 2001. Patterns in habitat quality for the white-throated sparrow (*Zonotrichia albicollis*) in a recently logged landscape. University of Alberta.
- Hannon, S. J. 2005. Effect of stand vs. landscape level forest structure on species abundance and distribution. Sustainable Forest Management Network, Edmonton, Alberta.
- Hannon, S. J., S. E. Cotterill, and F. K. A. Schmiegelow. 2004. Identifying rare species of songbirds in managed forests: application of an ecoregional template to a boreal mixedwood system. Forest Ecology and Management 191:157-170.
- Hannon, S. J., C. A. Paszkowski, S. Boutin, J. DeGroot, S. E. Macdonald, M. Wheatley, and B. R. Eaton. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. Canadian Journal of Forest Research 32:1784-1800.

- Hanowski, J., N. Danz, and J. Lind. 2006. Response of breeding bird communities to forest harvest around seasonal ponds in northern forests, USA. *Forest Ecology and Management* 229:63-72.
- Hanowski, J., N. Danz, J. Lind, and G. Niemi. 2003. Breeding bird response to riparian forest harvest and harvest equipment. *Forest Ecology and Management* 174:315-328.
- Harris, A. G., S. C. McMurray, P. W. C. Uhlig, J. K. Jeglum, R. F. Foster, and G. D. Racey. 1996. Field guide to the wetland ecosystem classification for northwestern Ontario. Ontario Ministry of Natural Resources, Northwest Science and Technology, Thunder Bay, Ontario. NWST Field Guide FG-01.
- Hillebrand, H. and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12:1405-1419.
- Hobson, K. 1996. The influence of forest management practices on boreal forest bird habitat use and productivity: a community approach., Prince Albert Model Forest Association Inc.
- Hobson, K. A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixedwoods of western Canada. *Wilson Bulletin* 112:373-387.
- Hobson, K. A. and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecological Applications* 9:849-863.
- Hobson, K. A., E. M. Bayne, and S. L. Van Wilgenburg. 2002. Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. *Conservation Biology* 16:1530-1541.

- Hobson, K. A., D. A. Kirk, and A. R. Smith. 2000. A multivariate analysis of breeding bird species of western and central Canadian boreal forests: stand and spatial effects. *Ecoscience* 7:267-280.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-23.
- Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. *Ecological Monographs* 56:201-220.
- Hooper, D. U., F. S. Chapin, III, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, and A. J. Symstad. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3-35.
- Houlahan, J. E., and C. S. Findlay. 2004. Estimating the 'critical' distance at which adjacent land-use degrades wetland water and sediment quality. *Landscape Ecology* 19:677-690.
- Houseman, G. R., G. G. Mittlebach, H. L. Reynolds, and K. L. Gross. 2008. Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology* 89:2172-2180.
- Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124:301-310.

- Hughes, J. B. 2000. The Scale of Resource Specialization and the Distribution and Abundance of Lycaenid Butterflies. *Oecologia* 123:375-383.
- Hunt, L. M. and W. Haider. 2004. Aesthetic impacts of disturbances on selected boreal forested shorelines. *Forest Science* 50:729-738.
- Ilhardt, B. L., E. S. Verry, and B. J. Palik. 2000. Defining riparian areas. p. 23-42. *In* E. S. Verry, J. W. Hornbeck, and A. Dolloff (eds.) *Riparian management in forests of the continental eastern United States*. Lewis Publishers, Boca Raton, Florida.
- Imbeau, L., P. Drapeau, and M. Mönkönen. 2003. Are forest birds categorised as “edge species” strictly associated with edges? *Ecography* 26:514-520.
- Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters* 9:1237-1244.
- Karant, K. K., J. D. Nichols, J. R. Sauer, and J. E. Hines. 2006. Comparative dynamics of avian communities across edges and interiors of North American ecoregions. *Journal of Biogeography* 33:674-682.
- Kardynal, K. J., J. L. Morissette, S. L. VanWilgenburg, E. M. Bayne, and K. A. Hobson. 2011. Avian response to experimental harvest in southern boreal mixedwood shoreline forests: implications for riparian buffer management. *Canadian Journal of Forest Research* 41:2375-2388.
- Kardynal, K., K. A. Hobson, S. L. Van Wilgenburg, and J. L. Morissette. 2009. Moving riparian management guidelines towards a natural disturbance model: an example using boreal

- riparian and shoreline forest bird communities. *Forest Ecology and Management* 257:54-65.
- Karp, D. S., G. Ziv, J. Zook, P. R. Ehrlich, and G. C. Daily. 2011. Resilience and stability in bird guilds across a tropical countryside. *Proceedings of the National Academy of Sciences* 108:21134-21139.
- Keith, D. A. 2010. The interpretation, assessment and conservation of ecological communities. *Ecological Management and restoration* 10:S3-S15.
- Kelly, C. K., M. G. Bowler, O. Pybus, and P. H. Harvey. 2008. Phylogeny, niches and relative abundance in natural communities. p. 962-970.
- Kennedy, C. M., E. H. C. Grant, M. C. Neel, W. F. Fagan, and P. P. Marra. 2011. Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores. *Ecological Applications* 21:1837-1850.
- King, R. S., M. E. Baker, P. F. Kazzyak, and D. E. Weller. 2010. How novel is too novel? Stream community thresholds at exceptionally low levels of catchment urbanization. *Ecological Applications* 21:1659-1678.
- Kirk, D. A., A. W. Diamond, K. A. Hobson, and A. R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Canadian Journal of Zoology* 74:1749-1770.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880-883.

- Laliberté, E. and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305.
- Lambeets, K., M. L. Vandegheuchte, J. P. Maelfait, and D. Bonte. 2008. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology* 77:1162-1174.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5-13.
- Larue, P., L. Bélanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. *Canadian Journal of Forest Research* 25:555-566.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177-192
- Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. *Journal of Environmental Management* 70:165-180.
- Legendre, P. and L. Legendre. 2002. *Numerical Ecology*, 2nd Edition edition. Elsevier, Amsterdam.
- Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435-450.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.

- Lemelin, L.-V. 2007. L'habitat de la sauvagine en nidification dans le Québec forestier. Université du Québec.
- Lindenmayer, D. B., J. Fischer, A. Felton, R. Montague-Drake, A. D. Manning, D. Simberloff, K. Youngentob, D. Saunders, D. Wilson, A. M. Felton, C. Blackmore, A. Lowe, S. Bond, N. Munro, and C. P. Elliott. 2007. The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos* 116:1220-1226.
- Locky, D. A. 2005. Boreal plains peatlands: characterization, plant diversity, biogeography, and impacts from logging. University of Alberta (Canada).
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters* 3:73-76.
- Lougheed, V. L., M. D. McIntosh, C. A. Parker, and R. J. Stevenson. 2008. Wetland degradation leads to homogenization of the biota at local and landscape scales. *Freshwater Biology* 53:2402-2413.
- Macdonald, E., C. J. Burgess, G. J. Scrimgeour, S. Boutin, S. Reedyk, and B. Kotak. 2004. Should riparian buffers be part of forest management based on emulation of natural disturbance? *Forest Ecology and Management* 187:185-196.
- Macdonald, S. E., B. Eaton, C. S. Machtans, C. Paszkowski, S. Hannon, and S. Boutin. 2006. Is forest close to lakes ecologically unique? Analysis of vegetation, small mammals, amphibians, and songbirds. *Forest Ecology and Management* 223:1-17.
- Magurran, A. E. 2003. *Measuring Biological Diversity*. Blackwell Science, Malden, MA.

- Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* 10:1366-1379.
- MacNally, R. and C. A. R. Timewell. 2005. Resource availability controls bird-assemblage composition through interspecific aggression. *The Auk* 122:1097-1111.
- MacNally, R. C. 1995. On large-scale dynamics and community structure in forest birds: lessons from some eucalypt forests of southeastern Australia. *Philosophical Transactions of the Royal Society of London* 350:369-379.
- Manly, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. 2nd Edition ed. Chapman and Hall, London Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. R. Wood, and J. S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecological Applications* 20:126-134.
- Margules, C. R. and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.
- Marquis, R. J. and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007-2014.
- Mason, N. W. H., K. MacGillivray, J. B. Steel, and J. B. Wilson. 2003. An index of functional diversity. *Journal of Vegetation Science* 14:571-578.
- Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112-118.

- McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.
- McGarigal, K. and W. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. *Journal of Wildlife Management* 56:10-23.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution* 21:178-185.
- McKinney, M. L. and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *TRENDS in Ecology and Evolution* 14:450-453.
- McParland, C. E. 2004. Food web interactions of waterbirds and fish in eutrophic wetlands of Alberta's aspen parkland. University of Alberta (Canada).
- Meynard, C. N. and J. F. Quinn. 2008. Bird metacommunities in temperate south american forest: vegetation structure, area and climate effects. *Ecology* 89:981-990.
- Mills, P. F. 1994. The agricultural potential of northwestern Canada and Alaska and the impact of climatic change. *Arctic* 47:115-123.
- Mitsch, W. J. and J. G. Gosselink. 2007. *Wetlands*, 2nd edition. Van Nostrand Reinhold, New York.
- Mönkönnen, M. and D. A. Welsh. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the forest bird communities of Europe and North America. *Annales Zoologici Fennici* 31:61-70.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, Malden, MA.

- Morissette, J. L., K. J. Kardynal, E. M. Bayne, and K. Hobson. 2013. Comparing bird community composition among boreal wetlands: is wetland classification a missing piece of the puzzle? *Wetlands* 33:653-665.
- Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research* 32:2169-2183.
- Mouchet, M., F. Guilhaumon, S. Villeger, N. W. H. Mason, J.-A. Tomasini, and D. Mouillot. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117:794-800.
- Murakami, M. and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through predation by birds. *Ecology Letters* 5: 333-337.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734-737.
- Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia - ecology, conservation, and management of streamside communities*. Elsevier Academic Press, Burlington, MA.
- Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209-212.
- National Council for Air Stream Improvement, I. N. 2007. Synthesis of technical information on forest wetlands in Canada. National Council for Air and Stream Improvement, Inc., Research Triangle Park, N.C. Technical Bulletin No. 938.

- National Wetlands Working Group (NWWG). 1997. The Canadian wetland classification system. Canada Committee on Ecological Land Classification, Environment Canada.
- Niemi, G., J. Hanowski, P. Helle, R. Howe, M. Mönkkönen, L. Vernier, and D. Welsh. 1998. Ecological sustainability of birds in boreal forests. *Conservation Ecology* 2:17.
- Norton, M. R., S. J. Hannon, and F. K. A. Schmiegelow. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. *Ecography* 23:209-223.
- Nur, N., G. Ballard, and G. Geupel. 2008. Regional analysis of riparian bird species responds to vegetation and local habitat features. *The Wilson Journal of Ornithology* 120:840-855.
- Pandit, S. N. and J. Kolasa. 2012. Opposite effects of environmental variability and species richness on temporal turnover of species in a complex habitat mosaic. *Hydrobiologia* 685:145-154.
- Pasari, J. R., T. Levi, E. S. Zavaleta, and D. Tilman. 2013. Several scales of biodiversity affect ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* 110:10219-10222.
- Paszkowski, C. A. and W. M. Tonn. 2006. Foraging guilds of aquatic birds on productive boreal lakes: environmental relations and concordance patterns. *Hydrobiologia* 567:19-30.
- Pearson, S. F. and D. A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed pacific northwest Douglas-fir forests. *Ecological Applications* 11:840-853.

- Pélissier, R., P. Couteron, and S. Dray. 2008. Analyzing or explaining beta diversity? comment. *Ecology* 89:3227-3232.
- Petchey, O. L. and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402-411.
- Petchey, O. L. and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741-758.
- Petchey, O. L., K. L. Evans, I. S. Fishburn, and K. J. Gaston. 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology* 76:977-985.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Petrone, R. M., U. Silins, and K. J. Devito. 2007. Potential impacts of catchment microclimatic variability on pond evaporation in the western boreal plain, Alberta, Canada. *Hydrological Processes* 21:1391-1401.
- Pierre, J. P. 2001. Effects of forest harvesting disturbance on aquatic birds in the boreal forest of Alberta. University of Alberta (Canada).
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands - a test of biodiversity theory. *Ecology* 79:94-105.
- Poole, A. e. 2005. The birds of North America Online. Cornell Laboratory of Ornithology, Ithaca, New York.

- Poos, M. S., S. C. Walker, and D. A. Jackson. 2009. Functional-diversity indices can be driven by methodological choices and species richness. *Ecology* 90:341-347.
- Post, D. M., J. P. Taylor, J. F. Kitchell, M. H. Olson, D. E. Schindler, and B. R. Herwig. 1998. The Role of Migratory Waterfowl as Nutrient Vectors in a Managed Wetland. *Conservation Biology* 12:910-920.
- Quinn, G. P. and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, United Kingdom.
- Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124:317-337.
- Rao, C. R. 1982. Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* 21:24-43.
- Reeves, G. H., P. A. Bisson, B. E. Rieman, and L. E. Benda. 2006. Postfire logging in riparian areas. *Conservation Biology* 20:994-1004.
- Rempel, R. S., K. F. Abraham, T. R. Gadawski, S. Gabor, and R. K. Ross. 1997. A simple wetland habitat classification for boreal forest waterfowl. *Journal of Wildlife Management* 61:746-757.
- Rice, J., R. D. Ohmart, and B. W. Anderson. 1983. Turnovers in species composition of avian communities in contiguous riparian habitats. *Ecology* 64:1444-1455.

- Ries, L., R. J. Fletcher, Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35:491-522.
- Riffell, S., T. Burton, and M. Murphy. 2006. Birds in depression forested wetlands: area and habitat requirements and model uncertainty. *Wetlands* 26:107-118.
- Rodewald, A. D. and M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? *Biological Conservation* 128:193-200.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9:135-151.
- Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* 86:56-62.
- Sargeant, A. B., and D. G. Raveling. 1992. Mortality during the breeding season, p. 396-422. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, USA.
- Schieck, J. and K. A. Hobson. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. *Canadian Journal of Forest Research* 30:1281-1295.

- Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Canadian Journal of Fish and Aquatic Science* 58:18-29
- Schleuter, D., M. Daufresne, F. Massol, and C. Argiller. 2010. A user's guide to functional diversity indices. *Ecological Monographs* 80:469-484.
- Schmera, D. and J. Podani. 2013. Components of beta diversity in hierarchical sampling designs: a new approach. *Ecological Indicators* 26:126-136.
- Schneider, R. R., J. B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land-uses in the western Canadian sedimentary basin: a modelling approach. *Conservation Ecology* 7:8.
- Schulte, L. A. and G. J. Niemi. 1998. Bird communities of early successional burned and logged forest. *Journal of Wildlife Management* 62:1418-1429.
- Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7:491-508.
- Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. *Trends in Ecology & Evolution* 21:464-471.
- Simon, N. P., A. W. Diamond, and F. E. Schwab. 2003. Do northern forest bird communities show more ecological plasticity than southern forest bird communities in eastern Canada? *Ecoscience* 10:289-296.

- Smith, K. B., Smith Christopher E., S. F. Forest, and Richard Alain J. 2007. A field guide to the wetlands of the boreal plains ecozone of Canada. Ducks Unlimited Canada.
- Song, S. 2002. The ecological basis for stand management: a summary and synthesis of ecological responses to wildfire and harvesting in boreal forests. Alberta Research Council, Vegreville, Alberta.
- Srivastava, D. S. and M. Vellend. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution and Systematics* 36:267-294.
- Steedman, R. J., R. S. Kushneriuk, and R. L. France. 2001. Littoral water temperature response to experimental shoreline logging around small boreal forest lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1638-1647.
- Swift, T. L., and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. *Biological Reviews* 85:35-53.
- Sundstrom, S. M., C. R. Allen, and C. Barichiev. 2012. Species, Functional Groups, and Thresholds in Ecological Resilience. *Conservation Biology* 26:305-314.
- Swift, T. L. and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. *Biological Reviews* 85:35-53.
- Tarnocai, C. 2001. Eastern Cereal and Oilseed Research Centre Research Branch, Agriculture and Agri-Food Canada, Ottawa, Canada.

- Thrush, S. F., Hallida Jane, J. E. Hewitt, and A. M. Lohrer. 2008. The effects of habitat loss, fragmentation, and community homogenization on resilience in estuarries. *Ecological Applications* 18:12-21.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843-808.
- Toner, M. and P. Keddy. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications* 7:236-246.
- Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89:944-951.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding patterns. *Journal of Experimental Marine Biology and Ecology* 250:97-115.
- Väckär, D., B. ten Brink, J. Loh, J. E. M. Baillie, and B. Reyers. 2012. Review of multispecies indices for monitoring human impacts on biodiversity. *Ecological Indicators* 17:58-67.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99:3-9.

- Villard, M.-A., F. K. A. Schmiegelow, and M. K. Trzcinski. 2007. Short-term response of forest birds to experimental clearcut edges. *The Auk* 124:828-840.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116:882-892.
- Virkkala, R., M. Luoto, R. K. Heikkinen, and N. Leikola. 2005. Distribution patterns of boreal marshland birds: modelling the relationships to land cover and climate. *Journal of Biogeography* 32:1957-1970.
- Wardwell, D. A., C. R. Allen, G. D. Peterson, and A. J. Tyre. 2008. A test of the cross-scale resilience model: Functional richness in Mediterranean-climate ecosystems. *Ecological Complexity* 5:165-182.
- Welsh, D. A. and S. C. Lougheed. 1996. Relationships of bird community structure and species distributions of two environmental gradients in the northern boreal forest. *Ecography* 19:194-208.
- Whitaker, D. M. and W. A. Montevecchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a Balsam fir ecosystem. *Canadian Journal of Forest Research* 27:1159-1167.
- Whitehouse, H. E. and S. E. Bayley. 2005. Vegetation patterns and biodiversity of peatland plant communities surrounding mid-boreal wetland ponds in Alberta, Canada. *Canadian Journal of Botany* 83:621-637.

- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.
- Wiens, J. A. 1989. The ecology of bird communities. Volume 1. Foundations and patterns. University Press, Cambridge.
- Wilson, W. H., Jr. 1996. The birds of North America: palm warbler (*Dendroica palmarum*). The Academy of Natural Sciences; The American Ornithologist's Union, Philadelphia; Washington D.C.
- With, K. A. and A. W. King. 2004. The effect of landscape structure on community self-organization and critical biodiversity. *Ecological Modelling* 179:349-366.
- Wohl, D. L., S. Arora, and J. R. Gladstone. 2004. Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. *Ecology* 85:1534-1540.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *TRENDS in Ecology and Evolution*.
- Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences* 96:1463-1468.
- Yarrow, M. M. and V. H. Marín. 2007. Toward conceptual cohesiveness: a historical analysis of the theory and utility of ecological boundaries and transition zones. *Ecosystems* 10:462-476.

APPENDIX 1: SUPPLEMENTARY MATERIALS FOR ASSESSING THE COMPOSITION OF RIPARIAN ASSEMBLAGES (CHAPTER 2)

Table A1.1 Complete Indicator Species Analysis results and associated Species Specialization Index (SSI) values

AOU	Full Transect					Shoreline Forest & Upland Forest					SSI
	Max Group	Ind Val	Mean	StDev	p	Max Group	Ind Val	Mean	StDev	P	
LISP	Rip	59.5	19.4	4.66	0.0002	Rip	31.2	15.6	6.14	0.033	0.46
LCSP	Rip	35.6	13.2	4.37	0.002	Rip	9.7	7.5	4.39	0.293	0.878
LEYE	Rip	32.2	12.5	4.41	0.005	Rip	11.3	8.1	4.47	0.167	1.002
ALFL	Rip	28.5	12.7	4.39	0.009	Rip	22.6	12	5.61	0.059	0.472
COYE	Rip	24.1	10.2	4.02	0.012	Rip	16.1	9.8	5.27	0.113	0.473
SOSA	Rip	23	9.8	3.88	0.013	Rip	4.8	5.4	3.56	0.581	0.955
SWSP	Rip	25.6	11.9	4.27	0.014	Rip	9.3	10.9	5.43	0.511	0.547
COSN	Rip	24.5	13.2	4.24	0.023	Rip	4.8	5.5	3.73	0.609	0.543
CHSP	Rip	39.1	29.8	4.09	0.033	Rip	37.7	26.4	6.05	0.055	0.349
WTSP	Rip	37.8	28.6	4.35	0.042	Rip	25.8	20.7	6.25	0.162	0.398
CCSP	Rip	14.9	7.6	3.68	0.044	Rip	12.9	8.9	4.86	0.176	0.754
KILL	Rip	13.8	7.4	3.51	0.045	NA	NA	NA	NA	NA	1.277

AOU	Full Transect					Shoreline Forest & Upland Forest					SSI
	Max Group	Ind Val	Mean	StDev	p	Max Group	Ind Val	Mean	StDev	P	
YWAR	Rip	27.8	17.9	4.92	0.046	Rip	25.8	17.9	6.37	0.108	0.793
BOGU	Rip	13.8	7.5	3.57	0.049	NA	NA	NA	NA	NA	1.116
RWBL	Rip	16.2	8.9	4	0.055	Rip	6.5	6.3	3.84	0.445	0.358
SOSP	Rip	11.5	6.5	3.53	0.079	Rip	6.5	6.5	3.91	0.513	0.356
AMRO	Rip	10.8	7.2	3.48	0.138	Rip	4.8	5.5	3.67	0.646	0.266
BRBL	Rip	9.2	5.7	3.15	0.149	NA	NA	NA	NA	NA	1.047
WPWA	Rip	17.3	14.3	4.39	0.189	NA	NA	NA	NA	NA	0.832
TEWA	Rip	35.9	33.6	3.05	0.196	Rip	42.4	32.4	4.74	0.043	0.473
OSFL	Rip	8.7	7.2	3.46	0.205	Low	10.1	7	4.05	0.101	1.002
BLTE	Rip	6.9	5.1	2.94	0.24	Rip	9.7	7.6	4.2	0.200	1.208
BOCH	Rip	10.4	9.2	3.96	0.294	NA	NA	NA	NA	NA	0.855
WIWA	Rip	4.6	4.2	2.49	0.386	Low	10.4	6.9	3.91	0.129	1.331
SPSA	Rip	4.6	4.3	2.53	0.404	NA	NA	NA	NA	NA	1.632
SCJU	Rip	17.9	18.5	4.81	0.439	Rip	22	15.4	6.06	0.115	0.547
RUBL	Rip	4.6	4.2	2.41	0.474	NA	NA	NA	NA	NA	NA
CAWA	Rip	4.2	5.1	2.89	0.506	Rip	4.2	7.1	4.05	0.898	0.943
BCCH	Rip	10.1	12	4.23	0.588	Rip	14.3	11.6	5.5	0.214	0.834
COTE	Rip	3.4	3.7	2.24	0.630	NA	NA	NA	NA	NA	NA
CMWA	Rip	3.4	3.7	2.37	0.665	NA	NA	NA	NA	NA	1.601
SACR	Rip	3.4	3.7	2.34	0.666	NA	NA	NA	NA	NA	NA

AOU	Full Transect					Shoreline Forest & Upland Forest					SSI
	Max Group	Ind Val	Mean	StDev	p	Max Group	Ind Val	Mean	StDev	P	
TTWO	Rip	3.4	3.8	2.43	0.684	Rip	5.9	7.5	4.37	0.586	2.173
MAWA	Rip	5.9	7.6	3.62	0.686	Rip	8.1	7.1	3.97	0.350	0.681
AMRE	Rip	10.1	12.8	4.44	0.715	Up	7.3	11.3	5.38	0.783	0.684
CEDW	Rip	3.5	5.2	2.96	0.717	Rip	6	7.1	4.4	0.486	0.580
NOFL	Rip	4.6	7.3	3.57	0.802	Rip	6.5	6.3	3.69	0.533	0.690
BHCO	Rip	2.9	4.7	2.6	1	Up	4.9	10.6	5.31	0.987	0.436
WAVI	Rip	2	4.3	2.49	1	NA	NA	NA	NA	NA	NA
OVEN	Up	53.7	29.9	4.05	0.0002	Up	49.9	26.7	6.07	0.006	0.740
REVI	Up	56	31.7	3.69	0.0002	Up	39.1	28.4	5.6	0.054	1.124
PHVI	Up	34.4	16.5	4.57	0.008	Up	30.6	16.1	6.38	0.038	1.148
RUGR	Up	15.1	6.1	3.36	0.029	NA	NA	NA	NA	NA	1.272
LEFL	Up	18.9	17.6	4.84	0.299	Up	21.5	19.4	6.61	0.288	0.509
BHVI	Up	11.5	12.3	4.44	0.476	Rip	7.6	8.8	4.93	0.416	0.670
CONW	Up	8.4	9.2	3.83	0.488	Rip	5.8	8.2	4.76	0.658	1.003
BAWW	Up	17.2	18.7	4.77	0.543	Up	12.9	17.4	6.05	0.777	0.645
RBGR	Up	13.3	15.7	4.52	0.646	Low	7.1	12.2	5.6	0.893	0.757
MOWA	Up	6.3	9	3.92	0.726	Rip	7.4	10.3	5.36	0.663	0.613
HOWR	Up	3.7	4.3	2.41	0.727	NA	NA	NA	NA	NA	0.793
BLPW	Up	1.4	3.7	2.41	1	Rip	4.8	5.5	3.59	0.618	NA
MYWA	Low	46.8	31.7	3.51	0.001	Low	46.6	28.4	5.76	0.012	0.510

AOU	Full Transect					Shoreline Forest & Upland Forest					SSI
	Max Group	Ind Val	Mean	StDev	p	Max Group	Ind Val	Mean	StDev	P	
WWCR	Low	20.1	5.1	3.03	0.005	NA	NA	NA	NA	NA	1.656
HETH	Low	40	23.1	4.87	0.009	Low	24.3	20.2	6.42	0.200	0.834
WEWP	Low	14	6.2	3.24	0.031	Low	19.9	7	3.89	0.030	0.723
RCKI	Low	35.4	25.6	4.57	0.044	Rip	24.3	20.7	6.12	0.21	1.038
RBNU	Low	16.2	10.8	4.25	0.099	Low	13.5	10.1	5.16	0.201	1.038
OCWA	Low	5.3	3.7	2.29	0.209	NA	NA	NA	NA	NA	1.148
WETA	Low	11	8.9	3.86	0.238	NA	NA	NA	NA	NA	1.632
SWTH	Low	30.1	29.5	4.08	0.35	Low	23.2	26.1	6.25	0.623	0.617
WIWR	Low	4.5	5	2.86	0.403	Rip	16.8	15.3	5.91	0.305	0.978
YBFL	Low	4	5.1	3.04	0.498	Up	2.4	6.4	3.96	1	1.981
YBSA	Low	6.5	7.6	3.58	0.537	Up	5.2	7	4.16	0.647	0.730

Figure A1.1 Comparison of SSI for landbirds and waterbirds counted during the study.



APPENDIX 2: SUPPLEMENTARY MATERIAL SUPPORTING THE CHARACTERIZATION OF BIRD ASSEMBLAGES AMONG BOREAL WETLAND CLASSES IN CHAPTER 3

Table A2.1 Table number of birds counted for each species in each wetland class during the study.

Common Name	Scientific Name	AOU Code	Wetland Class											Harvested	TOTAL
			Marsh	Thicket Swamp	Treed Poor Fen	Treed Rich Fen	Shrubby Rich Fen	Graminoid Rich Fen	Tamarack Swamp	Mixedwood Swamp	Conifer Swamp	Treed Bog			
Alder Flycatcher	<i>Empidonax alnorum</i>	ALFL	0	10	0	2	3	0	2	0	0	0	0	9	26
American Bittern	<i>Botaurus lentiginosus</i>	AMBI	0	0	0	0	1	0	0	0	0	0	0	0	1
American Crow	<i>Corvus brachyrhynchos</i>	AMCR	0	0	0	1	0	0	0	0	0	0	0	0	1
American Goldfinch	<i>Spinus tristis</i>	AMGO	0	1	0	0	0	0	0	0	0	0	0	6	7
American Redstart	<i>Setophaga ruticilla</i>	AMRE	1	0	0	0	0	0	0	4	0	0	5	10	
American Robin	<i>Turdus migratorius</i>	AMRO	0	0	0	0	0	0	1	1	2	0	2	6	
American White Pelican	<i>Pelecanus erythrorhynchos</i>	AWPE	0	0	0	0	1	0	0	0	0	0	0	1	
Barn Swallow	<i>Hirundo rustica</i>	BARS	0	1	0	0	0	0	0	0	0	0	0	1	
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH	0	0	0	0	0	0	0	1	0	0	0	1	
Belted Kingfisher	<i>Ceryle alcyon</i>	BEKI	1	0	0	0	1	0	0	0	0	0	0	2	
Blue-headed Vireo	<i>Vireo solitaries</i>	BHVI	1	0	0	3	0	0	1	0	2	0	0	7	

Common Name	Scientific Name	AOU Code	Wetland Class											Harvested	TOTAL
			Marsh	Thicket Swamp	Treed Poor Fen	Treed Rich Fen	Shrubby Rich Fen	Graminoid Rich Fen	Tamarack Swamp	Mixedwood Swamp	Conifer Swamp	Treed Bog			
Blackburnian Warbler	<i>Setophaga fusca</i>	BLBW	0	0	0	0	1	0	0	1	0	0	0	2	
Blue Jay	<i>Cyanocitta cristata</i>	BLJA	0	1	0	0	0	0	0	0	0	1	0	2	
Boreal Chickadee	<i>Poecile hudsonicus</i>	BOCH	0	0	0	1	0	0	0	0	2	0	0	3	
Bonaparte's Gull	<i>Larus Philadelphia</i>	BOGU	1	0	0	0	0	0	0	0	0	0	0	1	
Brown Creeper	<i>Certhia Americana</i>	BRCR	0	1	0	0	0	0	1	3	2	0	0	7	
Black-throated Green Warbler	<i>Setophaga virens</i>	BTNW	0	0	0	0	0	0	0	3	0	0	0	3	
Canada Warbler	<i>Cardellina Canadensis</i>	CAWA	0	0	0	0	0	0	0	2	0	0	0	2	
Clay-colored Sparrow	<i>Spizella pallida</i>	CCSP	0	2	0	0	0	0	0	0	0	0	0	2	
Chipping Sparrow	<i>Spizella passerine</i>	CHSP	0	3	2	8	0	0	4	0	11	3	0	31	
Cape May Warbler	<i>Setophaga tigrina</i>	CMWA	0	0	0	0	0	0	0	1	0	0	0	1	
Connecticut Warbler	<i>Oporornis agilis</i>	CONW	0	0	0	1	0	0	0	0	1	0	0	2	
Common Tern	<i>Sterna hirundo</i>	COTE	0	0	1	0	0	0	0	0	0	0	0	1	
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE	5	27	7	4	15	0	5	0	1	0	14	78	
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	CSWA	0	0	0	0	0	1	0	2	0	0	15	18	
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU	0	0	8	14	2	0	2	0	10	4	0	40	
Great Blue Heron	<i>Ardea Herodias</i>	GBHE	1	0	0	0	2	0	0	0	0	0	0	3	

Common Name	Scientific Name	AOU Code	Wetland Class											Harvested	TOTAL
			Marsh	Thicket Swamp	Treed Poor Fen	Treed Rich Fen	Shrubby Rich Fen	Graminoid Rich Fen	Tamarack Swamp	Mixedwood Swamp	Conifer Swamp	Treed Bog			
Golden-crowned Kinglet	<i>Regulus satrapa</i>	GCKI	0	0	0	0	0	0	0	0	0	4	0	0	4
Gray Jay	<i>Perisoreus Canadensis</i>	GRAJ	0	1	2	7	3	0	1	0	7	2	0	23	
Hermit Thrush	<i>Catharus guttatus</i>	HETH	0	0	0	5	0	0	3	0	4	2	0	14	
House Wren	<i>Troglodytes aedon</i>	HOWR	1	0	0	0	0	0	0	0	0	0	3	4	
Le Conte's Sparrow	<i>Ammodramus leconteii</i>	LCSP	8	3	0	0	15	2	0	0	0	0	0	28	
Least Flycatcher	<i>Empidonax minimus</i>	LEFL	1	0	0	0	0	0	0	0	0	0	0	1	
Lincoln's Sparrow	<i>Melospiza lincolni</i>	LISP	3	7	3	5	1	0	0	0	0	0	3	22	
Magnolia Warbler	<i>Setophaga magnolia</i>	MAWA	0	1	0	0	0	1	0	1	0	0	4	7	
Mourning Dove	<i>Zenaida macroura</i>	MODO	0	1	0	1	0	0	0	0	0	0	0	2	
Mourning Warbler	<i>Geothlypis Philadelphia</i>	MOWA	1	1	0	0	0	1	0	2	0	0	8	13	
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	NAWA	0	2	8	9	0	0	6	3	6	5	0	39	
Northern Flicker	<i>Colaptes auratus</i>	NOFL	0	1	0	0	0	0	0	0	0	0	0	1	
Northern Waterthrush	<i>Parkesia noveboracensis</i>	NOWA	2	6	0	1	0	0	3	1	2	0	1	16	
Nelson's Sparrow	<i>Ammodramus nelson</i>	NSTS	1	0	0	0	5	0	0	0	0	0	0	6	
Orange-crowned Warbler	<i>Oreothlypis celata</i>	OCWA	0	1	2	2	0	0	0	0	0	0	0	5	
Ovenbird	<i>Seiurus aurocapilla</i>	OVEN	0	0	0	0	0	0	0	9	0	1	0	10	

Common Name	Scientific Name	AOU Code	Wetland Class											Harvested	TOTAL
			Marsh	Thicket Swamp	Treed Poor Fen	Treed Rich Fen	Shrubby Rich Fen	Graminoid Rich Fen	Tamarack Swamp	Mixedwood Swamp	Conifer Swamp	Treed Bog			
Palm Warbler	<i>Setophaga palmarum</i>	WPWA	0	0	10	10	2	0	0	0	1	2	0	25	
Pied-billed Grebe	<i>Podilymbus podiceps</i>	PBGR	1	0	0	0	0	0	0	0	0	0	0	1	
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	RBGR	0	0	0	0	0	0	0	0	0	0	1	1	
Ring-billed Gull	<i>Larus delawarensis</i>	RBGU	4	0	0	0	0	0	0	0	0	0	0	4	
Ruby-crowned Kinglet	<i>Regulus calendula</i>	RCKI	0	1	3	11	1	0	4	1	17	5	0	43	
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	1	0	0	0	0	0	1	7	0	0	4	13	
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	9	1	0	0	0	3	0	0	0	0	0	13	
Sedge Wren	<i>Cistothorus platensis</i>	SEWR	5	8	0	0	12	0	0	0	0	0	0	25	
Sora	<i>Porzana Carolina</i>	SORA	8	0	0	0	1	2	0	0	0	0	0	11	
Solitary Sandpiper	<i>Tringa solitaria</i>	SOSA	0	0	0	0	0	0	0	0	0	1	0	1	
Song Sparrow	<i>Melospiza melodia</i>	SOSP	2	5	0	0	0	0	0	0	0	0	6	13	
Spotted Sandpiper	<i>Actitis macularia</i>	SPSA	0	0	0	2	1	0	0	0	0	0	0	3	
Swamp Sparrow	<i>Melospiza georgiana</i>	SWSP	18	21	2	1	28	4	2	0	2	0	0	78	
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH	0	0	0	0	0	0	1	2	3	1	0	7	
Tennessee Warbler	<i>Oreothlypis peregrine</i>	TEWA	0	1	0	1	0	0	3	0	1	0	0	6	
Three-toed Woodpecker	<i>Picoides dorsalis</i>	TTWO	0	0	0	1	0	0	0	0	0	0	0	1	

Common Name	Scientific Name	AOU Code	Wetland Class											Harvested	TOTAL
			Marsh	Thicket Swamp	Treed Poor Fen	Treed Rich Fen	Shrubby Rich Fen	Graminoid Rich Fen	Tamarack Swamp	Mixedwood Swamp	Conifer Swamp	Treed Bog			
Virginia Rail	<i>Rallus limicola</i>	VIRA	1	0	0	0	1	1	0	0	0	0	0	0	3
Wilson's Warbler	<i>Cardellina pusilla</i>	WIWA	0	2	1	0	0	0	0	0	0	0	0	0	3
Winter Wren	<i>Troglodytes troglodytes</i>	WIWR	0	0	0	0	0	0	1	0	2	0	0	0	3
White-throated Sparrow	<i>Zonotrichia albicollis</i>	WTSP	1	12	6	1	4	0	1	7	2	0	29	63	
White-winged Crossbill	<i>Loxia leucoptera</i>	WWCR	0	0	0	0	0	0	1	2	3	1	0	7	
Wilson's Snipe	<i>Gallinago gallinago</i>	COSN	0	2	0	2	3	1	0	0	0	0	0	8	
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	YBFL	0	0	6	10	0	0	1	1	4	1	0	23	
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	YBSA	0	0	0	0	0	0	0	0	0	0	2	2	
Yellow Rail	<i>Coturnicops noveboracensis</i>	YERA	0	0	0	0	1	0	0	0	0	0	0	1	
Yellow-rumped Warbler	<i>Setophaga coronate</i>	MYWA	0	0	2	5	1	0	1	0	16	1	1	27	
Yellow Warbler	<i>Setophaga petechial</i>	YWAR	1	0	0	0	1	0	0	0	0	0	1	3	
Total Birds Detected			78	123	63	108	106	16	45	54	105	30	114	842	

APPENDIX 3: SUPPLEMENTARY MATERIALS USED FOR CALCULATING FUNCTIONAL DIVERSITY AND RESILIENCE INDICES IN CHAPTER 4

Table A3.1 Species list and functional traits and weight classes assigned to each species. The full list was used to assess potential FD relative to actual FD and so that Weight class clusters could be used for other components of the thesis.

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
AGWT	American Green-winged Teal	<i>Anas crecca</i>	GRANI	DABBL	WATER	1	25
AMAV	American Avocet	<i>Recurvirostra americana</i>	OMNI	FORAG	WAMAR	1	NA
AMBI	American Bittern	<i>Botaurus lentiginosus</i>	CARNI/INSEC	AMBUS	WATER	1	1
AMCO	American Coot	<i>Fulica Americana</i>	OMNI	DABBL/DIVER	WATER	1	NA
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	OMNI	FORAG	GRND	1	1
AMKE	American Kestrel	<i>Falco sparverius</i>	CARNI/INSEC	HAWKR	AIRIA/GRND	1	NA
BDOW	Barred Owl	<i>Strix varia</i>	CARNI	HAWKR	GRND	1	NA
BUFF	Bufflehead	<i>Bucephala albeola</i>	INSEC	GLEAN	WATBOT	1	84
BWHA	Broad-winged Hawk	<i>Buteo platypterus</i>	CARNI	HAWKR	GRND	1	NA
BWTE	Blue-winged Teal	<i>Anas discors</i>	OMNI	DABBL	WATER	1	75

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
COHA	Cooper's Hawk	<i>Accipiter cooperii</i>	CARNI	HAWKR	AIRIA/GRND	1	NA
EAGR	Eared Grebe	<i>Podiceps nigricollis</i>	INSEC	DIVER	WATER	1	1
FRGU	Franklin's Gull	<i>Larus pipixcan</i>	INSEC	HAWKR	AIRIA	1	NA
HOGR	Horned Grebe	<i>Podiceps auritus</i>	INSEC/PISC	DIVER	WATER	1	3
HOME	Hooded Merganser	<i>Lophodytes cucullatus</i>	INSEC/PISC	DIVER/GLEAN	WATBOT/WATER	1	NA
MAGO	Marbled Godwit	<i>Limosa fedoa</i>	INSEC/MOLL	PROBE	WASHO	1	NA
NOHA	Northern Harrier	<i>Circus cyaneus</i>	CARNI	HAWKR	GRND	1	NA
NSHO	Northern Shoveler	<i>Anas clypeata</i>	OMNI	STRAN	WATER	1	30
PBGR	Pied-billed Grebe	<i>Podilymbus podiceps</i>	CRUST/INSEC	DIVER	WATER	1	7
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	INSEC	EXCVA	BARK	1	3
RBGU	Ring-billed Gull	<i>Larus delawarensis</i>	INSEC/PISC	GLEAN/HAWKR	GRND/WATER	1	NA
	Red-breasted						
RBME	Merganser	<i>Mergus serrator</i>	PISC	DIVER	WATER	1	NA
RNDU	Ring-necked Duck	<i>Aythya collaris</i>	OMNI	FORAG	WATBOT	1	140
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>	OMNI	FORAG	WATBOT	1	2
RUGR	Ruffed Grouse	<i>Bonasa umbellus</i>	OMNI	FORAG	GRND	1	12
WODU	Wood Duck	<i>Aix sponsa</i>	GRANI	GLEAN	GRND/WASUR	1	NA

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
AMWI	American Wigeon	<i>Anas Americana</i>	HERB	DABBL/GRAZE	GRND/WATER	2	65
BAGO	Barrow's Goldeneye	<i>Bucephala islandica</i>	OMNI	FORAG	WATBOT	2	NA
CAGU	California Gull	<i>Larus californicus</i>	CARNI/INSEC	GLEAN/HAWKR	GRND	2	NA
CANV	Canvasback	<i>Aythya valisineria</i>	OMNI	FORAG	WATBOT	2	NA
COGO	Common Goldeneye	<i>Bucephala clangula</i>	OMNI	FORAG	WATBOT	2	32
COME	Common Merganser	<i>Mergus merganser</i>	PISC	DIVER	WATER	2	NA
CORA	Common Raven	<i>Corvus corax</i>	OMNI	SCAV	GRND	2	NA
	Double-crested						
DCCO	Cormorant	<i>Phalacrocorax auritus</i>	PISC	DIVER	WATER	2	NA
GADW	Gadwall	<i>Anas strepera</i>	HERB	DABBL	WATER	2	NA
GBHE	Great Blue Heron	<i>Ardea Herodias</i>	PISC	AMBUS	WATER	2	2
GGOW	Great Gray Owl	<i>Strix nebulosa</i>	CARNI	HAWKR	GRND	2	NA
GHOW	Great Horned Owl	<i>Bubo virginianus</i>	CARNI	HAWKR	GRND	2	NA
GRSC	Greater Scaup	<i>Aythya marila</i>	OMNI	GLEAN	WATBOT	2	NA
LESC	Lesser Scaup	<i>Aythya affinis</i>	CRUST	GLEAN	WATBOT	2	19
MALL	Mallard	<i>Anas platyrhynchos</i>	GRANI	DABBL/GLEAN	GRND/WATER	2	46
NOGO	Northern Goshawk	<i>Accipiter gentilis</i>	CARNI	HAWKR	AIRIA/GRND	2	NA

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
NOPI	Northern Pintail	<i>Anas acuta</i>	GRANI	DABBL	WATER	2	1
OSPR	Osprey	<i>Pandion haliaetus</i>	PISC	FPLUN	WATER	2	NA
REDH	Redhead	<i>Aythya Americana</i>	HERB	DIVER	WATER	2	2
RNGR	Red-necked Grebe	<i>Podiceps grisegena</i>	CRUST/PISC	DIVER	WATER	2	56
RTHA	Red-tailed Hawk	<i>Buteo jamaicensis</i>	CARNI	HAWKR	GRND	2	2
WEGR	Western Grebe	<i>Aechmophorus occidentalis</i>	PISC	DIVER	WATER	2	NA
	American White						
AWPE	Pelican	<i>Pelecanus erythrorhynchos</i>	PISC	GLEAN	WASUR	3	NA
BAEA	Bald Eagle	<i>Haliaeetus leucocephalus</i>	CARNI/PISC	FPLUN/SCAV	GRND/WATER	3	NA
CAGO	Canada Goose	<i>Branta Canadensis</i>	HERB	DABBL/GRAZE	GRND/WATER	3	20
COLO	Common Loon	<i>Gavia immer</i>	PISC	DIVER	WATER	3	74
SACR	Sandhill Crane	<i>Grus Canadensis</i>	OMNI	FORAG	GRND/WAMAR	3	4
TRUS	Trumpeter Swan	<i>Cygnus buccinators</i>	Herbivore	DABBL	WATER	3	NA
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	INSEC	SALLY	AIRIA	4	53
AMGO	American Goldfinch	<i>Carduelis tristis</i>	OMNI	FORAG	GRND/LCNSH	4	1
	Black-and-white						
BAWW	Warbler	<i>Mniotilta varia</i>	INSEC	GLEAN	BARK	4	74

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
BBWA	Bay-breasted Warbler	<i>Dendroica castanea</i>	INSEC	GLEAN	UPCAN	4	NA
	Black-capped						
BCCH	Chickadee	<i>Poecile atricapillus</i>	INSEC	GLEAN	LCNSH	4	40
BLBW	Blackburnian Warbler	<i>Dendroica fusca</i>	INSEC	GLEAN	UPCAN	4	3
BLPW	Blackpoll Warbler	<i>Dendroica striata</i>	INSEC	GLEAN	UPCAN	4	NA
BOCH	Boreal Chickadee	<i>Poecile hudsonicus</i>	INSEC	GLEAN	LCNSH	4	NA
CAWA	Canada Warbler	<i>Wilsonia canadensis</i>	INSEC	GLEAN	LCNSH	4	7
CCSP	Clay-colored Sparrow	<i>Spizella pallida</i>	OMNI	FORAG	GRND/LCNSH	4	15
CHSP	Chipping Sparrow	<i>Spizella passerine</i>	OMNI	FORAG	GRND	4	215
CMWA	Cape May Warbler	<i>Dendroica tigrina</i>	INSEC	GLEAN	UPCAN	4	3
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	INSEC	GLEAN	LCNSH	4	31
	Chestnut-sided						
CSWA	Warbler	<i>Dendroica pensylvanica</i>	INSEC	GLEAN	LCNSH	4	NA
HOWR	House Wren	<i>Troglodytes aedon</i>	INSEC	GLEAN	LCNSH	4	4
LCSP	Le Conte's Sparrow	<i>Ammodramus leconteii</i>	OMNI	FORAG	GRND	4	48
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	INSEC	GLEAN/SALLY	AIRIA/UPCAN	4	101
MAWR	Marsh Wren	<i>Cistothorus palustris</i>	INSEC	GLEAN	WAMAR	4	1

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
MOWA	Mourning Warbler	<i>Oporornis philadelphia</i>	INSEC	GLEAN	GRND	4	21
	Yellow-rumped						
MYWA	Warbler	<i>Dendroica coronata</i>	INSEC	GLEAN	LCNSH	4	262
PHVI	Philadelphia Vireo	<i>Vireo philadelphicus</i>	INSEC	GLEAN	UPCAN	4	57
PISI	Pine Siskin	<i>Carduelis pinus</i>	OMNI	FORAG	GRND/UPCAN	4	1
RBNU	Red-breasted Nuthatch	<i>Sitta Canadensis</i>	INSEC	GLEAN	BARK	4	28
WEWP	Western Wood-Pewee	<i>Contopus sordidulus</i>	INSEC	SALLY	AIRIA	4	16
WIFL	Willow Flycatcher	<i>Empidonax traillii</i>	INSEC	SALLY	AIRIA	4	NA
WPWA	Palm Warbler	<i>Dendroica palmarum</i>	INSEC	GLEAN	GRND	4	51
	Yellow-bellied						
YBFL	Flycatcher	<i>Empidonax flaviventris</i>	INSEC	SALLY	AIRIA	4	6
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	INSEC	GLEAN	LCNSH	4	102
AMRE	American Redstart	<i>Setophaga ruticilla</i>	INSEC	GLEAN/SALLY	AIRIA/LCNSH	5	40
BRCR	Brown Creeper	<i>Certhia Americana</i>	INSEC	GLEAN	BARK	5	2
	Black-throated Green						
BTNW	Warbler	<i>Dendroica virens</i>	INSEC	GLEAN	UPCAN	5	1
GCKI	Golden-crowned	<i>Regulus satrapa</i>	INSEC	GLEAN	LCNSH	5	NA

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
	Kinglet						
	Golden-winged						
GWWA	Warbler	<i>Vermivora chrysoptera</i>	INSEC	GLEAN	UPCAN	5	NA
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>	INSEC	GLEAN	LCNSH	5	16
NAWA	Nashville Warbler	<i>Vermivora ruficapilla</i>	INSEC	GLEAN	LCNSH	5	NA
	Orange-crowned						
OCWA	Warbler	<i>Vermivora celata</i>	INSEC	GLEAN	LCNSH	5	4
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	INSEC	GLEAN	LCNSH/UPCAN	5	174
	Ruby-throated						
RTHU	Hummingbird	<i>Archilochus colubris</i>	OMNI	HOVGL	FLORA	5	NA
SEWR	Sedge Wren	<i>Cistothorus platensis</i>	INSEC	GLEAN	GRND	5	NA
TEWA	Tennessee Warbler	<i>Vermivora peregrina</i>	INSEC	GLEAN	UPCAN	5	368
WIWA	Wilson's Warbler	<i>Wilsonia pusilla</i>	INSEC	GLEAN/SALLY	AIRIA/LCNSH	5	5
WIWR	Winter Wren	<i>Troglodytes troglodytes</i>	INSEC	GLEAN	GRND	5	9
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	OMNI	FORAG	UPCAN	6	2
BBCU	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	INSEC	GLEAN	LCNSH	6	NA
BHCO	Brown-headed	<i>Molothrus ater</i>	OMNI	FORAG	GRND	6	5

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
	Cowbird						
BOBO	Bobolink	<i>Dolichonyx oryzivorus</i>	OMNI	FORAG	GRND	6	20
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>	FRUGI/INSEC	GLEAN/SALLY	AIRIA/UPCAN	6	31
CLSW	Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	INSEC	SCREE	AIRIA	6	NA
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	FRUGI/INSEC	GLEAN	BARK/LCNSH	6	2
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	INSEC	SALLY	AIRIA	6	NA
	Great Crested						
GCFL	Flycatcher	<i>Myiarchus crinitus</i>	INSEC	SALLY	AIRIA	6	NA
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	OMNI	FORAG	GRND/LCNSH	6	NA
HETH	Hermit Thrush	<i>Catharus guttatus</i>	INSEC	GLEAN	GRND	6	123
HOSP	House Sparrow	<i>Passer domesticus</i>	GRANI	GLEAN	GRND	6	NA
MOBL	Mountain Bluebird	<i>Sialia currucoides</i>	INSEC	GLEAN	GRND	6	NA
OSFL	Olive-sided Flycatcher	<i>Contopus cooperi</i>	INSEC	SALLY	AIRIA	6	16
PIGR	Pine Grosbeak	<i>Pinicola enucleator</i>	OMNI	FORAG	UPCAN	6	NA
PUFI	Purple Finch	<i>Carpodacus purpureus</i>	FRUGI/GRANI	GLEAN	UPCAN	6	NA
	Rose-breasted						
RBGR	Grosbeak	<i>Pheucticus ludovicianus</i>	OMNI	FORAG	UPCAN	6	52

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
RECR	Red Crossbill	<i>Loxia curvirostra</i>	OMNI	FORAG	UPCAN	6	NA
RNPH	Red-necked Phalarope	<i>Phalaropus lobatus</i>	INSEC	GLEAN	WASUR	6	NA
SOSA	Solitary Sandpiper	<i>Tringa solitaria</i>	CRUST/INSEC	GLEAN	WATER	6	33
SPSA	Spotted Sandpiper	<i>Actitis macularia</i>	INSEC	GLEAN	WASHO	6	5
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	OMNI	FORAG	GRND/LCNSH	6	216
	Three-toed						
TTWO	Woodpecker	<i>Picoides tridactylus</i>	INSEC	SCALE	BARK	6	3
VEER	Veery	<i>Catharus fuscescens</i>	OMNI	FORAG	GRND/LCNSH	6	NA
VESP	Vesper Sparrow	<i>Pooecetes gramineus</i>	OMNI	FORAG	GRND	6	NA
WEKI	Western Kingbird	<i>Tyrannus verticalis</i>	INSEC	SALLY	AIRIA	6	NA
WETA	Western Tanager	<i>Piranga ludoviciana</i>	INSEC/OMNI	FORAG/SALLY	AIRIA/UPCAN	6	20
WIPH	Wilson's Phalarope	<i>Phalaropus tricolor</i>	INSEC	GLEAN	WASHO	6	NA
	White-throated						
WTSP	Sparrow	<i>Zonotrichia albicollis</i>	OMNI	FORAG	GRND	6	168
	White-winged						
WWCR	Crossbill	<i>Loxia leucoptera</i>	OMNI	FORAG	UPCAN	6	6
YBSA	Yellow-bellied	<i>Sphyrapicus varius</i>	OMNI	EXCVA	BARK	6	15

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
	Sapsucker						
BARS	Barn Swallow	<i>Hirundo rustica</i>	INSEC	SCREE	AIRIA	7	NA
BHVI	Blue-headed Vireo	<i>Vireo solitaries</i>	INSEC	GLEAN	LCNSH	7	33
CONW	Connecticut Warbler	<i>Oporornis agilis</i>	INSEC	GLEAN	GRND	7	24
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	FRUGI/INSEC	GLEAN/SALLY	AIRIA/LCNSH	7	2
EAWP	Eastern Wood-Pewee	<i>Contopus virens</i>	INSEC	SALLY	AIRIA	7	NA
LISP	Lincoln's Sparrow	<i>Melospiza lincolnii</i>	OMNI	FORAG	GRND	7	94
NOWA	Northern Waterthrush	<i>Seiurus noveboracensis</i>	INSEC	GLEAN	WATER	7	2
	Nelson's Sharp-tailed						
NSTS	Sparrow	<i>Ammodramus nelsoni</i>	OMNI	FORAG	GRND	7	NA
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	INSEC/MOLL	GLEAN	GRND	7	295
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	INSEC	GLEAN	UPCAN	7	307
SAPH	Say's Phoebe	<i>Sayornis saya</i>	INSEC	SALLY	AIRIA	7	NA
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	OMNI	FORAG	GRND	7	NA
SCJU	Dark-eyed Junco	<i>Junco hyemalis</i>	OMNI	FORAG	GRND	7	87
SOSP	Song Sparrow	<i>Melospiza melodia</i>	OMNI	FORAG	GRND/LCNSH	7	11
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	OMNI	FORAG	GRND	7	56

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
TRES	Tree Swallow	<i>Tachycineta bicolor</i>	INSEC	SCREE	AIRIA	7	NA
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	INSEC	GLEAN	UPCAN	7	4
	White-breasted						
WBNU	Nuthatch	<i>Sitta carolinensis</i>	INSEC	GLEAN	BARK	7	1
YTVI	Yellow-throated Vireo	<i>Vireo flavifrons</i>	INSEC	GLEAN	UPCAN	7	NA
AMRO	American Robin	<i>Turdus migratorius</i>	OMNI/VERMI	FORAG/GLEAN	GRND/LCNSH	8	14
	Black-backed						
BBWO	Woodpecker	<i>Picoides arcticus</i>	INSEC	SCALE	BARK	8	NA
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	OMNI	FORAG	GRND/UPCAN	8	NA
BLTE	Black Tern	<i>Chlidonias niger</i>	INSEC	GLEAN/HAWKR	AIRIA/WATER	8	32
BOOW	Boreal Owl	<i>Aegolius funereus</i>	CARNI	HAWKR	GRND	8	NA
BRBL	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	OMNI	FORAG	GRND	8	9
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	OMNI	FORAG	GRND/LCNSH	8	NA
CONI	Common Nighthawk	<i>Chordeiles minor</i>	INSEC	SCREE	AIRIA	8	4
EUST	European Starling	<i>Sturnus vulgaris</i>	OMNI	FORAG	GRND	8	NA
EVGR	Evening Grosbeak	<i>Coccothraustes vespertinus</i>	OMNI	FORAG	UPCAN	8	NA
GRAJ	Gray Jay	<i>Perisoreus canadensis</i>	OMNI	FORAG	GRND/UPCAN	8	2

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
HAWO	Hairy Woodpecker	<i>Picooides villosus</i>	FRUGI/INSEC	GLEAN	BARK/LCNSH	8	NA
KILL	Killdeer	<i>Charadrius vociferus</i>	INSEC	GLEAN	GRND	8	16
LEYE	Lesser Yellowlegs	<i>Tringa flavipes</i>	CRUST/INSEC	GLEAN	WASUR	8	72
	Northern Saw-whet						
NSWO	Owl	<i>Aegolius acadicus</i>	CARNI	HAWKR	GRND	8	NA
PESA	Pectoral Sandpiper	<i>Calidris melanotos</i>	INSEC	GLEAN	GRND	8	NA
PUMA	Purple Martin	<i>Progne subis</i>	INSEC	SCREE	AIRIA	8	NA
RUBL	Rusty Blackbird	<i>Euphagus carolinus</i>	INSEC	GLEAN	GRND	8	4
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	OMNI	FORAG	GRND	8	37
SORA	Sora	<i>Porzana Carolina</i>	OMNI	FORAG	WAMAR	8	15
SSHA	Sharp-shinned Hawk	<i>Accipiter striatus</i>	CARNI	HAWKR	AIRIA/GRND	8	NA
VIRA	Virginia Rail	<i>Rallus limicola</i>	INSEC/MOLL	PROBE	WAMAR	8	NA
WEME	Western Meadowlark	<i>Sturnella neglecta</i>	INSEC	GLEAN	GRND	8	NA
		<i>Coturnicops</i>					
YERA	Yellow Rail	<i>noveboracensis</i>	OMNI	FORAG	WAMAR	8	NA
	Yellow-headed	<i>Xanthocephalus</i>					
YHBL	Blackbird	<i>xanthocephalus</i>	OMNI	FORAG	GRND	8	NA

AOU CODE	Common Name	Scientific Name	Prey^a	Style^b	Substrate^c	Aggregation	N
BBMA	Black-billed Magpie	<i>Pica pica</i>	INSEC	GLEAN	GRND	9	NA
BEKI	Belted Kingfisher	<i>Ceryle alcyon</i>	CRUST/PISC	PLUNG	WATER	9	2
BOGU	Bonaparte's Gull	<i>Larus Philadelphis</i>	INSEC	GLEAN/HAWKR	AIRIA/GRND	9	25
COGR	Common Grackle	<i>Quiscalus quiscula</i>	OMNI	FORAG	GRND	9	2
COSN	Common Snipe	<i>Gallinago gallinago</i>	OMNI/VERMI	FORAG/PROBE	GRND/MUDDY	9	39
COTE	Common Tern	<i>Sterna hirundo</i>	PISC	PLUNG	WATER	9	8
GRYE	Greater Yellowlegs	<i>Tringa melanoleuca</i>	INSEC/PISC	AMBUS/GLEAN	WASUR/WATER	9	5
MERL	Merlin	<i>Falco columbarius</i>	CARNI	HAWKR	AIRIA	9	NA
MODO	Mourning Dove	<i>Zenaidura macroura</i>	GRANI	GLEAN	GRND	9	NA
NOFL	Northern Flicker	<i>Colaptes auratus</i>	INSEC	GLEAN	GRND	9	12
WILL	Willet	<i>Catoptrophorus semipalmatus</i>	CRUST/INSEC	PROBE	WASHO	9	NA

- a. Food type abbreviations: INSEC = insectivore, GRANI = granivore, OMNI=omnivore, CRUST=crustacivore, MOLLU= molluscivore, PISC = piscivore, VERMI = vermivore, FRUGI = frugivore
- b. Foraging style abbreviations: GLEAN = Gleaner, AMBUS =Ambusher, HAWKR=Hawker, SALLY = Sallier, PROBE = Prober, STRAN = Strangler, PLUNG = Plunger, FPLUNG = Foot plunger, FORAG = Forager, SCAV = Scavenger, DABB = dabbler, DIVE = diver, GRAZE = grazer, SCALE = scaler, EXCAV = excavator
- c. Foraging substrate abbreviations: GRND=Ground, LCNSH=Lower canopy and shrub, UPCAN=Upper canopy, AIRIA=Aerial, BARK=bark, FLOR=floral, WATER=Water, WASUR=water surface, WABOT=water bottom, WASHOR=water shore, WASUR=water surface, WAMAR=water/marsh

Table A3.2 Complete results for trait-based Indicator Species Analysis

Functional Trait	Type	IV	MEAN	STD	p	Trait Type
CRUST	Riparian	48.3	17	4.8	0.0004	Food
OMNI	Riparian	47.7	36.1	1.87	0.0002	Food
VERMI	Riparian	33	16.4	4.53	0.0074	Food
AIRIA	Riparian	45.3	30.5	4.79	0.0126	Habit
FORAG	Riparian	48	36.1	1.88	0.0002	Habit
HAWKR	Riparian	21.8	10.7	4.52	0.0312	Habit
PROBE	Riparian	24.3	13.6	4.46	0.0292	Habit
SALLY	Riparian	38.5	29.4	4.77	0.0476	Habit
GRND	Riparian	41.1	35.6	1.41	0.0014	Location
MUDDY	Riparian	24.3	13.6	4.46	0.0292	Location
WASUR	Riparian	33.3	13.1	4.46	0.0036	Location
WATER	Riparian	35.6	14.4	4.95	0.0046	Location
PISCI	Riparian	5.7	4.8	2.82	0.3131	Food
PLUNG	Riparian	4.6	4.3	2.58	0.4147	Habit
WAMAR	Riparian	4.6	4.3	2.4	0.4191	Location
WASHO	Riparian	4.6	4.4	2.53	0.4201	Location
AMBUS	Riparian	4.6	4.4	2.53	0.4771	Habit
FRUGI	Riparian	5.1	6.6	3.41	0.6079	Food
CARNI	Riparian	3.4	3.8	2.23	0.6695	Food
SCALE	Riparian	3.4	3.8	2.37	0.6697	Habit
SCREE	Riparian	2.3	3.2	2.15	0.833	Habit
MOLLU	Upland	56.1	29.9	3.99	0.0002	Food
UPCAN	Upland	40.5	35.6	1.59	0.006	Location
GLEAN	Upland	37.9	35.2	1.2	0.0232	Habit
INSEC	Upland	36.8	35.2	1.23	0.0912	Food
BARK	Upland	22.4	24.6	4.46	0.6415	Location
LCNSH	Lowland Edge	36.2	35.7	1.46	0.2991	Location
EXCVA	Lowland Edge	5.8	8.2	3.8	0.7305	Habit

APPENDIX 4: INDIVIDUAL SPECIES RESULTS FROM TITAN IN RESPONSE TO A GRADIENT IN TOTAL DISTURBANCE BY AGRICULTURE IN NEAB AND DMMB STUDY AREAS

Table A4.1 Species codes, English names scientific names, indicator scores (IndVal), change points (env.cp) and percentiles (5 %, 50 %, 95 %), for declining (-) and increasing taxa (+) in response to increasing agricultural conversion at the landscape and 500 m scales in NEAB. Note that all significant indicator species are shown but that only species that met significance criteria for P (≤ 0.05), purity (≥ 0.95), and reliability (≥ 0.95 , and ≥ 0.9 for at 0.05, and 0.01, respectively) are included in the figures. P is the probability of getting an equal or larger IndVal using 250 random permutations. IndVal is the unstandardized indicator score, z is the standardized indicator value and N = frequency of species occurrence among blocks/wetlands sampled.

Species Code	English Name	Scientific name	"+/-		5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
			"	env.cp										
NEAB Landscape														
BUFF	Bufflehead	<i>Bucephala albeola</i>	-	0.19	0.14	0.51	0.72	2.70	67.50	0.02	0.99	0.96	0.61	17
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	-	0.29	0.19	0.28	0.66	3.17	67.91	0.01	1.00	0.94	0.68	18
COLO	Common Loon	<i>Gavia immer</i>	-	0.51	0.22	0.54	0.72	3.83	68.28	0.00	0.99	0.95	0.75	16
CONW	Connecticut Warbler	<i>Oporornis agilis</i>	-	0.28	0.14	0.28	0.56	2.36	55.44	0.03	0.99	0.92	0.52	13
GRAJ	Gray Jay	<i>Perisoreus canadensis</i>	-	0.28	0.16	0.27	0.53	4.50	59.20	0.00	1.00	0.92	0.69	8

Species Code	English Name	Scientific name	"+/-											
			"	env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
GRYE	Greater Yellowlegs	<i>Tringa melanoleuca</i>	-	0.26	0.14	0.25	0.37	4.17	44.44	0.01	1.00	0.78	0.48	4
HETH	Hermit Thrush	<i>Catharus guttatus</i>	-	0.72	0.16	0.54	0.72	2.37	77.27	0.03	0.87	0.78	0.52	17
		<i>Ammodramus</i>												
LCSP	Le Conte's Sparrow	<i>leconteii</i>	-	0.23	0.14	0.26	0.60	3.18	68.48	0.01	0.94	0.88	0.59	17
LEYE	Lesser Yellowlegs	<i>Tringa flavipes</i>	-	0.16	0.14	0.19	0.70	5.53	81.65	0.00	0.86	0.78	0.61	10
	Yellow-rumped													
MYWA	Warbler	<i>Dendroica coronata</i>	-	0.19	0.14	0.46	0.70	2.06	59.11	0.02	0.89	0.70	0.33	23
NOFL	Northern Flicker	<i>Colaptes auratus</i>	-	0.29	0.14	0.28	0.57	3.42	52.51	0.02	0.91	0.82	0.51	8
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	-	0.51	0.28	0.51	0.70	5.58	81.66	0.00	1.00	1.00	0.97	16
	Rose-breasted	<i>Pheucticus</i>												
RBGR	Grosbeak	<i>ludovicianus</i>	-	0.46	0.19	0.51	0.70	3.96	66.82	0.00	0.98	0.96	0.84	16
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	-	0.53	0.16	0.54	0.72	3.65	65.49	0.01	0.96	0.85	0.64	17
RNDU	Ring-necked Duck	<i>Aythya collaris</i>	-	0.72	0.16	0.66	0.72	2.79	70.84	0.01	0.93	0.83	0.58	23
SACR	Sandhill Crane	<i>Grus canadensis</i>	-	0.46	0.26	0.36	0.53	2.32	35.71	0.02	0.89	0.51	0.22	5
SCJU	Dark-eyed Junco	<i>Junco hyemalis</i>	-	0.53	0.29	0.53	0.60	6.39	88.43	0.00	1.00	0.99	0.99	18
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	-	0.72	0.14	0.50	0.72	1.65	68.01	0.02	0.78	0.62	0.41	19
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	-	0.54	0.29	0.53	0.66	4.52	70.59	0.00	0.98	0.95	0.66	12

Species Code	English Name	Scientific name	"+/-											
			"	env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
TEWA	Tennessee Warbler	<i>Vermivora peregrina</i>	-	0.54	0.23	0.46	0.70	3.85	73.23	0.01	1.00	1.00	0.90	19
WETA	Western Tanager	<i>Piranga ludoviciana</i>	-	0.28	0.16	0.27	0.46	3.00	36.36	0.04	0.98	0.63	0.40	4
WPWA	Palm Warbler	<i>Dendroica palmarum</i>	-	0.51	0.14	0.36	0.66	2.29	49.36	0.03	0.96	0.78	0.45	10
	White-throated													
WTSP	Sparrow	<i>Zonotrichia albicollis</i>	-	0.66	0.16	0.56	0.72	2.08	60.26	0.04	0.82	0.67	0.34	25
AGWT	Green-winged Teal	<i>Anas crecca</i>	+	0.70	0.14	0.53	0.72	2.95	62.51	0.01	0.70	0.62	0.42	8
AMCO	American Coot	<i>Fulica americana</i>	+	0.29	0.25	0.29	0.53	4.93	79.90	0.00	1.00	0.99	0.95	16
AMRO	American Robin	<i>Turdus migratorius</i>	+	0.25	0.14	0.25	0.54	2.44	62.51	0.03	0.86	0.67	0.41	20
	Black-and-white													
BAWW	Warbler	<i>Mniotilta varia</i>	+	0.66	0.16	0.55	0.72	2.08	52.59	0.05	0.78	0.50	0.20	9
	Brown-headed													
BHCO	Cowbird	<i>Molothrus ater</i>	+	0.66	0.25	0.54	0.72	3.62	72.14	0.00	1.00	0.96	0.69	13
BWTE	Blue-winged Teal	<i>Anas discors</i>	+	0.54	0.16	0.36	0.60	2.50	63.41	0.02	0.94	0.79	0.50	20
KILL	Killdeer	<i>Charadrius vociferus</i>	+	0.70	0.16	0.66	0.72	3.72	77.91	0.00	0.84	0.76	0.42	13
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	+	0.29	0.14	0.28	0.60	1.85	58.92	0.04	0.89	0.70	0.34	19
MALL	Mallard	<i>Anas platyrhynchos</i>	+	0.14	0.14	0.14	0.60	3.62	76.20	0.01	0.96	0.87	0.63	22
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>	+	0.26	0.16	0.27	0.66	3.68	69.53	0.01	0.97	0.88	0.62	14

Species Code	English Name	Scientific name	"+/-		env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
			"												
			<i>Oporornis</i>												
MOWA	Mourning Warbler	<i>philadelphia</i>	+		0.70	0.14	0.66	0.72	3.70	66.00	0.02	0.80	0.67	0.42	6
NOPI	Northern Pintail	<i>Anas acuta</i>	+		0.70	0.28	0.66	0.72	4.67	69.60	0.01	0.94	0.75	0.44	5
NSHO	Northern Shoveler	<i>Anas clypeata</i>	+		0.54	0.28	0.53	0.66	6.95	87.45	0.00	1.00	0.99	0.98	11
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>	+		0.51	0.27	0.46	0.56	5.09	75.48	0.00	0.99	0.98	0.87	12
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	+		0.25	0.14	0.25	0.29	4.85	72.23	0.00	1.00	1.00	0.96	22
			<i>Passerculus</i>												
SAVS	Savannah Sparrow	<i>sandwichensis</i>	+		0.51	0.28	0.51	0.56	7.54	86.66	0.00	1.00	1.00	0.98	10
SORA	Sora	<i>Porzana carolina</i>	+		0.28	0.19	0.27	0.53	4.03	70.63	0.00	0.99	0.99	0.94	20
SOSP	Song Sparrow	<i>Melospiza melodia</i>	+		0.29	0.16	0.27	0.57	4.79	70.00	0.00	1.00	0.99	0.91	17
VESP	Vesper Sparrow	<i>Poocetes gramineus</i>	+		0.70	0.54	0.70	0.72	10.00	100.00	0.00	0.96	0.88	0.82	4
			<i>Xanthocephalus</i>												
YHBL	Yellow-headed Blackbird	<i>xanthocephalus</i>	+		0.56	0.29	0.56	0.72	4.38	53.23	0.00	0.99	0.89	0.70	5
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	+		0.25	0.14	0.25	0.36	5.90	79.73	0.00	1.00	1.00	0.97	20
NEAB-500m															
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	-		0.78	0.13	0.60	0.83	2.25	35.89	0.04	0.91	0.84	0.50	41
BOCH	Boreal Chickadee	<i>Poecile hudsonicus</i>	-		0.13	0.03	0.12	0.15	7.22	22.73	0.00	1.00	0.97	0.82	5

Species Code	English Name	Scientific name	"+/-											
			"	env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
BOGU	Bonaparte's Gull	<i>Larus philadelphia</i>	-	0.41	0.03	0.34	0.52	3.72	19.53	0.01	1.00	0.95	0.72	13
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	-	0.65	0.08	0.19	0.73	2.85	28.37	0.02	0.97	0.89	0.54	26
COLO	Common Loon	<i>Gavia immer</i>	-	0.11	0.06	0.12	0.30	8.48	57.83	0.00	1.00	1.00	1.00	29
CONW	Connecticut Warbler	<i>Oporornis agilis</i>	-	0.35	0.15	0.34	0.42	4.18	22.20	0.00	0.93	0.91	0.78	16
GRAJ	Gray Jay	<i>Perisoreus canadensis</i>	-	0.06	0.03	0.07	0.29	6.93	27.03	0.01	1.00	0.94	0.77	6
HETH	Hermit Thrush	<i>Catharus guttatus</i>	-	0.42	0.11	0.37	0.51	6.66	37.58	0.00	1.00	1.00	0.98	27
		<i>Ammodramus</i>												
LCSP	Le Conte's Sparrow	<i>leconteii</i>	-	0.21	0.12	0.27	0.91	3.64	31.04	0.01	0.81	0.76	0.61	29
LISP	Lincoln's Sparrow	<i>Melospiza lincolnii</i>	-	0.58	0.10	0.53	0.83	3.11	41.05	0.02	1.00	0.95	0.72	45
	Yellow-rumped													
MYWA	Warbler	<i>Dendroica coronata</i>	-	0.19	0.05	0.24	0.87	2.92	38.46	0.02	0.88	0.84	0.63	47
NOFL	Northern Flicker	<i>Colaptes auratus</i>	-	0.34	0.09	0.31	0.87	1.97	8.96	0.02	0.77	0.49	0.26	6
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	-	0.21	0.13	0.27	0.56	7.14	42.53	0.00	1.00	1.00	0.99	28
	Rose-breasted	<i>Pheucticus</i>												
RBGR	Grosbeak	<i>ludovicianus</i>	-	0.45	0.13	0.42	0.54	4.51	20.63	0.00	1.00	0.97	0.86	13
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	-	0.47	0.15	0.54	0.76	4.21	30.51	0.00	1.00	1.00	0.83	29
RNDU	Ring-necked Duck	<i>Aythya collaris</i>	-	0.10	0.07	0.35	0.64	3.92	50.11	0.00	1.00	0.99	0.87	42

Species Code	English Name	Scientific name	"+/-											
			"	env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
RNGR	Red-necked Grebe	<i>Podiceps grisegena</i>	-	0.64	0.36	0.62	0.73	5.17	45.77	0.00	0.97	0.97	0.91	40
SACR	Sandhill Crane	<i>Grus canadensis</i>	-	0.11	0.04	0.11	0.30	4.70	20.50	0.00	1.00	0.88	0.67	6
SCJU	Dark-eyed Junco	<i>Junco hyemalis</i>	-	0.34	0.17	0.31	0.47	7.28	40.20	0.00	1.00	1.00	1.00	31
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	-	0.10	0.06	0.24	0.64	2.82	35.42	0.03	0.95	0.90	0.66	29
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	-	0.30	0.13	0.31	0.47	5.87	27.44	0.00	0.97	0.97	0.95	17
TEWA	Tennessee Warbler	<i>Vermivora peregrina</i>	-	0.35	0.12	0.36	0.68	4.73	34.57	0.00	0.95	0.94	0.83	31
WPWA	Palm Warbler	<i>Dendroica palmarum</i>	-	0.03	0.03	0.20	0.38	4.11	33.22	0.03	0.99	0.92	0.79	11
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	-	0.34	0.03	0.34	0.69	5.38	52.71	0.00	0.99	0.99	0.89	63
	Yellow-bellied													
YBSA	Sapsucker	<i>Sphyrapicus varius</i>	-	0.05	0.03	0.06	0.87	4.32	27.88	0.02	0.86	0.63	0.40	9
AGWT	Green-winged Teal	<i>Anas crecca</i>	+	0.69	0.03	0.54	0.81	2.03	16.37	0.03	0.69	0.55	0.32	10
AMCO	American Coot	<i>Fulica americana</i>	+	0.15	0.12	0.30	0.56	4.90	43.49	0.01	1.00	1.00	0.96	39
AMCR	American Crow	<i>Corvus</i>	+	0.89	0.27	0.73	0.91	5.58	65.21	0.01	0.98	0.96	0.79	15
		<i>brachyrhynchos</i>												
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	+	0.47	0.22	0.50	0.73	4.38	16.97	0.01	1.00	0.94	0.67	9
BBMA	Black-billed Magpie	<i>Pica pica</i>	+	0.67	0.41	0.64	0.87	4.45	21.32	0.00	0.95	0.89	0.75	8

Species Code	English Name	Scientific name	"+/-											
			"	env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
	Brown-headed													
BHCO	Cowbird	<i>Molothrus ater</i>	+	0.14	0.14	0.34	0.83	3.78	25.00	0.00	1.00	1.00	0.79	19
BWTE	Blue-winged Teal	<i>Anas discors</i>	+	0.55	0.22	0.48	0.62	6.34	56.66	0.00	1.00	0.98	0.95	61
CCSP	Clay-colored Sparrow	<i>Spizella pallida</i>	+	0.55	0.12	0.56	0.79	3.80	42.57	0.00	0.99	0.97	0.74	44
EAGR	Eared Grebe	<i>Podiceps nigricollis</i>	+	0.60	0.52	0.62	0.83	4.62	12.00	0.02	0.96	0.74	0.52	3
GADW	Gadwall	<i>Anas strepera</i>	+	0.76	0.03	0.67	0.84	3.47	15.15	0.03	0.67	0.52	0.35	5
HOWR	House Wren	<i>Troglodytes aedon</i>	+	0.55	0.23	0.55	0.83	3.33	13.91	0.01	1.00	0.88	0.56	7
KILL	Killdeer	<i>Charadrius vociferus</i>	+	0.56	0.15	0.54	0.81	4.36	26.27	0.00	0.94	0.91	0.72	18
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	+	0.30	0.06	0.29	0.88	2.32	27.81	0.05	0.79	0.68	0.39	32
MALL	Mallard	<i>Anas platyrhynchos</i>	+	0.14	0.04	0.15	0.86	2.15	39.91	0.04	0.98	0.86	0.46	52
	<i>Oporornis</i>													
MOWA	Mourning Warbler	<i>philadelphia</i>	+	0.73	0.29	0.69	0.91	3.60	17.51	0.02	0.96	0.86	0.55	7
NOPI	Northern Pintail	<i>Anas acuta</i>	+	0.55	0.17	0.54	0.78	2.76	11.24	0.01	0.87	0.51	0.25	6
NSHO	Northern Shoveler	<i>Anas clypeata</i>	+	0.54	0.33	0.52	0.60	7.79	45.82	0.00	1.00	1.00	0.96	27
	Nelson's Sharp-tailed													
NSTS	Sparrow	<i>Ammodramus nelsoni</i>	+	0.30	0.21	0.31	0.57	2.24	8.77	0.05	0.91	0.43	0.18	5
PBGR	Pied-billed Grebe	<i>Podilymbus podiceps</i>	+	0.51	0.09	0.47	0.91	3.25	25.87	0.01	0.91	0.84	0.58	23

Species Code	English Name	<i>Scientific name</i>	"+/-											
			"	env.cp	5%	50%	95%	z	IndVal	p	Purity	rel05	rel01	N
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	+	0.35	0.14	0.38	0.56	1.61	8.59	0.04	0.80	0.48	0.23	6
REDH	Redhead	<i>Aythya americana</i>	+	0.55	0.17	0.52	0.65	5.91	33.02	0.00	0.99	0.98	0.90	21
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	+	0.13	0.11	0.16	0.88	2.06	35.88	0.04	0.73	0.58	0.33	42
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>	+	0.36	0.13	0.37	0.52	6.50	38.98	0.00	1.00	1.00	1.00	32
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	+	0.38	0.23	0.36	0.43	10.54	67.10	0.00	1.00	1.00	1.00	66
		<i>Passerculus</i>												
SAVS	Savannah Sparrow	<i>sandwichensis</i>	+	0.65	0.25	0.54	0.69	7.96	45.15	0.00	1.00	1.00	1.00	23
SORA	Sora	<i>Porzana carolina</i>	+	0.35	0.07	0.33	0.47	4.64	52.68	0.00	1.00	1.00	0.91	70
SOSA	Solitary Sandpiper	<i>Tringa solitaria</i>	+	0.89	0.21	0.88	0.91	3.84	42.99	0.04	0.88	0.65	0.40	8
SOSP	Song Sparrow	<i>Melospiza melodia</i>	+	0.69	0.21	0.56	0.81	9.35	67.42	0.00	1.00	1.00	1.00	42
VESP	Vesper Sparrow	<i>Poocetes gramineus</i>	+	0.76	0.42	0.67	0.81	10.38	45.70	0.00	1.00	1.00	0.99	13
		<i>Xanthocephalus</i>												
YHBL	Yellow-headed Blackbird	<i>xanthocephalus</i>	+	0.45	0.42	0.49	0.67	5.88	18.92	0.00	1.00	0.99	0.89	7
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	+	0.30	0.10	0.29	0.57	4.72	42.96	0.00	1.00	0.98	0.86	44

Table A4.2 Species codes, English names scientific names, indicator scores (IndVal), change points (env.cp) and percentiles(5 %, 50 %, 95 %), for declining (-) and increasing taxa (+) in response to increasing agricultural conversion at the landscape and 500m scales in DMMB. Note that all significant indicator species are shown but that only species that met significance criteria for $P (\leq 0.05)$, purity (≥ 0.95), and reliability (≥ 0.95 , and ≥ 0.9 for at 0.05, and 0.01, respectively) are included in the figures. P is the probability of getting an equal or larger IndVal using 250 random permutations. IndVal is the unstandardized indicator score, z is the standardized indicator value and N= frequency of species occurrence among blocks/wetlands sampled.

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
DMMB Landscape														
<i>Pelecanus</i>														
AWPE	American White Pelican	<i>erythrorhynchos</i>	-	0.01	0.01	0.01	0.69	3.37	53.32	0.02	0.86	0.71	0.39	4
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	-	0.56	0.01	0.31	0.67	4.22	69.23	0.01	1	0.98	0.83	9
BLBW	Blackburnian Warbler	<i>Dendroica fusca</i>	-	0.21	0.01	0.21	0.56	5.2	71.79	0	0.99	0.98	0.85	8
BOGU	Bonaparte's Gull	<i>Larus philadelphia</i>	-	0.08	0.01	0.14	0.69	0.92	24.36	0.03	0.58	0.35	0.17	3
BRCR	Brown Creeper	<i>Certhia americana</i>	-	0.03	0.01	0.03	0.21	5.18	66.67	0.01	1	0.88	0.64	4
Black-throated Green														
BTNW	Warbler	<i>Dendroica virens</i>	-	0.08	0.01	0.03	0.31	4.26	57.14	0.02	1	0.86	0.55	4

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
CAWA	Canada Warbler	<i>Wilsonia canadensis</i>	-	0.01	0.01	0.02	0.31	5.25	74.33	0	0.95	0.83	0.61	5
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	-	0.4	0.08	0.45	0.67	4.76	75.93	0	1	0.98	0.84	13
COLO	Common Loon	<i>Gavia immer</i>	-	0.31	0.08	0.31	0.6	5.09	79.6	0	1	1	0.99	15
		<i>Perisoreus</i>												
GRAJ	Gray Jay	<i>canadensis</i>	-	0.14	0.01	0.14	0.4	5.83	75	0	1	0.98	0.83	6
LISP	Lincoln's Sparrow	<i>Melospiza lincolnii</i>	-	0.03	0.01	0.14	0.67	2.24	52.94	0.05	0.89	0.67	0.36	8
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>	-	0.01	0.01	0.01	0.4	4.58	71.34	0.01	1	0.75	0.56	4
		<i>Oporornis</i>												
MOWA	Mourning Warbler	<i>philadelphia</i>	-	0.4	0.01	0.21	0.56	5.45	77.24	0	1	0.98	0.91	10
MYWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>	-	0.14	0.01	0.21	0.56	5.25	86.44	0	1	1	0.96	12
		<i>Vermivora</i>												
NAWA	Nashville Warbler	<i>ruficapilla</i>	-	0.4	0.01	0.21	0.57	4.36	68.28	0	0.98	0.97	0.83	9
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	-	0.03	0.01	0.21	0.64	2.96	71.81	0.01	0.98	0.92	0.61	15
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	-	0.08	0.01	0.08	0.41	6.15	88.89	0	0.96	0.95	0.89	9
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	-	0.14	0.01	0.14	0.4	7.09	87.5	0	1	1	0.94	7

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	-	0.31	0.03	0.31	0.5	8.32	100	0	1	1	1	10
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	-	0.68	0.01	0.69	0.69	2.5	66.27	0.04	0.89	0.77	0.39	20
SCJU	Dark-eyed Junco	<i>Junco hyemalis</i>	-	0.03	0.01	0.03	0.69	3.5	59.75	0	0.87	0.73	0.45	6
RNDU	Ring-necked Duck	<i>Aythya collaris</i>	-	0.68	0.03	0.67	0.69	2.81	66.19	0.03	0.75	0.57	0.28	20
		<i>Melospiza</i>												
SWSP	Swamp Sparrow	<i>georgiana</i>	-	0.5	0.01	0.36	0.68	3.07	63.73	0	1	0.93	0.65	20
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	-	0.14	0.01	0.03	0.64	5.37	77.95	0	0.94	0.94	0.91	9
		<i>Vermivora</i>												
TEWA	Tennessee Warbler	<i>peregrina</i>	-	0.03	0.01	0.14	0.57	2.4	41.28	0.05	0.98	0.55	0.23	4
TRES	Tree Swallow	<i>Tachycineta bicolor</i>	-	0.68	0.01	0.64	0.69	2.73	70.59	0.03	0.94	0.67	0.28	12
		<i>Troglodytes</i>												
WIWR	Winter Wren	<i>troglodytes</i>	-	0.03	0.01	0.08	0.57	4.77	74.51	0	0.95	0.92	0.75	7
		<i>Zonotrichia</i>												
WTSP	White-throated Sparrow	<i>albicollis</i>	-	0.6	0.31	0.6	0.69	5.42	82.82	0	1	1	0.99	16
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	+	0.4	0.01	0.4	0.68	2.42	61.65	0.02	0.97	0.83	0.49	19

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
AMCO	American Coot	<i>Fulica americana</i>	+	0.6	0.08	0.56	0.68	5.97	87	0	1	1	0.99	10
AMGO	American Goldfinch	<i>Carduelis tristis</i>	+	0.4	0.08	0.4	0.67	7.41	90	0	1	1	1	9
AMRO	American Robin	<i>Turdus migratorius</i>	+	0.64	0.31	0.64	0.69	2.67	64.03	0.02	0.95	0.9	0.56	19
BARS	Barn Swallow	<i>Hirundo rustica</i>	+	0.14	0.01	0.21	0.67	3.52	61.54	0.01	1	0.91	0.55	8
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	+	0.56	0.07	0.56	0.67	3.49	72.43	0.01	1	0.94	0.66	14
BLTE	Black Tern	<i>Chlidonias niger</i>	+	0.56	0.14	0.6	0.69	2.59	52.68	0.02	0.89	0.7	0.42	8
BUFF	Bufflehead	<i>Bucephala albeola</i>	+	0.21	0.01	0.14	0.69	2.99	67.89	0.02	0.98	0.89	0.65	16
BWTE	Blue-winged Teal	<i>Anas discors</i>	+	0.31	0.08	0.4	0.64	5.69	83.01	0	1	1	0.97	12
CCSP	Clay-colored Sparrow	<i>Spizella pallida</i>	+	0.21	0.03	0.21	0.56	7.43	100	0	1	1	1	12
COSN	Common Snipe	<i>Gallinago gallinago</i>	+	0.64	0.03	0.6	0.68	2.86	70.47	0.01	0.96	0.89	0.55	15
EUST	European Starling	<i>Sturnus vulgaris</i>	+	0.68	0.3	0.67	0.69	2.92	48.61	0.04	0.94	0.54	0.18	3
		<i>Dumetella</i>												
GRCA	Gray Catbird	<i>carolinensis</i>	+	0.6	0.4	0.6	0.68	8.05	100	0	1	0.99	0.99	7
HOWR	House Wren	<i>Troglodytes aedon</i>	+	0.5	0.03	0.5	0.64	5	77.95	0	0.99	0.97	0.89	10

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
<i>Charadrius</i>														
KILL	Killdeer	<i>vociferus</i>	+	0.4	0.03	0.4	0.69	3.07	53.58	0.02	0.98	0.83	0.43	7
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	+	0.14	0.01	0.4	0.68	4.13	69.23	0	0.99	0.97	0.78	9
LESC	Lesser Scaup	<i>Aythya affinis</i>	+	0.14	0.03	0.4	0.67	4.22	69.23	0.01	1	0.93	0.72	9
MALL	Mallard	<i>Anas platyrhynchos</i>	+	0.08	0.01	0.14	0.5	4.33	72.75	0	1	0.99	0.96	19
MAWR	Marsh Wren	<i>Cistothorus palustris</i>	+	0.64	0.5	0.67	0.69	5.15	66.67	0.01	0.99	0.94	0.78	4
MODO	Mourning Dove	<i>Zenaida macroura</i>	+	0.08	0.01	0.18	0.67	2.6	57.14	0.03	0.98	0.79	0.41	8
REDH	Redhead	<i>Aythya americana</i>	+	0.56	0.4	0.64	0.69	5.23	62.5	0	1	0.94	0.81	5
RNGR	Red-necked Grebe	<i>Podiceps grisegena</i>	+	0.21	0.01	0.21	0.5	4.52	74.26	0	1	1	1	19
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>	+	0.6	0.21	0.6	0.68	5.46	80.7	0	1	1	0.91	8
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	+	0.4	0.01	0.31	0.6	3.47	63.7	0	1	1	0.92	20
<i>Passerculus</i>														
SAVS	Savannah Sparrow	<i>sandwichensis</i>	+	0.4	0.08	0.5	0.67	6.38	80	0	1	1	0.97	8
SORA	Sora	<i>Porzana carolina</i>	+	0.4	0.03	0.4	0.6	4.8	74.84	0	1	1	0.99	18

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
SOSP	Song Sparrow	<i>Melospiza melodia</i>	+	0.08	0.01	0.08	0.31	4.98	79.81	0	1	1	0.99	17
WEWP	Western Wood-Pewee	<i>Contopus sordidulus</i>	+	0.69	0.4	0.67	0.69	5.34	90	0.02	0.96	0.88	0.62	5
		<i>Xanthocephalus</i>												
YHBL	Yellow-headed Blackbird	<i>xanthocephalus</i>	+	0.6	0.4	0.64	0.69	5.37	71.43	0	1	0.95	0.79	5
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	+	0.08	0.01	0.31	0.67	3.95	75.75	0	1	1	0.92	15

DMMB 500 m

AMRE	American Redstart	<i>Setophaga ruticilla</i>	-	0.68	0.01	0.59	0.77	2.94	26.8	0.02	0.95	0.84	0.53	17
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	-	0.01	0	0.01	0.32	6.85	34.8	0	1	0.94	0.81	5
BLBW	Blackburnian Warbler	<i>Dendroica fusca</i>	-	0.43	0	0.01	0.5	5.01	21.43	0	1	0.95	0.84	6
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	-	0.7	0	0.46	0.77	3.5	24.84	0.01	1	0.95	0.79	13
CAWA	Canada Warbler	<i>Wilsonia canadensis</i>	-	0.02	0	0.02	0.92	5.08	19.63	0.01	0.72	0.62	0.44	4
		<i>Bombycilla</i>												
CEDW	Cedar Waxwing	<i>cedrorum</i>	-	0.24	0	0.17	0.8	6.63	35.51	0	0.94	0.93	0.85	9

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	-	0.28	0.01	0.2	0.59	8.05	51.78	0	1	0.99	0.99	15
COLO	Common Loon	<i>Gavia immer</i>	-	0.02	0.01	0.06	0.42	7.68	62.61	0	0.99	0.99	0.99	21
		<i>Oporornis</i>												
MOWA	Mourning Warbler	<i>philadelphia</i>	-	0.17	0.01	0.24	0.47	11.2	60.06	0	1	1	1	14
MYWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>	-	0.02	0	0.02	0.31	11.4	66.36	0	1	1	1	11
		<i>Vermivora</i>												
NAWA	Nashville Warbler	<i>ruficapilla</i>	-	0.32	0	0.15	0.35	9.44	36.36	0	1	1	1	8
		<i>Seiurus</i>												
NOWA	Northern Waterthrush	<i>noveboracensis</i>	-	0.59	0.01	0.69	0.92	2.24	18.68	0.02	0.76	0.62	0.37	12
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	-	0.17	0.02	0.32	0.56	9.85	64.02	0	1	1	1	23
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	-	0.01	0	0.04	0.46	9.95	72.84	0	1	1	1	12
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	-	0.72	0.01	0.69	0.89	2.78	38.99	0.03	0.81	0.71	0.44	33
RNDU	Ring-necked Duck	<i>Aythya collaris</i>	-	0.69	0.01	0.4	0.77	2.97	42.88	0.01	0.91	0.87	0.53	36
		<i>Melospiza</i>												
SWSP	Swamp Sparrow	<i>georgiana</i>	-	0.28	0	0.17	0.67	5.03	54.71	0	0.99	0.98	0.96	39

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	-	0.06	0	0.02	0.31	8.06	45.44	0	1	1	0.97	8
TRES	Tree Swallow	<i>Tachycineta bicolor</i>	-	0.06	0.01	0.29	0.76	4.19	32.13	0.01	0.98	0.9	0.76	13
		<i>Troglodytes</i>												
WIWR	Winter Wren	<i>troglodytes</i>	-	0.01	0	0.01	0.28	9.19	48.67	0	1	0.93	0.85	5
		<i>Zonotrichia</i>												
WTSP	White-throated Sparrow	<i>albicollis</i>	-	0.56	0.35	0.5	0.69	13.5	73.13	0	1	1	1	28
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	+	0.56	0.02	0.54	0.78	4.08	42.8	0.01	1	1	0.87	34
		<i>Botaurus</i>												
AMBI	American Bittern	<i>lentiginosus</i>	+	0.79	0.02	0.78	0.87	3.5	21.93	0.02	0.7	0.54	0.35	8
AMCO	American Coot	<i>Fulica americana</i>	+	0.68	0.4	0.64	0.78	8.03	50.55	0	1	1	1	22
		<i>Corvus</i>												
AMCR	American Crow	<i>brachyrhynchos</i>	+	0.89	0.72	0.88	0.92	6.81	89.23	0	1	0.98	0.9	15
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	+	0.81	0.67	0.79	0.87	5.54	21.87	0.01	0.94	0.76	0.58	4
BARS	Barn Swallow	<i>Hirundo rustica</i>	+	0.92	0.5	0.88	0.92	5.64	63.35	0.01	0.99	0.92	0.66	6
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	+	0.17	0.06	0.35	0.77	2.33	29.09	0.04	0.87	0.81	0.34	16

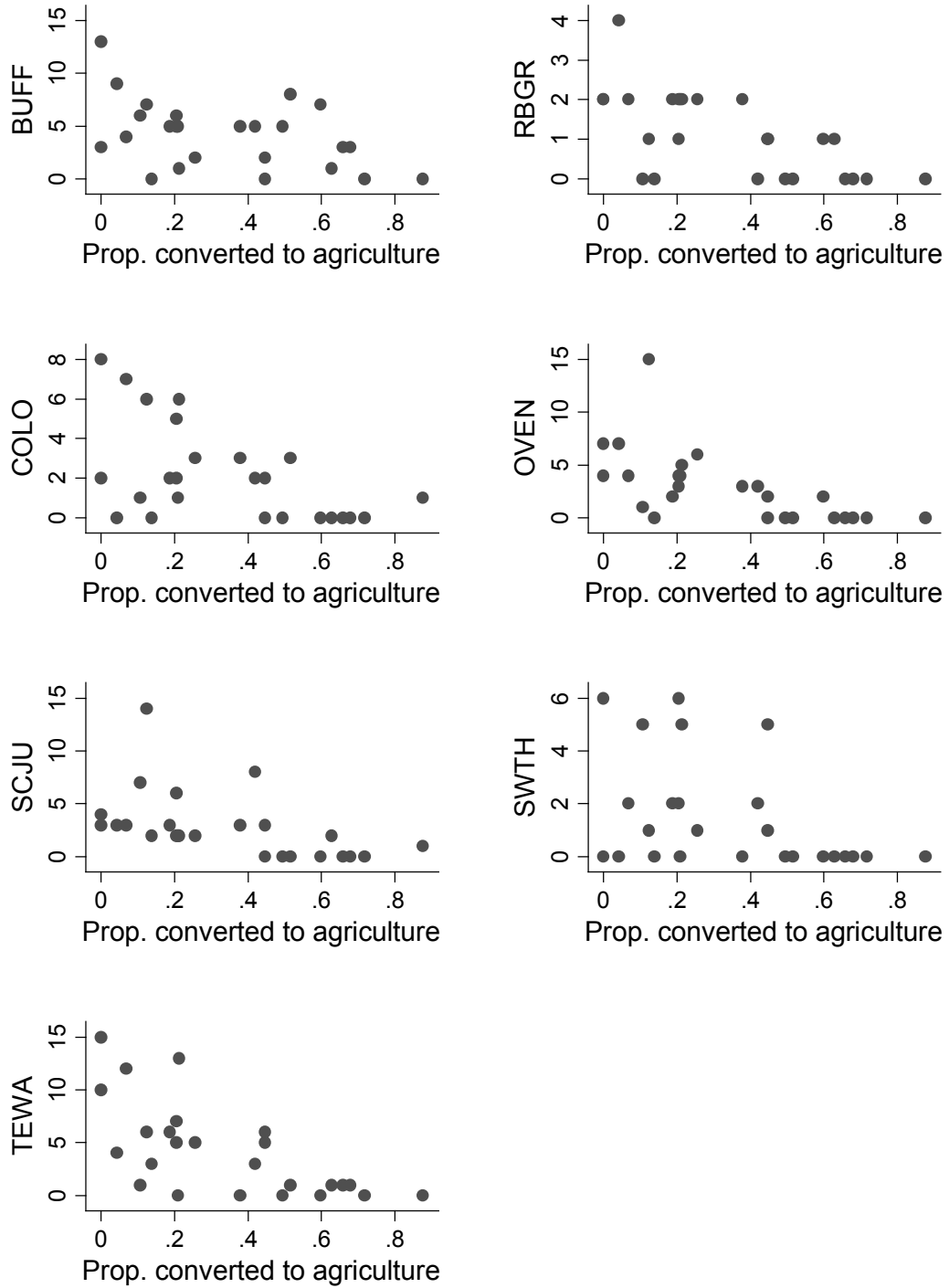
Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
BUFF	Bufflehead	<i>Bucephala albeola</i>	+	0.87	0.46	0.83	0.89	3.9	54.46	0.01	0.93	0.91	0.67	25
BWTE	Blue-winged Teal	<i>Anas discors</i>	+	0.38	0.31	0.67	0.85	4.93	40.71	0	1	1	0.96	24
CANV	Canvasback	<i>Aythya valisineria</i>	+	0.68	0.49	0.73	0.87	2.54	11.76	0.05	0.98	0.71	0.38	4
CCSP	Clay-colored Sparrow	<i>Spizella pallida</i>	+	0.43	0.33	0.54	0.78	10.2	65.73	0	1	1	1	31
COSN	Common Snipe	<i>Gallinago gallinago</i>	+	0.83	0	0.82	0.89	2.65	39.48	0.04	0.86	0.76	0.42	23
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	+	0.92	0	0.74	0.92	1.71	28.4	0.02	0.6	0.31	0.13	5
GADW	Gadwall	<i>Anas strepera</i>	+	0.88	0.43	0.85	0.89	4.02	30.56	0.03	0.93	0.71	0.32	5
		<i>Dumetella</i>												
GRCA	Gray Catbird	<i>carolinensis</i>	+	0.54	0.42	0.68	0.76	5.06	25.64	0	1	0.99	0.86	10
HOWR	House Wren	<i>Troglodytes aedon</i>	+	0.17	0.06	0.4	0.77	3.39	32.73	0.01	1	0.97	0.63	18
		<i>Charadrius</i>												
KILL	Killdeer	<i>vociferus</i>	+	0.5	0.29	0.62	0.83	2.38	17.56	0.04	0.97	0.71	0.37	9
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	+	0.33	0.06	0.38	0.88	2.51	23.82	0.03	0.96	0.89	0.46	14
LESC	Lesser Scaup	<i>Aythya affinis</i>	+	0.32	0.28	0.43	0.89	3.38	28	0.01	0.99	0.96	0.65	14

Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
MAWR	Marsh Wren	<i>Cistothorus palustris</i>	+	0.88	0.78	0.83	0.88	6.78	40.93	0.01	0.98	0.91	0.79	5
NOFL	Northern Flicker	<i>Colaptes auratus</i>	+	0.74	0.43	0.75	0.83	2.84	16.31	0.02	0.99	0.67	0.49	6
		<i>Podilymbus</i>												
PBGR	Pied-billed Grebe	<i>podiceps</i>	+	0.44	0.28	0.54	0.79	3.16	33.05	0.01	0.98	0.96	0.73	21
PHVI	Philadelphia Vireo	<i>Vireo philadelphicus</i>	+	0.78	0.29	0.77	0.87	2.92	21.11	0.04	0.93	0.73	0.39	8
REDH	Redhead	<i>Aythya americana</i>	+	0.74	0.69	0.76	0.88	5.44	23.08	0	1	0.96	0.79	6
RNGR	Red-necked Grebe	<i>Podiceps grisegena</i>	+	0.06	0.01	0.28	0.77	4.89	56.55	0	1	1	0.97	37
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>	+	0.44	0.32	0.46	0.76	5.62	41.86	0	1	1	1	18
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	+	0.42	0.28	0.42	0.6	7.68	68.94	0	0.99	0.99	0.99	52
		<i>Passerculus</i>												
SAVS	Savannah Sparrow	<i>sandwichensis</i>	+	0.43	0.32	0.48	0.87	5.06	33.89	0	1	0.99	0.9	17
SORA	Sora	<i>Porzana carolina</i>	+	0.17	0.02	0.31	0.83	4.09	54.27	0.01	1	0.99	0.91	38
SOSP	Song Sparrow	<i>Melospiza melodia</i>	+	0.24	0.02	0.28	0.7	8.49	76.66	0	1	1	1	53
		<i>Pooecetes</i>												
VESP	Vesper Sparrow	<i>gramineus</i>	+	0.67	0.46	0.7	0.77	4.92	20	0	1	0.93	0.69	7

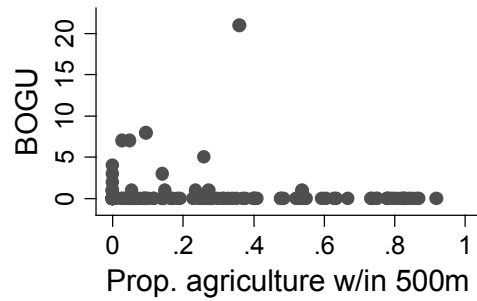
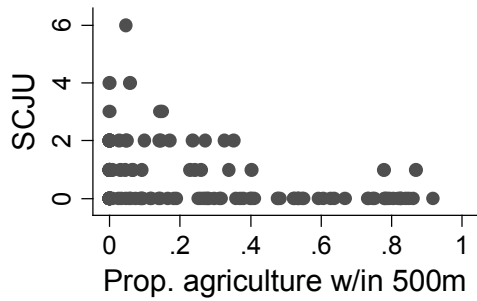
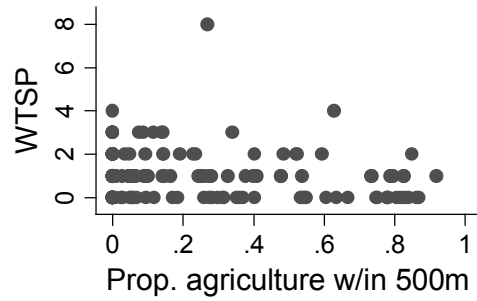
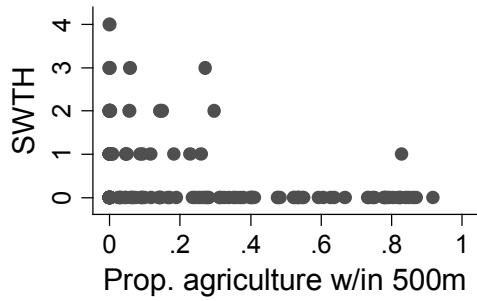
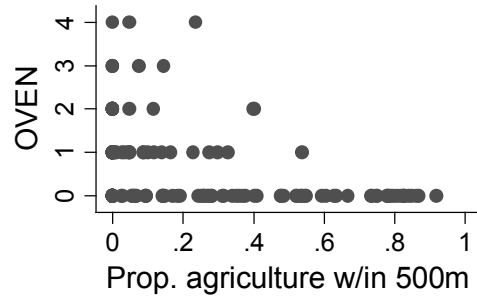
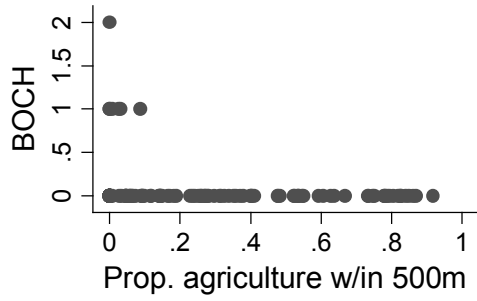
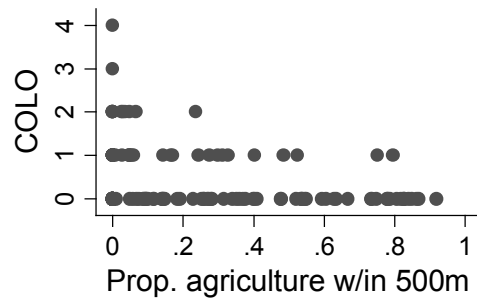
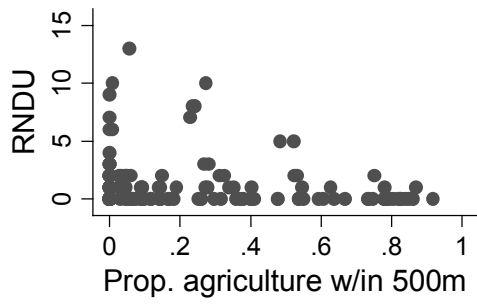
Species														
Code	English Name	Scientific name	"+/-"	env.cp	5%	50%	95%	z	IndVal	P	Purity	rel05	rel01	N
WEME	Western Meadowlark	<i>Sturnella neglecta</i>	+	0.44	0.4	0.73	0.92	2.42	13.95	0.02	0.96	0.63	0.38	6
		<i>Xanthocephalus</i>												
YHBL	Yellow-headed Blackbird	<i>xanthocephalus</i>	+	0.78	0.75	0.77	0.83	7.63	33.33	0	0.99	0.97	0.91	6
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	+	0.69	0.06	0.64	0.77	4.4	45.23	0	0.99	0.99	0.89	32

Figure A4.1 Scatter plots representing abundance of species that were significant negative (z-) indicators of a gradient of increasing agricultural conversion NEAB and DMMB at landscape and wetland scales.

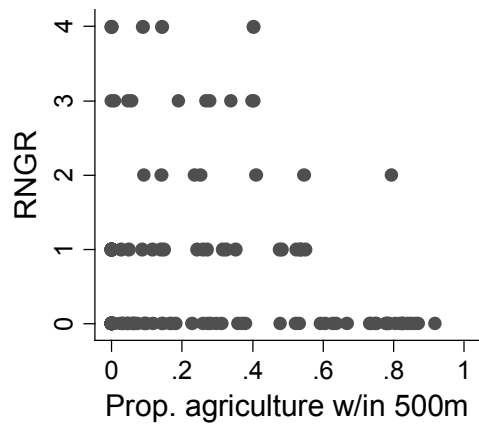
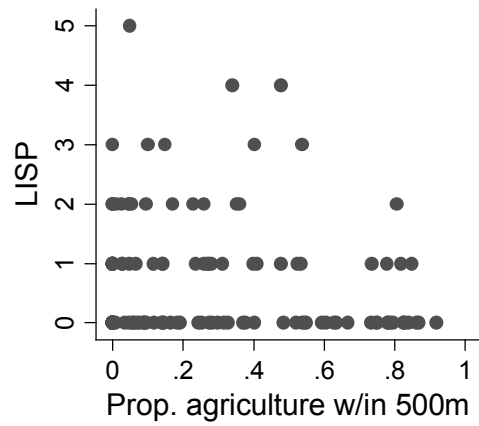
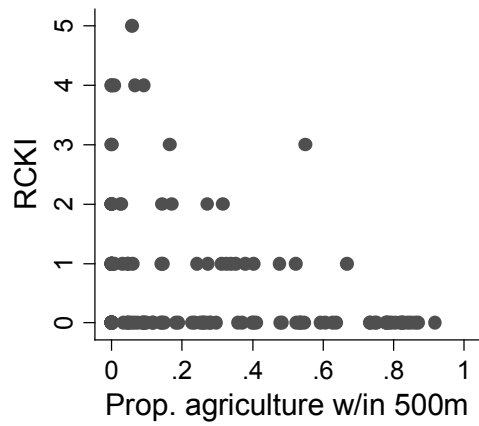
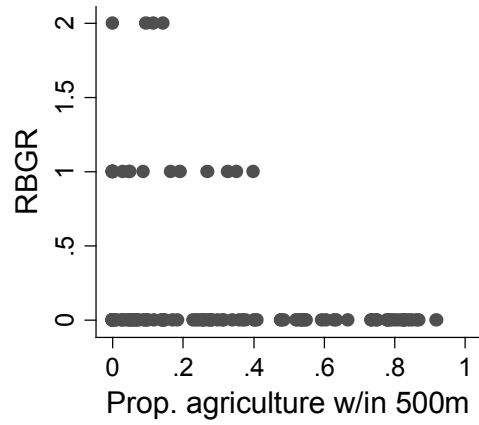
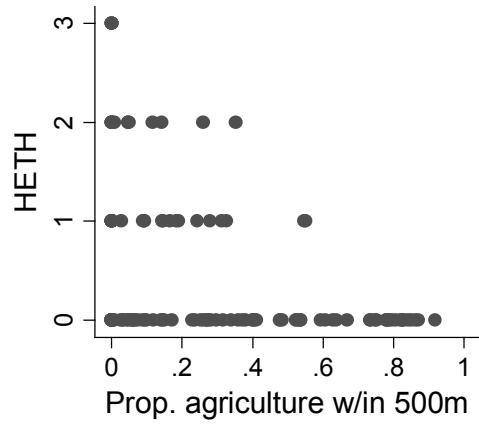
NEAB Landscape



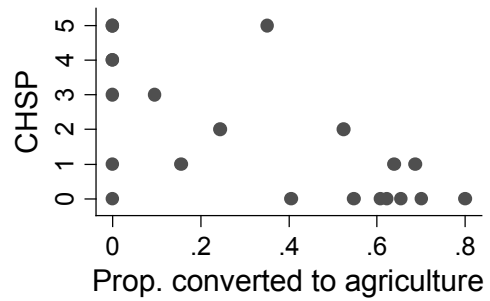
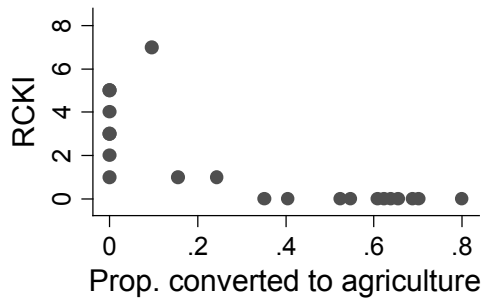
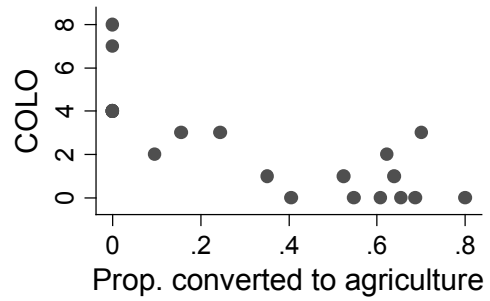
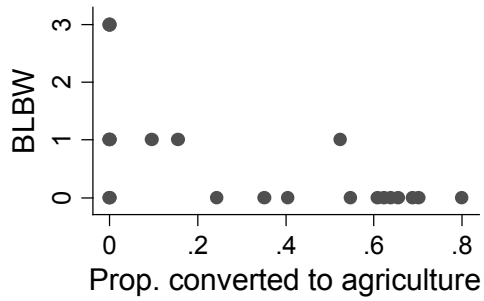
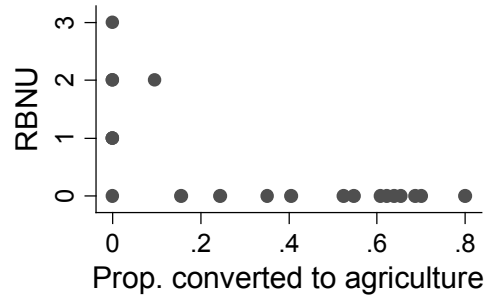
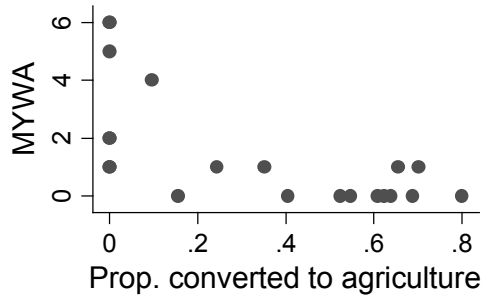
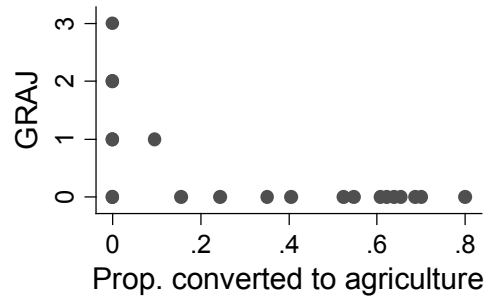
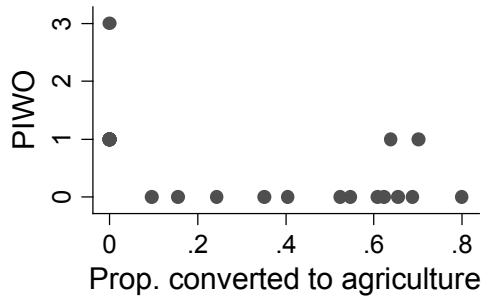
NEAB Wetland



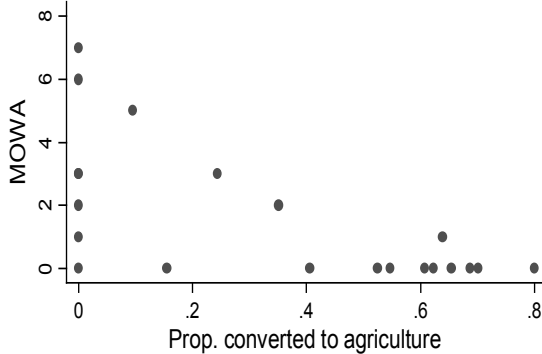
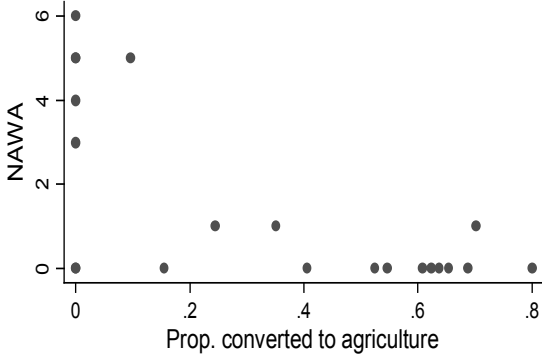
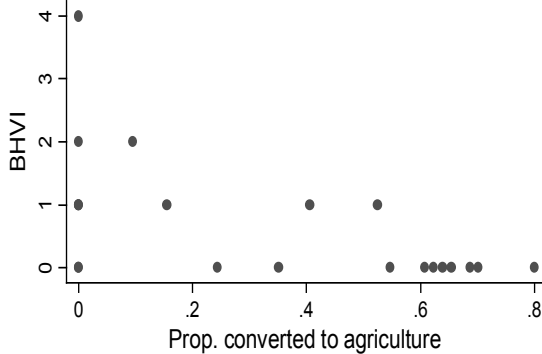
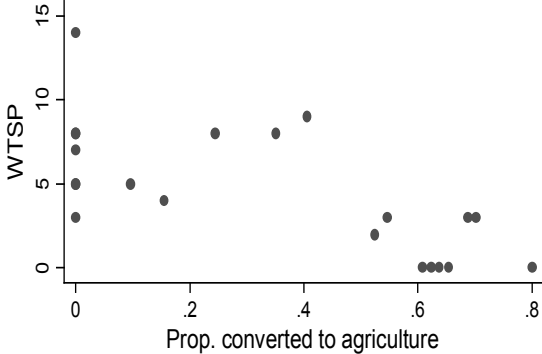
NEAB Wetland



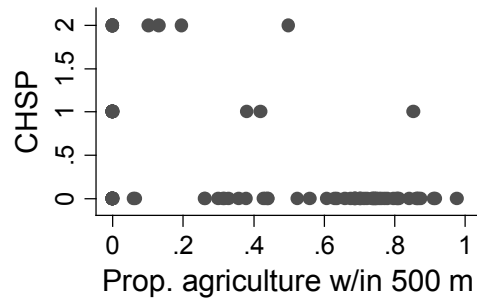
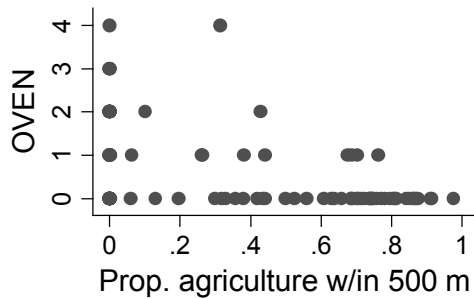
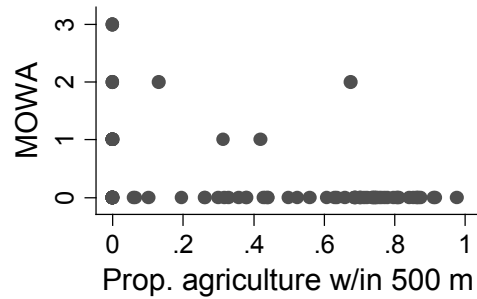
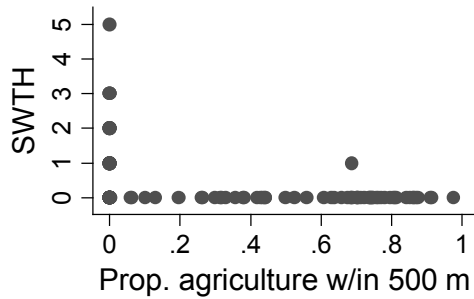
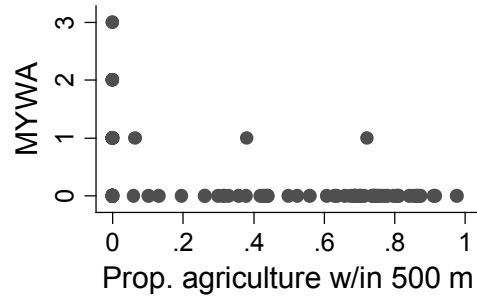
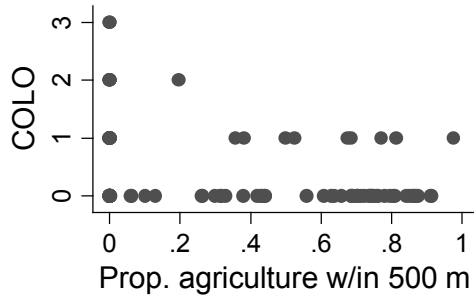
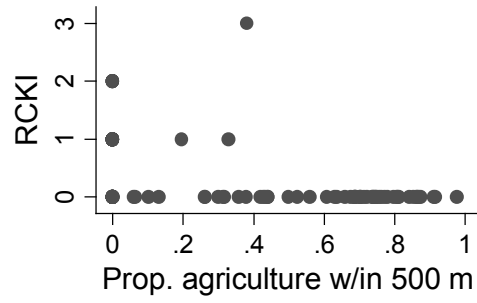
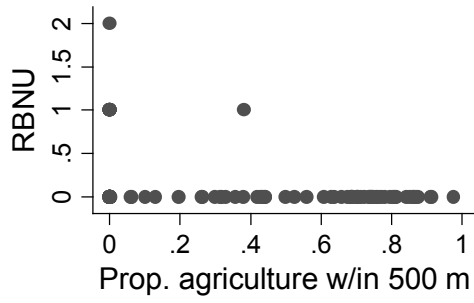
DMMB Landscape



DMMB Landscape



DMMB Wetland



DMMB Wetland

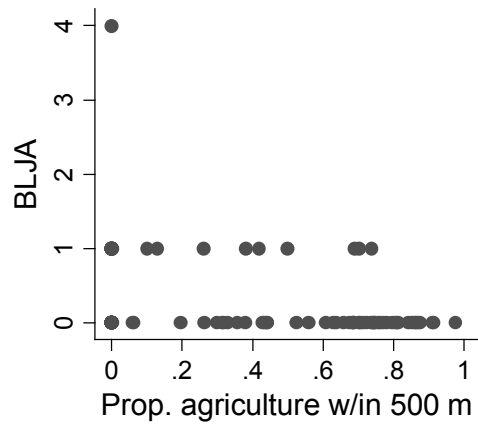
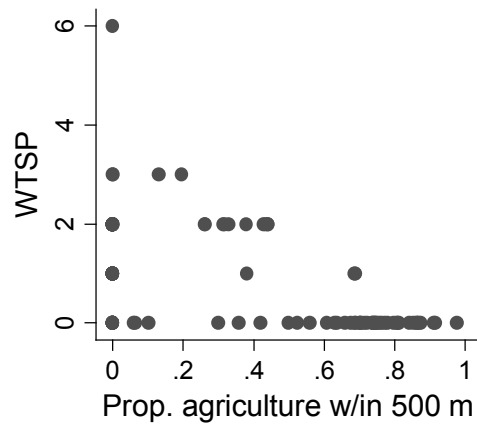
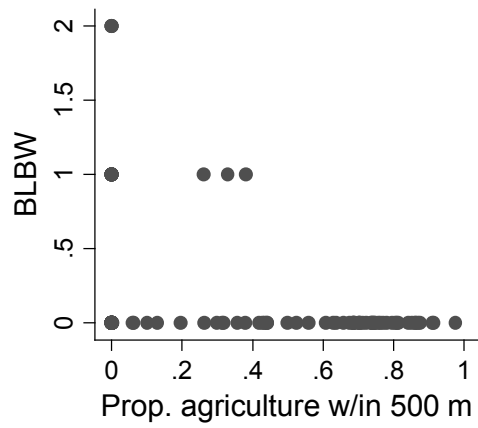
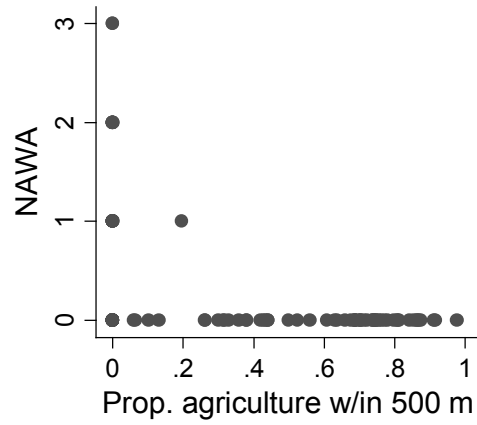
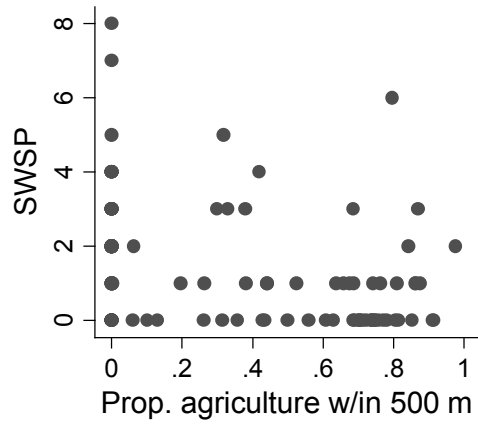
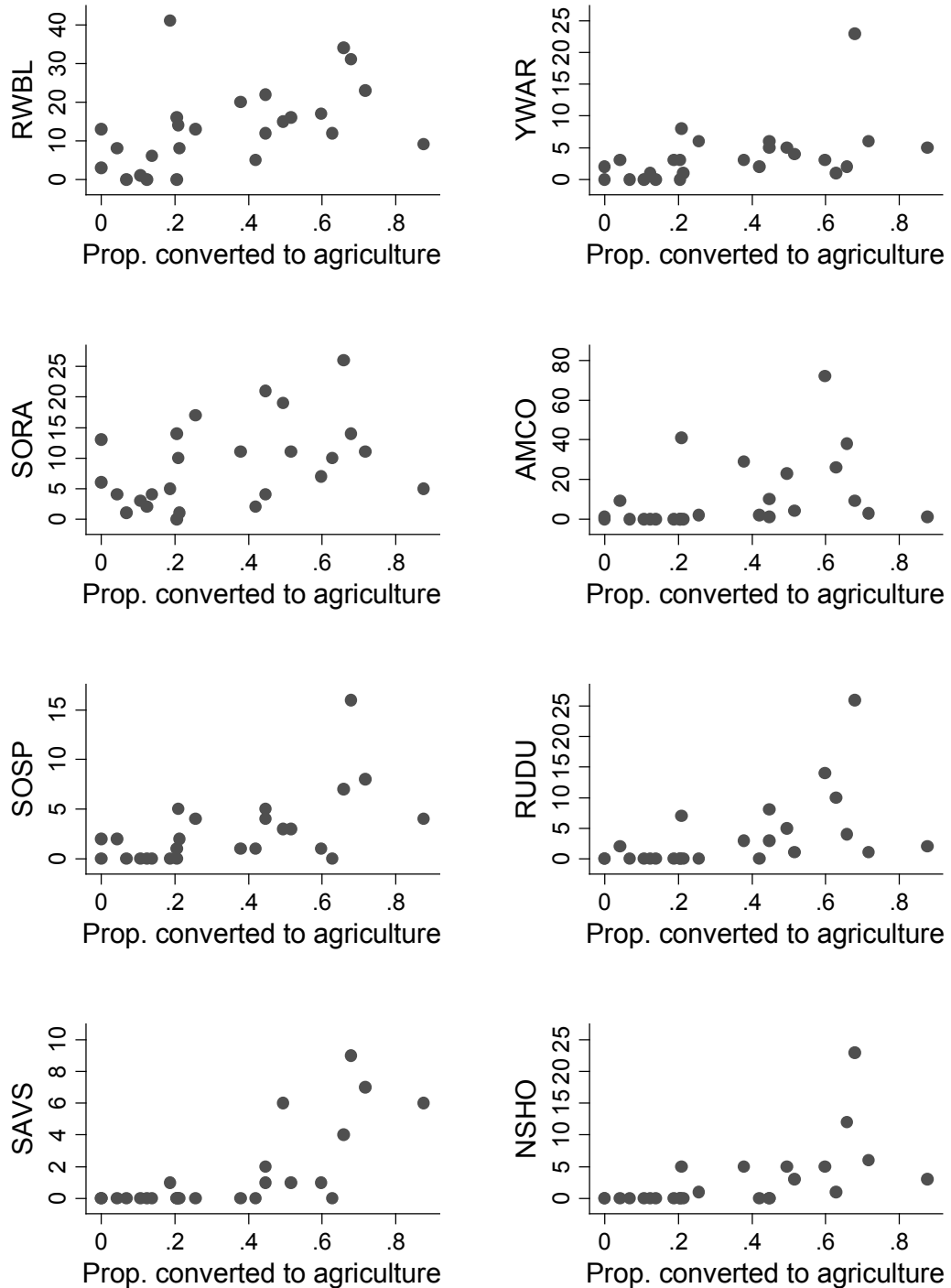
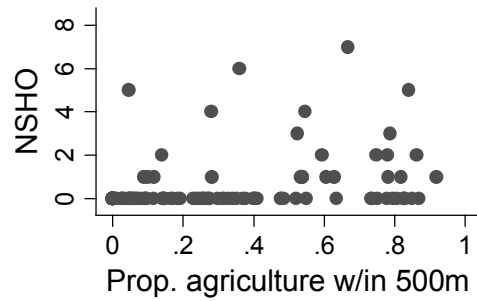
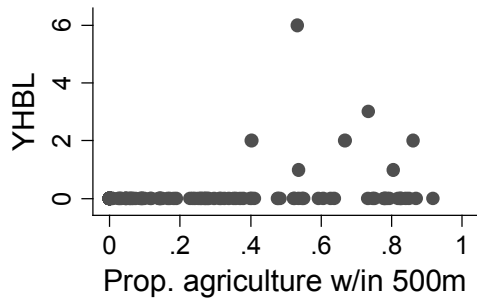
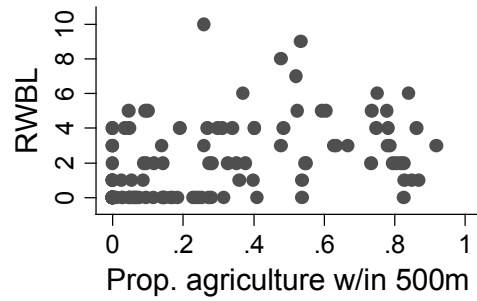
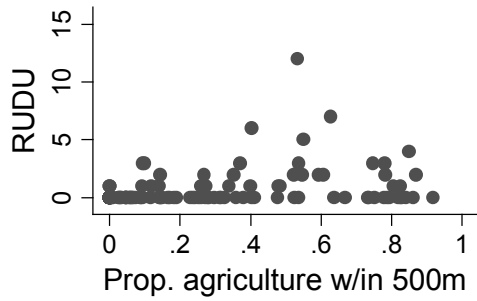
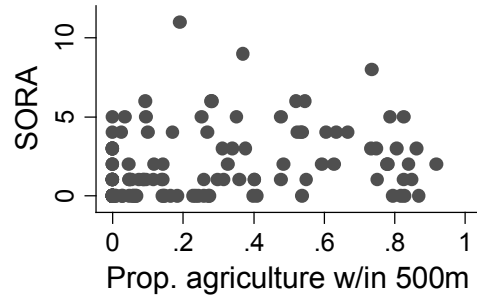
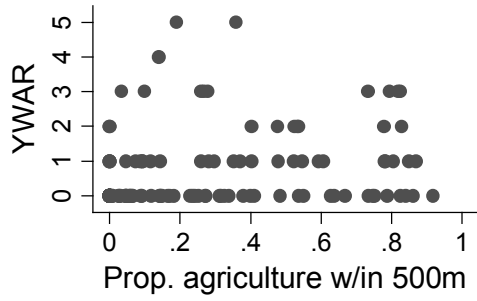
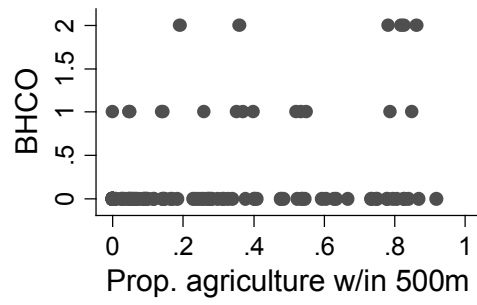
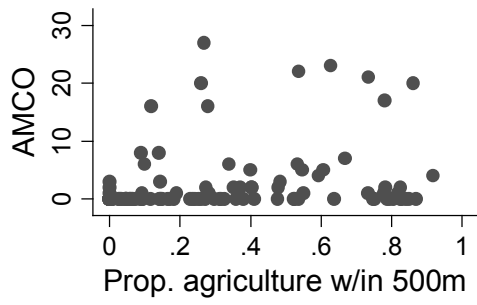


Figure A4.2 Scatter plots representing abundance of species with significant positive (z^+) responses to a gradient of increasing agricultural conversion for NEAB and DMMB at landscape and wetland scales.

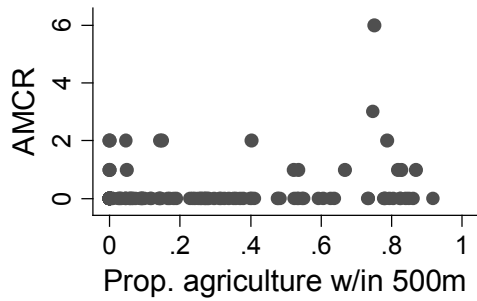
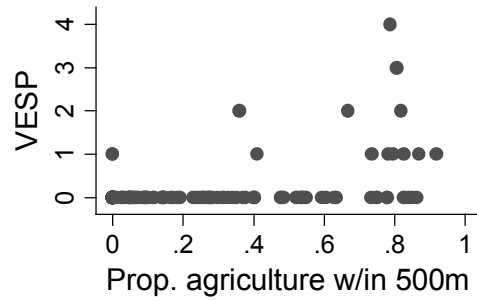
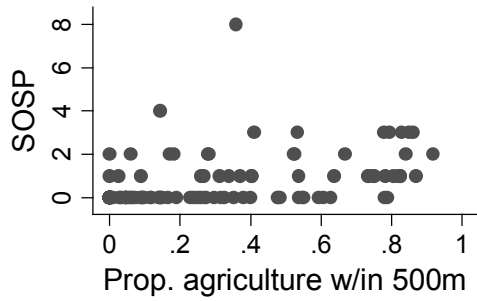
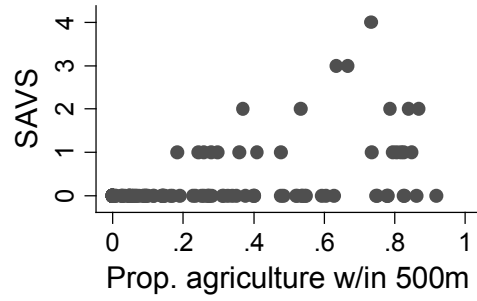
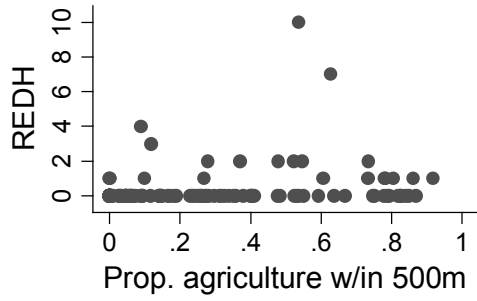
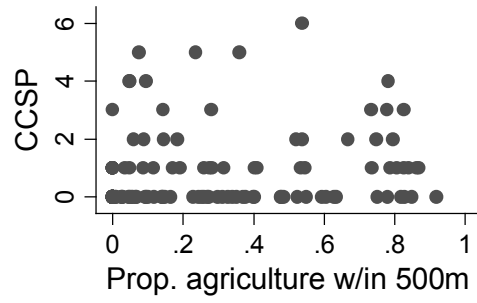
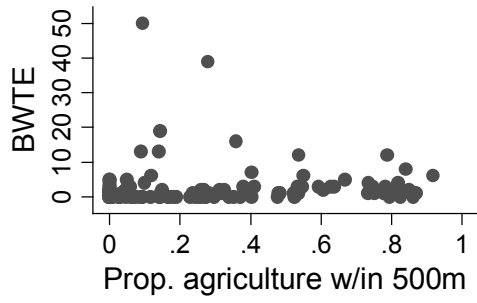
NEAB Landscape



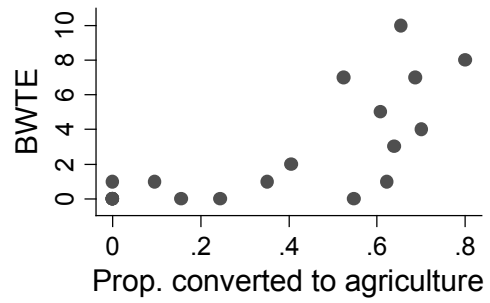
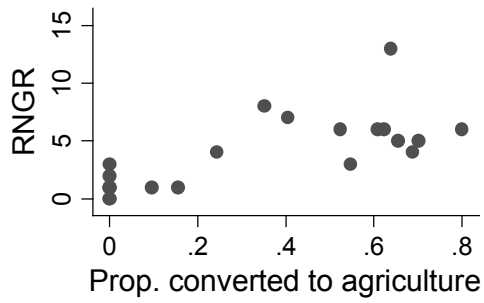
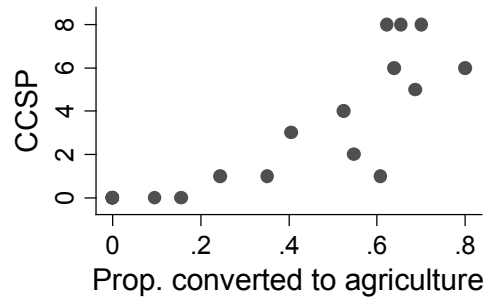
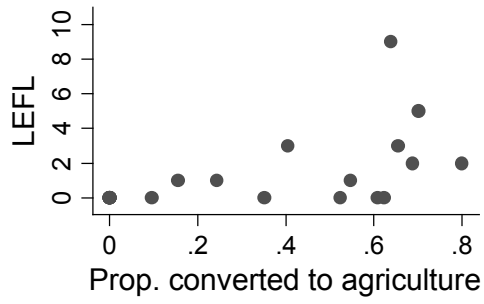
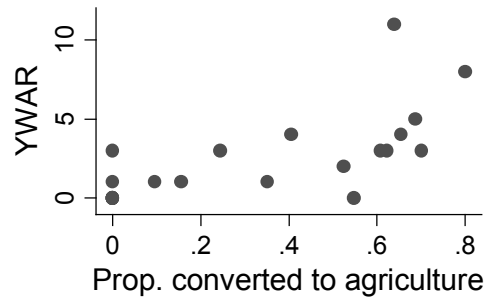
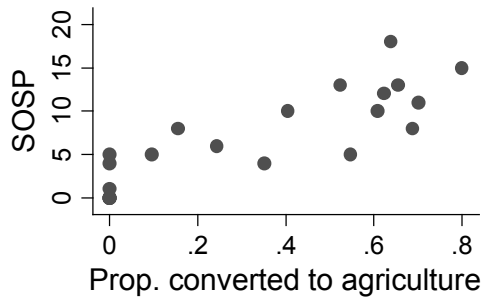
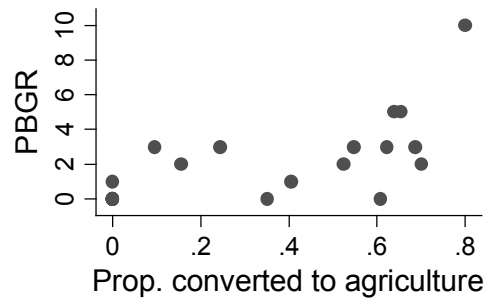
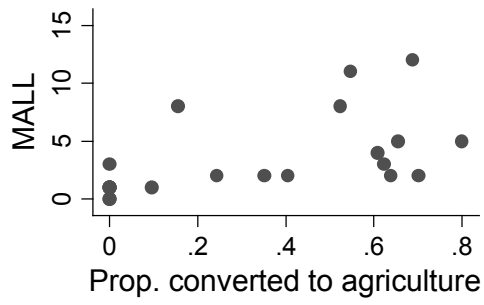
NEAB Wetland



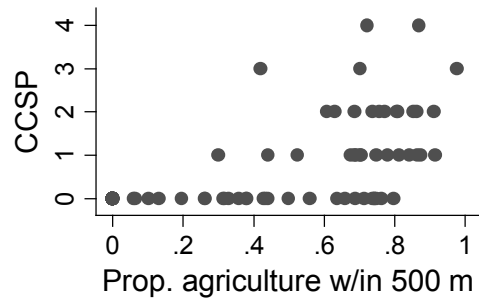
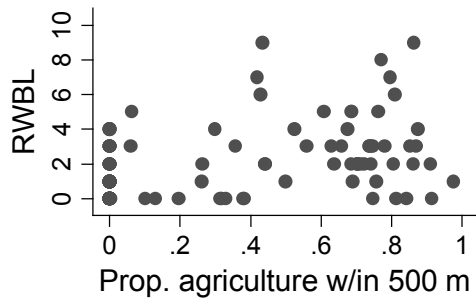
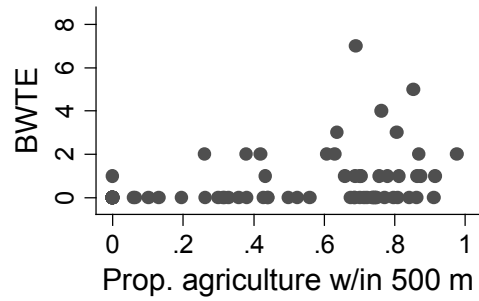
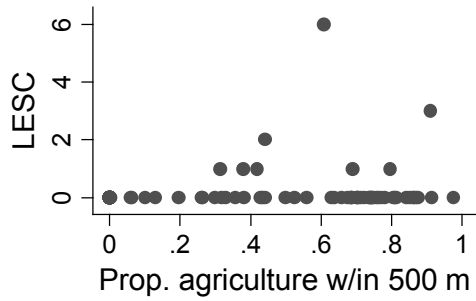
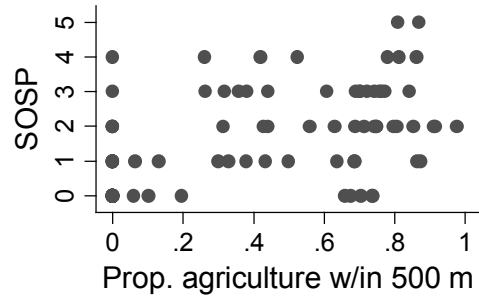
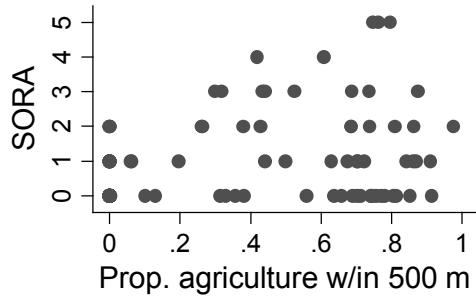
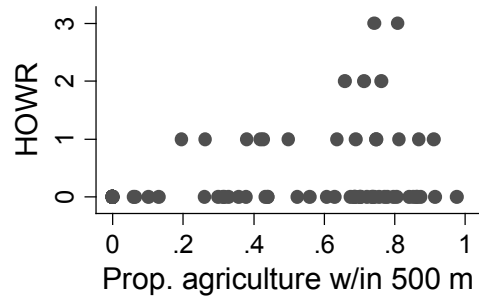
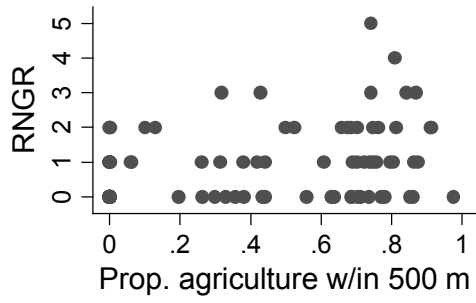
NEAB Wetland



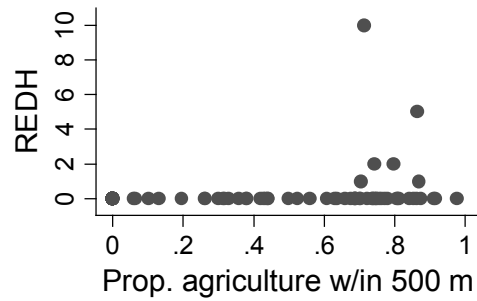
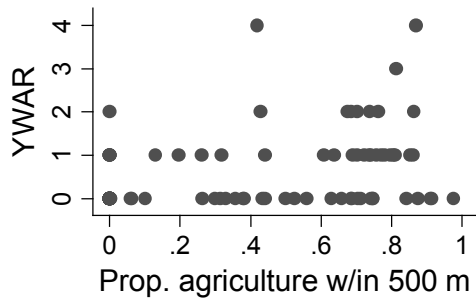
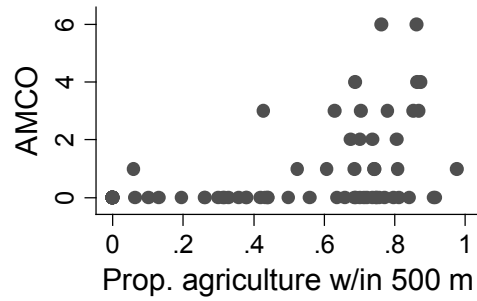
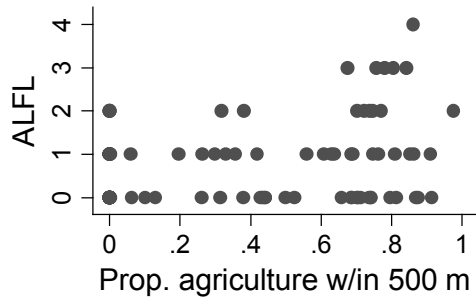
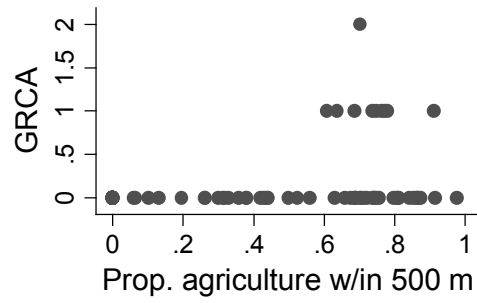
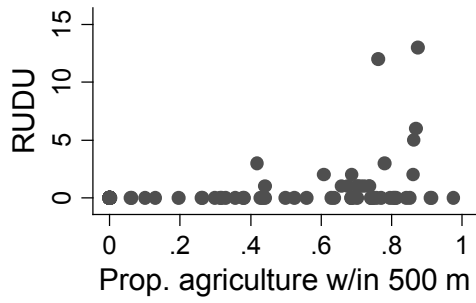
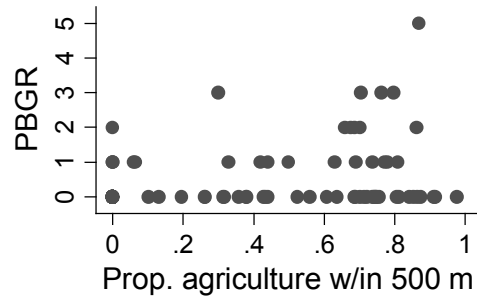
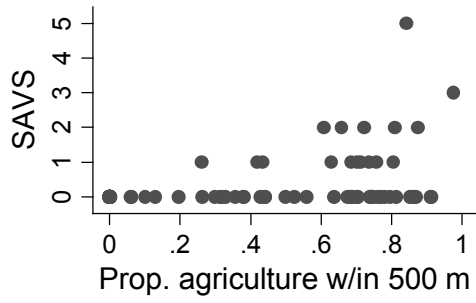
DMMB Landscape



DMMB Wetland



DMMB Wetland



DMMB Wetland

