

DETERMINANTS OF BREEDING BIRD DIVERSITY IN ONTARIO'S FAR NORTH

A Thesis Submitted to the Committee on Graduate Studies

in Partial Fulfillment of the Requirements for the Degree of Master of Science in the Faculty of

Arts and Science

TRENT UNIVERSITY

Peterborough, Ontario, Canada

© Copyright by Timothy R. Irvin 2022

Environmental and Life Sciences MSc Graduate Program

May 2022

Abstract

Determinants of breeding bird diversity in Ontario's far north

Timothy R. Irvin

190 species of birds are known to breed in Ontario's far north making the region an important nursery for boreal birds. Digital point count data were collected using two different autonomous recording units (ARUs): one model with two standard microphones to detect birds and anurans, and one model with one standard microphone and one ultrasonic microphone for detecting bats. ARUs were deployed either in short or long-term plots, which were four to six days or approximately 10 weeks, respectively. I assessed differences in breeding bird richness detections between ARU and plot types. I also tested the relative impact of the habitat heterogeneity and species-energy hypotheses in relation to breeding birds and created predictive maps of breeding bird diversity for Ontario's far north. I found no difference in species richness estimates between the two ARU models but found that long-term plots detected about 7 more bird species and 1.5 more anuran species than short-term plots. I found support for both the species-energy and habitat heterogeneity hypotheses, but support for each hypothesis varied with the resolution of the analysis. Species-energy models were better predictors of breeding bird diversity at coarser resolutions and habitat heterogeneity models were better predictors at finer resolutions. Breeding bird diversity was highest in the Ontario Shield Ecozone compared with the Hudson Bay Lowlands Ecozone, but concentrated areas of higher diversity found in the Lowlands were associated with large rivers and the associated coastlines.

Keywords:

Hill diversity, biodiversity, diversity index, species richness, autonomous recording unit, breeding birds, Ontario, boreal forest, species-energy hypothesis, habitat heterogeneity hypothesis, Hudson Bay Lowlands, Ontario Shield.

Acknowledgements

I wish to acknowledge that this research was conducted in the territory of the Nishnawbe Aski Nation. I specifically want to thank the communities of Attawapiskat, Fort Albany, Fort Severn, Keewaywin, Kitchenuhmaykoosib Inninuwug (Big Trout Lake), Nibinamik (Summer Beaver), Ogoki (Marten Falls), Peawanuk (Weenusk), Sandy Lake, and Webequie for their support and warm hospitality while working in their communities and on their traditional lands. I am grateful for all the assistance the communities provided and hope that the information this project produces may be useful for the First Nations people of Ontario's far north.

Thank you to my long-suffering supervisors Ken Abraham and Bruce Pond, who stuck with me for far longer than was reasonable. Special thanks to Bruce for his friendship, kindness, and guidance as I grappled with all the analytics, and for his expertise in creating the predictive diversity distribution maps. When my compass started spinning—as it often did—Bruce was always there to steer me back on course. Without his help, I never (ever!) could have completed this project.

I thank the Ontario Ministry of Natural Resources Northeast Science and Information Section and Wildlife Research & Development Section for coordinating my field work and for the opportunity to participate in Far North Biodiversity Project. I am especially grateful to Dean Phoenix, John Ringrose and Derek Goertz for their humour, expertise, and company during our field seasons. I am also grateful for Dean's support and patience while answering all my questions about project logistics, data, or otherwise during many long phone

calls long after it was his job to do so. I also owe a debt to Kevin Chan and Erica Newton for their expert assistance as I grappled with statistics.

Thanks also to Linda Cardwell and Mary-Lynn Sriver, the foundation of the Environmental and Life Sciences Graduate Program! Your support is so critical for ENLS students.

Lastly—and without question most importantly—thank you Heidi, Nico and Phoebe for struggling through this with me.

Table of Contents

| | |
|--|-------------|
| Abstract | ii |
| Acknowledgements | iii |
| Table of Contents..... | v |
| List of figures..... | vii |
| List of tables..... | viii |
| Chapter 1 – Introduction | 1 |
| 1.1 General introduction..... | 1 |
| 1.2 Far north Biodiversity Project | 5 |
| 1.3 Modeling bird diversity in Ontario’s far north..... | 7 |
| Chapter 2 – Optimizing use of autonomous recording units for breeding birds and anurans in a large and remote study area..... | 11 |
| 2.1 Introduction | 11 |
| 2.2 Methods | 15 |
| Study Design | 15 |
| Plot types | 16 |
| Plot type comparisons (2012 data) | 21 |
| ARU type data comparisons using (2012 & 2014 data) | 22 |
| Statistical analysis..... | 23 |
| 2.3 Results | 24 |
| Bird species richness..... | 24 |
| Anuran species richness | 27 |
| 2.4 Discussion | 30 |
| ARU type comparison | 31 |
| Avian plot type comparison..... | 32 |
| Anuran plot type comparison..... | 33 |
| Conclusions..... | 34 |
| Chapter 3 – Determinants of songbird diversity in Ontario’s far north..... | 36 |
| 3.1 Introduction | 36 |
| Defining biodiversity..... | 36 |
| Measuring diversity | 37 |
| Biodiversity Distribution | 43 |
| Study area | 47 |
| Objective and hypotheses | 49 |
| 3.2 Methods | 50 |
| Avian data collection | 50 |
| Diversity Calculation | 55 |
| Covariates | 56 |
| Candidate model specification | 65 |

| | |
|---|------------|
| Predictive diversity mapping | 69 |
| 3.3 Results | 70 |
| Species richness..... | 70 |
| Hill-Shannon diversity..... | 75 |
| Predictive diversity maps..... | 79 |
| 3.4 Discussion | 81 |
| Species Richness | 82 |
| Hill-Shannon diversity..... | 84 |
| Hill-Gini-Simpson diversity | 84 |
| Implications of scale | 86 |
| Choice of diversity metrics and predictive maps | 87 |
| Conservation implications | 89 |
| Chapter 4 – General discussion..... | 92 |
| Literature Cited..... | 99 |
| Appendix 1 | 105 |

List of Figures

| | |
|---|----|
| Figure 1.1. Far north location map (Far North Science Advisory Panel , 2010)..... | 3 |
| Figure 2.1. Example of a Wildlife Acoustics, Inc. ARU showing microphones on opposite sides of device. | 16 |
| Figure 2.2. Long-term plot configuration showing SM2 and SM2BAT units at each sampling station. | 17 |
| Figure 2.3. Short-term plot showing configuration of SM2 and SM2BAT units at sampling stations. | 19 |
| Figure 2.4. Median bird richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) by plot type and ARU unit type in the Albany River Ecodistrict of Ontario’s far north in 2012..... | 25 |
| Figure 2.5. Median bird richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) by ARU unit type in Albany River Ecodistrict (2012) combined with Winisk River, Wood Creek and Dickey River Ecodistricts (2014) in Ontario's far north. | 25 |
| Figure 2.6. Median anuran richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) by plot type and ARU unit type in Albany River Ecodistrict (2012)..... | 28 |
| Figure 3.1. Dependence of shannon and gini-simpson index on a number of species in a perfectly even community (zeleny, n.d.) | 40 |
| Figure 3.2. Far North Biodiversity Project plot locations in Ontario’s far north 2010-2014 | 50 |
| Figure 3.3. Long-term plot configuration showing SM2 and SM2BAT units..... | 53 |
| Figure 3.4. Short-term plot showing configuration of SM2 and SM2BAT units. | 54 |
| Figure 3.5. Sampling effort (number of interpreted recording sessions) versus sampling year | 60 |
| Figure 3.6. R values of plot-level richness with independent variables from 0m to 10,000m grains. | 62 |
| Figure 3.7. PCA bi-plot of environmental variables and effort at 500m grain. | 64 |
| Figure 3.8. PCA bi-plot of environmental variables and effort at 10,000m grain. | 64 |
| Figure 3.9. Histograms showing distribution of i) species richness, and the effective numbers derived from ii) Shannon diversity index and iii) the Gini-Simpson index | 65 |
| Figure 3.10. R ² partitioning of habitat, energy, year, and effort contributions for a). Breeding bird richness and habitat, energy, and year contributions for b). Hill-Shannon diversity and c). Hill-Gini-Simpson diversity in Ontario’s far north, showing delta AIC values at 0 to 10,000m grains | 75 |
| Figure 3.11. Breeding bird species richness detected between 2010-2014 by autonomous recording units across Ontario’s far north at 500m grain. | 80 |
| Figure 3.12. Hill-Shannon diversity for breeding birds detected between 2010-2014 by autonomous recording units across Ontario’s far north at 500m grain. | 80 |
| Figure 3.13. Hill-Gini-Simpson diversity for breeding birds detected between 2010-2014 by autonomous recording units across Ontario’s far north at 500m grain. | 81 |

List of Tables

| | |
|--|-----|
| Table 2.1. Bird species richness sample effort and yield by plot type in the Albany Ecodistrict of Ontario's far north in 2012. | 22 |
| Table 2.2 Bird species richness sample effort, distribution among plot types and total recordings by automatic recording unit type in the Albany Ecodistrict of Ontario's far north in 2012. | 22 |
| Table 2.3. Bird species richness sample effort and total recordings by automated recording unit type using 2012 and 2014 data from the Albany River, Winisk River, Wood Creek and Dickey River Ecodistricts in Ontario's far north. | 23 |
| Table 2.4. Model results by a) plot type and aru unit type in Albany River Ecodistrict of Ontario's far north in 2012 and b) auotmated recording unit type in Albany Ecodistrict (2011) and Wood Creek, Dickey River, Winisk River Ecodistricts (2014). | 26 |
| Table 2.5. AICc results for the base, additive and interaction models of bird species richness in Albany Ecodistrict (2012) and Dickey River, Winisk River and Wood Creek Ecodistricts (2014) in Ontario's far north. | 27 |
| Table 2.6. Model results by a). Plot type and ARU unit type in Albany River Ecodistrict (2012) and b). ARU unit type in Albany Ecodistrict combined with Wood Creek, Dickey River, Winisk River Ecodistricts (2014). | 29 |
| Table 2.7. AICc results for the base, additive and interaction models of anuran richness in Albany Ecodistrict (2012) combined with data from Dickey River, Winisk River And Wood Creek Ecodistricts (2014). | 30 |
| Table 3.1. Conversion of diversity indices to effective number of species, where s = number of species, p_i represents the relative abundance of the i_{th} species, the number of individual species i at the plot divided by the total number of individuals of all s species. | 56 |
| Table 3.2. Candidate models for breeding bird species richness in Ontario's far north. | 66 |
| Table 3.3. Candidate models for the effective number of species derived from the shannon index and the effective number of species from the gini-simpson index. | 68 |
| Table 3.4. Model selection results for bird species richness (RICH): top model selected for each hypothesis, at each grain size, hypothesis abbreviations: H&E: energy and habitat heterogeneity; E: energy only; H: habitat heterogeneity only; E&Y: null model of only effort and year effects. Frequentist coefficient significance: $p < 0.001$ as ***; $p < 0.01$ as **; $p < 0.05$ as *; and $p < 0.10$ as ° | 72 |
| Table 3.5. Model selection results for Hill-Shannon index of bird species diversity (HILL-SHAN): top model selected for each hypothesis, at each grain size, hypothesis abbreviations: H&E: energy and habitat heterogeneity; E: energy only; H: habitat heterogeneity only; E&Y: null model of only effort and year effects. Frequentist coefficient significance: $p < 0.001$ as ***; $p < 0.01$ as **; $p < 0.05$ as *; and $p < 0.10$ as ° | 76 |
| Table 3.6. Model selection results for Hill-Gini-Simpson index of bird species diversity (HILL-Gs): top model selected for each hypothesis, at each grain size, hypothesis abbreviations: H&E: energy and habitat heterogeneity; E: energy only; H: habitat heterogeneity only; E&Y: null model of only effort and year effects. Frequentist coefficient significance: $p < 0.001$ as ***; $p < 0.01$ as **; $p < 0.05$ as *; and $p < 0.10$ as ° | 78 |
| Table 1A. The 125 breeding bird species detected on autonomous recording units during the far north biodiversity project between 2010-2014, showing the number of individuals of each species for long-term and short-term plots. | 105 |
| Table 2A. Anurans detected on autonomous recording units during the Far North Biodiversity Project between 2010-2014, showing the number of individuals of each species for long-term and short-term plots | 108 |
| Table 3A. The 17 land cover names and codes derived from the ontario land cover compilation v.2.0 used to calculate number of land classes and effective number for shannon diversity as indices for habitat heterogeneity* | 109 |
| Table 4A. Variance explained and component loadings from principal component analysis at 500m grain size. | 110 |

| | |
|---|-----|
| Table 4B. Variance explained and component loadings from principal component analysis at 10,000m grain size. | 110 |
| Table 5A. Correlation coefficients for all independent variables at 500m grain..... | 111 |
| Table 5B. Correlation coefficients for all independent variables at 10,000m grain..... | 111 |

Chapter 1 – Introduction

1.1 General introduction

Global biodiversity loss impacts the functioning of ecosystems and human well-being (Johnson et al., 2017). By signing the Convention on Biological Diversity in 2002, world leaders committed to achieve a significant reduction in the rate of biodiversity loss by 2010. However, in spite of this global commitment, and some local and regional successes, there has been little reduction in the rate of loss in global biodiversity (Butchart et al., 2010; Johnson et al., 2017). Birds are part of this decline. Rosenberg et al. (2019) suggested North America may have lost 3 billion birds, or 29% of 1970's abundance, representing a substantial loss of biodiversity.

Approximately 300 species of the continent's birds breed in the boreal forest, which has been referred to as North America's "bird nursery" (Stralberg et al., 2019; Wells et al., 2014). The boreal forest is the largest terrestrial ecosystem on Earth representing 25 percent of the world's remaining frontier forests (Bryant et al., 1997). Vast tracts of this biome are found in Canada, representing 30 percent of the biome's total global range (Gauthier et al., 2021). Compared to Nordic regions, large parts of the Canadian boreal landscape remain largely undeveloped (Östlund et al., 1997; Lee et al., 2007). In Canada there are still large pristine areas where forest fires, insect outbreaks, wind and beaver activity are the dominant disturbances, rather than human industry (Hansson, 1992; Krawchuk et al., 2006). This is particularly true of the northern reaches of the boreal where forests are too remote and sparse to support a forestry industry (Bryant et al., 1997). To ensure the boreal forest remains ecologically intact it has been recommended that large portions of it be protected from industrial disturbance (Locke, 2013),

and the International Boreal Conservation Science Panel has recommended that at least half of the boreal be protected from industrial disturbance (Badiou et al., 2013).

The dominant tree species in Canada's boreal forest include black and white spruce (*Picea mariana*, *Picea glauca*), jack pine (*Pinus banksiana*), aspen (*Populus tremuloides*), tamarack (*Larix laricina*) and white birch, (*Betula papyrifera*) which are highly influenced by disturbance regimes (The Far North Science Advisory Panel, 2010). Fire is the dominant disturbance in the more remote reaches of the forest where there is no fire suppression (Kirk et al., 1996), whereas in the southern areas of the forest where fire suppression is practiced, human forestry activities are the dominant disturbance (Telfer, 1993; Kirk et al., 1996). These disturbances create a mosaic of habitat patterns and age-classes that have important impacts on wildlife (Helle & Monkkonen, 1990).

Defined as Ontario's Far North by the Far North Act, 2010, S.O. 2010, c.18 s.2 (Fig. 1), the northern part of the province encompassing over 450 000 square kilometers of intact ecosystems, is composed predominantly of boreal forest, including swamps, bogs and fens, plus a zone of taiga and tundra at its highest latitudes (The Far North Science Advisory Panel, 2010). Unlike other parts of the province, the far north has very little industrial development (The Far North Science Advisory Panel, 2010). The region is characterized by two major ecozones: the Hudson Bay Lowlands (HBL) and the Ontario Shield (Crins et al., 2009). Limestone bedrock underlies the HBL which represents 54 percent of the far north (The Far North Science Advisory Panel, 2010). The Lowlands extend inland from the shores of Hudson and James Bay forming the third largest wetland in the world (Abraham & Keddy, 2005). The HBL area is dominated by vast

expanses of wetlands and poorly drained muskeg. Marshes, tidal flats and shallow water dominate the 1900 kilometers of salt-water shoreline along the coasts of Hudson Bay and James Bay (Ecological Stratification Working Group, 1995). Inland from the HBL, the Ontario Shield Ecozone represents the remaining 46 percent of the far north region and is underlain with Precambrian Shield, composed mostly of gneisses and granites (The Far North Science Advisory Panel, 2010). Collectively, the forests of the HBL and the Ontario Shield, and the adjacent forests of Manitoba, Quebec and Nunavut, represent the largest remaining block of boreal forest free from large-scale human disturbance in the world (The Far North Science Advisory Panel, 2010; World Resources Institute, 2010).

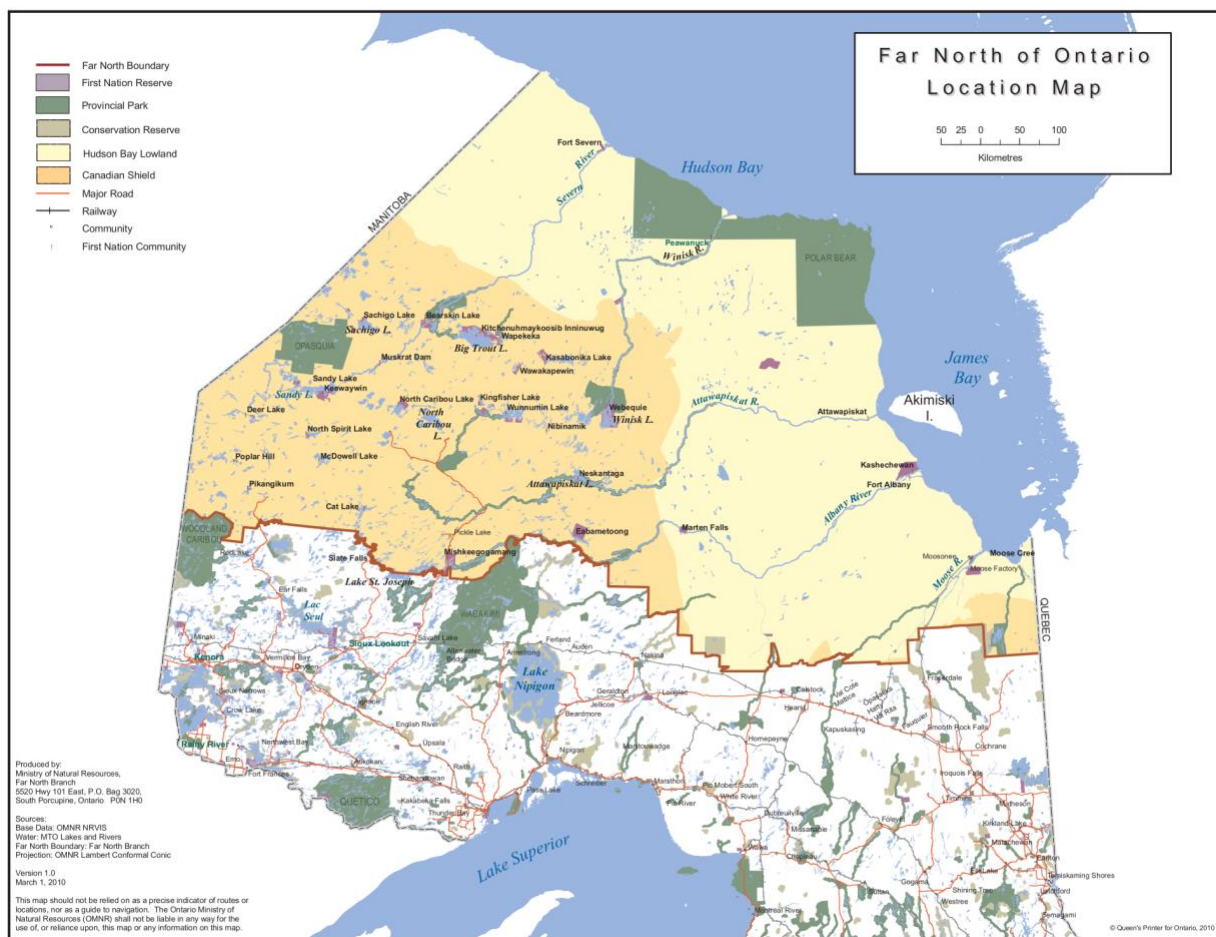


Figure 1.1. Far north location map (Far North Science Advisory Panel, 2010)

The human population of the Far north region is approximately 24 000 people spread over 31 small First Nation communities (The Far North Science Advisory Panel, 2010), which are not linked to each other or to the south by all-season roads. These Indigenous people still rely on the land for parts of their livelihood and engaging in traditional cultural practices including trapping, hunting, fishing, and gathering (e.g., Berkes et al., 1995, Tsuji et al., 2007). The lack of human disturbance across the vast ecosystems of the far north that are home to an intact suite of wildlife species, also makes the region globally unique from an ecological standpoint (Chetkiewicz & Lintner, 2014). However, because of the expense of conducting research in this remote area, few large-scale studies of the region's biota have been completed. In addition, the increasing industrial interest in this region means the opportunity for proactive conservation planning is time-limited.

Currently, Newmont's Musselwhite gold mine is the only operational mine in the region, since DeBeer's Victor diamond mine closed in 2019. However, plans to expand mineral extraction are progressing including the proposed development of the "Ring of Fire," a very large chromite deposit in the Hudson Bay Lowlands, which has been called the economic equivalent of the Athabasca oil sands with the potential to generate 120 billion dollars in economic benefits (Tencer, 2013). Partially in response to increasing industrial interests, the Ontario government created the Far North Act, which commits the province to engage with First Nations in a comprehensive land use planning process for the region. The Act adopted the recommendation of the International Boreal Conservation Science Panel to set aside at least half of the far north in protected areas, but also leaves provisions for enabling sustainable development (Ontario Ministry of Natural Resources, 2009).

1.2 Far north Biodiversity Project

In 2009, the Far North Biodiversity Project (FNBP), was initiated by the Ontario Ministry of Natural Resources (OMNR) to provide baseline data on the area's biodiversity, in support of the local First Nations' community-based land use planning activities and the provinces regulatory mandate for conservation. Over the course of six field seasons (2009-2014), the FNBP conducted a systematic multispecies inventory of birds, insects, fish, vegetation, reptiles, amphibians, and small and large mammals across the far north. While this five-year research project has generated data on numerous taxa, my study focused primarily on analyzing the avian data it produced, with some examination of anuran data in Chapter 2.

Canada-wide, most bird conservation is managed under the Migratory Birds Convention Act 1994 (MBCA) (non-migratory species are managed by the province's under provincial legislation (e.g., Ontario's Fish and Wildlife Conservation Act, 1997, c. 41). Canada is also part of the North American Bird Conservation Initiative and has designated Bird Conservation Regions nation-wide, which form the foundation of bird conservation planning across the country (Cooke, 2003; Rich et al., 2004). Collectively, these programs are critical for national and continent-level conservation planning (Cumming et al., 2010).

Three hundred and forty species of birds are known to be supported by Ontario's far north ecosystems during some point in their annual cycle (Abraham and McKinnon, 2011). Of those, 190 species have been documented breeding in the far north (Far North Science Advisory Panel, 2010), representing approximately one third of the species that breed north of Mexico in North

America (Blancher, 2003; Berlanga et al., 2010). Birds that breed in the far north including landbirds, waterbirds, waterfowl and shorebirds that have recognizable vocalizations are the focus of this study.

Birds occupy diverse niches across the northern landscape. This suggests that not only do they have large inherent ecological value, but they can be a link to understanding the ecosystems themselves (Niemi et al., 1997; Cumming et al., 2010). They may also act as indicators of ecosystem health (Diamond & Fillion, 1987; Furness & Greenwood, 1993) and even biodiversity in general (Freedman et al., 1994). Thus, studying the distribution of breeding birds in Ontario's far north, may give us new insights into northern ecosystems and help identify areas of particular biological value in this region.

Overall, the distribution and abundance of boreal birds is not well documented in the northern boreal region, including Ontario's far north (Cumming et al., 2010). By comparison, much more is known about avian communities in the southern reaches of the boreal (Schmiegelow & Monkkonen, 2002; Blancher, 2003; Stralberg et al., 2019). Most boreal bird research to date has been constrained by accessibility, primarily by road networks which are sparse or absent in much of the boreal, and almost completely absent in the far north. Thus, road-accessed research by itself does not provide adequate baseline data of the far north's boreal bird populations.

Additionally, findings on bird distribution in southern boreal landscapes that are subject to heavy human disturbance, may not apply to the fire and wetland-dominated ecosystems of far north (Venier et al., 2004). Likewise, latitudinal climatic variability may also have direct or indirect

impacts on the distribution of bird communities in southern versus northern reaches of the boreal forest (Venier et al., 1999).

The Ontario Breeding Bird Atlas (OBBA) is the largest and most comprehensive survey of breeding birds conducted in the province. Atlases were carried out between 1981-1985, 2001-2005 (Cadman et al., 1987; Cadman et al., 2007) and is currently being updated (2021-2025) again. The Atlases provide detailed information on the distribution and population status of Ontario birds including distribution maps for individual species. Until the FNBP was initiated, the two Atlases were the best available single source of information for far north avifauna. However, for the purposes of these Atlases, most research squares were accessed by road, or by canoe from a road access point. In the far north where this was not possible, researchers were flown into rivers, lakes or settlements to access survey points. Although efforts were made to sample the far north as widely as possible, sampling effort in this region was clustered around the lakes, rivers and settlements that provided access (Cadman et al., 2007). Because of these challenges, the far north region had the lowest sampling effort of any part of the province in the Atlas. In this context, the avian data produced by the FNBP is a particularly valuable addition to existing avian data resources for the far north.

1.3 Modeling bird diversity in Ontario's far north

Historical approaches to bird research and management have concentrated on single species or simple community-level studies measured over small areas (Freemark et al., 1995). However, given the scale of northern landscapes and industrial activities, researchers are shifting their focus to expand the scale of their research to address emerging landscape-level conservation

needs (Cumming et al., 2010; Stralberg et al., 2018; Stralberg et al., 2019). Some of this work is being tackled using modeling techniques that predict avian distribution based on multiple biophysical variables.

Energy, as derived from the sun, is thought to be largely responsible for patterns in distribution and productivity of terrestrial plants across the globe (Holdridge, 1967). This, in turn, influences patterns of other taxa, including vertebrates (Hawkins et al., 2003; Field et al., 2009) with variables like temperature directly limiting animal distributions by excluding individuals from regions where their physiological tolerances are exceeded (Root, 1988; Currie, 1991). Energy may also act indirectly on species distributions through energetic limitations on plant growth and food web development (Wright, 1983). Consequently, vegetation composition and structure are well-documented drivers of local and regional abundance and community composition of bird populations (MacArthur, 1966; Rotenberry & Wiens, 1980; Cody, 1981; Davidowitz & Rosenzweig, 1998). Beyond influencing bird habitat, energy variables also influence the distribution and abundance of insects (Venier et al., 1999). Since most boreal birds are insectivorous, this may be another mechanism by which energy influences avian distribution across the landscape (Venier et al., 1999; Kirk et al., 1996).

Years of research have illustrated how vegetation composition and structure influence bird distribution, abundance, and community composition in numerous ways (Willson, 1974; Anderson, 1981; Cody, 1985; Urban & Smith 1989; Lichstein et al., 2002). For example, at the level of a forest stand, birds respond to vegetation structure, foliage volume, and the proportions of deciduous and coniferous tree species (Willson 1974; Collins et al., 1982; James & Wamer.,

1982; Clark et al., 1983). In the boreal landscape specifically, the patterns and diversity of successional stages created by large-scale natural or human disturbances are major influences on avian species assemblages (Venier et al., 1999; Drapeau, 2000). Remote-sensed sources of land cover data can provide good information on these variables, and are improving all the time (Cummings et al., 2010).

Studies have shown strong associations between species distributions and energetic variables (Connell & Orias, 1964; Wright, 1983; Cumming et al., 2014; Stralberg et al., 2019). Venier et al. (1999) used data from the 1981-1985 OBBA (Cadman et al., 1987) and numerous macro-climate variables to model the distribution of five species of boreal songbirds. Results showed strong associations between the distributions of the five species in the study and the energy variables that were examined. This work suggests that macro-climate is an important factor influencing the distribution of breeding birds in Ontario's boreal forest. More recently, Cumming et al. (2010) and Stralberg et al. (2018) have also modeled boreal bird distributions across North America using variables related to energy available for biological productivity.

The interest in analysis of spatial data to support regional, national, and continental conservation planning has been increasing (Cumming et al., 2010; Stralberg et al., 2018; Stralberg et al., 2019). Cummings et al. (2010) and Stralberg et al. (2018) have modelled individual bird species distributions across North America's boreal forest. Their work covers Ontario's far north but they did not have access to the avian data collected during the FNBP, which represents the most comprehensive coverage of bird distribution data ever assembled for Ontario's far north. Using this dataset, I explore how to optimize collection of breeding bird data using autonomous

recording units (ARUs) over a large study area (Chapter 2). I also examine the relative contributions of the habitat heterogeneity and the species-energy hypotheses to the distribution of breeding birds across the far north and create predictive maps of avian diversity for my study area. Using FBNP data this study has the potential to provide the best available predictions of breeding bird diversity across the far north and contribute to conservation planning in the region (Chapter 3).

Chapter 2 – Optimizing use of autonomous recording units for breeding birds and anurans in a large and remote study area

2.1 Introduction

In today's world, most natural ecosystems have been reduced in size and are highly fragmented by human activities. The few large intact ecosystems that remain have high value for long-term biodiversity conservation (Noss et al., 2011; Watson & Venter, 2017; Stralberg et al., 2018;). Large intact landscapes provide high quality habitat for wildlife—especially for wide-ranging species—and may provide refugia from invasive species and pathogens and protect species from the impacts of climate change (Caro et al., 2012; Watson et al., 2018). Despite their value to wildlife conservation, many large remote regions have been under-studied by biologists because of the difficulty and expense involved in accessing and conducting research in these places (Cumming et al., 2010). There is often a lack of baseline biological data available to inform conservation planning for large remote areas compared with smaller and more readily accessible regions (Cumming et al., 2010; Stralberg et al., 2018). The far north of Ontario, Canada is an example of such a large and understudied region (Far North Science Advisory Panel, 2010).

Defined by Ontario's Far North Act, 2010, S.O. 2010, c. 18 s.2, the far north of Ontario encompasses over 450 000 square kilometres of intact ecosystems composed predominantly of boreal forest, swamp, bogs and fens (Figure 1.1, Far North Science Advisory Panel, 2010). Unlike other parts of the province, this region has had very little industrial development (Far North Science Advisory Panel 2010).

The region is comprised of two major ecozones: the Hudson Bay Lowlands and the Ontario Shield, which are further divided into 13 ecoregions based on biogeoclimatic characteristics (Wester et al., 2018). The Hudson Bay Lowlands comprise the third largest wetland in the world (Abraham & Keddy, 2005). This region is also the second-largest peatland in the world, making it a globally significant carbon sink (Far North Science Advisory Panel, 2010). In conjunction with neighbouring parts of Manitoba, Nunavut and Quebec, the far north of Ontario forms one of the largest pieces of intact forest in the world (The Far North Science Advisory Panel, 2010; World Resources Institute, 2010). The far north provides habitat for species at risk including woodland caribou (*Rangifer tarandus*), polar bears (*Ursus maritimus*), wolverines (*Gulo gulo*), olive-sided flycatchers (*Contopus cooperi*), rusty blackbirds (*Euphagus carolinus*), common nighthawks (*Chordeiles minor*), golden eagles (*Aquila chrysaetos*), peregrine falcons (*Falco peregrinus*) and more (FNBP preliminary report, 2014). This region is also an important nursery for North American boreal birds, which live in low densities across the landscape (Stralberg et al., 2018). Three hundred and forty species of birds are known to be supported by Ontario's far north ecosystems during some point in their annual cycle (Abraham and McKinnon, 2011). Of those, 190 species have been documented breeding in the region (Far North Science Advisory Panel, 2010), representing approximately one third of the species that breed north of Mexico in North America (Blancher, 2003; Berlanga et al., 2010).

The vast ecosystems of Ontario's far north and the substantial wildlife populations in the region represent an opportunity for proactive conservation planning that is no longer possible in regions where industrial activities have fragmented their landscapes (Cumming et al., 2010). However, there are significant mineral deposits in the region and the opportunity for comprehensive land

use planning before large-scale mining operations are developed may be time-limited (Far North Science Advisory Panel, 2010).

With the importance of intact large landscapes to long-term wildlife conservation – and the necessity for baseline biological data to inform conservation planning - it is valuable to explore the most efficient and cost-effective ways to sample large remote regions. In 2009, the Ontario Ministry of Natural Resources (OMNR) initiated the Far North Biodiversity Project (FNBP) - a five-year multi-species biological inventory project aimed at collecting baseline biodiversity data to help inform land use planning for the region. The project collected data on the distribution and abundance of numerous taxa including vertebrate, plant, insect and lichen species.

Point counts are used for collection of bird data because they provide a reasonable index of songbird abundance in boreal forest (Toms et al., 2005) and are among the most standardized of surveys methods (Cummings et al., 2010). Bioacoustic monitoring using autonomous recording units (ARUs) has become recognized as an efficient means of collecting species observations (L. A. Venier et al., 2012; R. Rempel, 2014; Shonfield & Bayne, 2017). Bioacoustic monitoring using ARUs has become recognized as an efficient means of collecting species observations (Rempel, 2014; Shonfield & Bayne, 2017; L. A. Venier et al., 2012), especially in remote areas where it is often more cost effective to leave a recording device in the field for an extended period of time, than to have a biologist return to a sampling site multiple times to conduct point counts (Shonfield & Bayne, 2017). Moreover, interpreting recordings from ARUs yields comparable results to conducting point counts in the field (Darras et al., 2018; Rempel et al., 2013) and can provide additional benefits for detecting rare species (Venier et al., 2012). As the

technology develops, automatic identification of birds from ARU recordings, using artificial intelligence (or machine learning) techniques may make interpretation of ARU data more efficient while reducing listener bias (Barath, 2021). Nonetheless, there are numerous makes and models of ARUs and these can be used in different configurations. With the increased application of these units, questions have arisen regarding the efficacy of different units in detecting birds (Rempel & Jackson, 2014). Rempel et al. (2013) investigated several commercially available units, including the Wildlife Acoustics SM2 songmeters used by the FNBP. Results indicated the SM2s performed as well as much more expensive units with respect to detection of birds.

Data from the FNBP provides an opportunity to test the efficacy of different Wildlife Acoustics ARUs in a large and remote study area and during two different sampling protocols. This study focuses on breeding birds, including landbirds, waterbirds, waterfowl and shorebirds that have recognizable calls used to defend territories and attract females throughout the breeding season. Since it was available, I also used anuran data produced by the FNBP. I analyzed breeding bird and anuran richness detections from two different ARU models (SM2 units that detect birds and anurans, and SM2BAT units that detect birds, anurans, and bats) and two different field protocols (long and short-term plots) to test the hypothesis that there are differences in species richness detections depending on the ARU model and plot types used.

2.2 Methods

Study Design

Sample plots across the far north of Ontario were located at the centre of randomly selected 20 km by 20 km grids taken from the National Forest Inventory (Gillis et al., 2005). Plots were stratified to ensure representative coverage for all 13 ecodevelopments in the region. Plots were accessed by helicopter and restricted to a 150 km radius from the closest staging community which was the maximum one-way flight distance for a helicopter loaded with field crews and equipment. If the designated random point location was too wet, too forested or otherwise inaccessible for helicopter landings, plots were relocated to the nearest possible landing area of similar habitat type. FSNP staff collected data from 2009 to 2014. However, because of different sampling methods across years, and technical problems with equipment, I only use data from 2012 and 2014 in these comparisons.

Recording Units

Two types of autonomous recording units (ARUs) were used to collect audio recordings of bird vocalizations: SM2 and SM2BAT units, both made by Wildlife Acoustics Inc. SM2 units have two microphones – one on each side of the device – to record bird and anuran vocalizations (Figure 2.1). SM2BAT units look identical but have one standard microphone for birds and anurans and one ultrasonic microphone to record bats. I did not analyze bat data in this study. All ARUs were programmed to record 10-minute point counts daily at 05:30, 06:00, 06:30,

07:30 to capture the dawn chorus, and at 22:00 and 23:00, to specifically target anurans and birds that vocalize at night.

ARUs were fixed to tree trunks or posts at each sampling station approximately 1.5 m off the ground. Care was taken to remove any vegetation within a one-metre radius of the microphones and to avoid setting up ARUs near moving water to reduce sound interference.



Figure 2.1. Example of a Wildlife Acoustics, Inc. ARU showing microphones on opposite sides of device.

Plot types

ARUs were deployed in two different configurations: long-term and short-term plots. These configurations were adapted from the Multiple Species Inventory and Monitoring (MSIM) Protocol developed by the US Forest Service (Manley et al., 1997). On long-term plots, four ARUs (three SM2 and one SM2BAT) were deployed in a 500m square configuration with one

ARU at a sampling station at each corner (Figure 2.2). Whenever possible SM2BAT units were placed at an aquatic, or other ecological edge, to target anurans, aquatic birds, and bats.

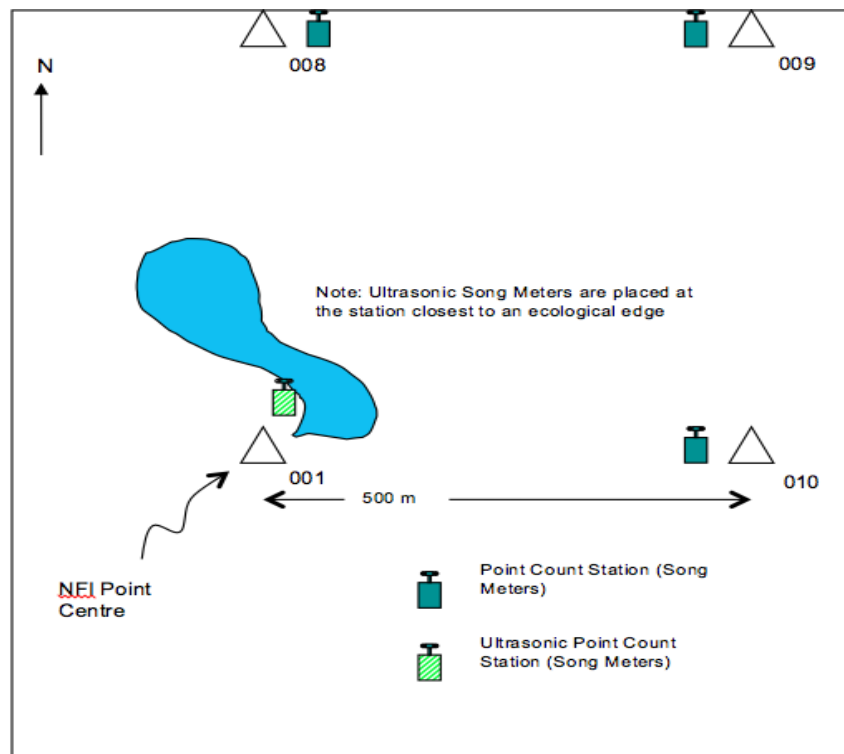


Figure 2.2. Long-term plot configuration used during the Far North Biodiversity Project in Ontario's far north showing SM2 and SM2BAT units at each sampling station.

The MSIM protocol prescribed 1000 m by 1000 m squares for sampling ((Manley et al., 1997). However, because of the large size of our study area and the expense of helicopter time, the FNBP opted for 500 m by 500 m squares. This arrangement allowed for faster plot set up, and enabled the deployment of extra plots, while still maintaining a sufficient distance between ARUs to avoid overlapping acoustic samples. Long-term plots were deployed in late May or early June at the beginning of the bird and anuran breeding season and left at the same location for the duration of the spring and summer before being collected in August.

On short-term plots, ARU were deployed in a 400 m diameter hexagon. Whereas each ARU on long-term plots was deployed in one location for weeks at a time, short-term plots were deployed for 6 days (2012) or 4 days (2014), and then relocated to sample a new area. Like long-term plots, short-term plots used ARUs to collect avian, anuran and bat data, but they also included extensive sampling of other taxa (plants, fish, insects, small mammals etc) by field crews who remained on site for the duration of the plots, which took place in June and July. ARUs were deployed in a 400 m diameter hexagon. Hexagons were oriented towards north with SM2 units placed at stations at the north, southeast, southwest and center locations (Figure 2.3). The center station was intended as backup in case other units failed and was offset 100 m from plot center to avoid disturbance by field crews conducting surveys of other taxa near plot centre. Lastly, an SM2BAT unit was placed at least 200 metres away from the other units at an ecological edge (edge of stream, lake, pond or interface between bog and forest or fen and forest) at the discretion of field crews, to target anurans, aquatic birds and bats.

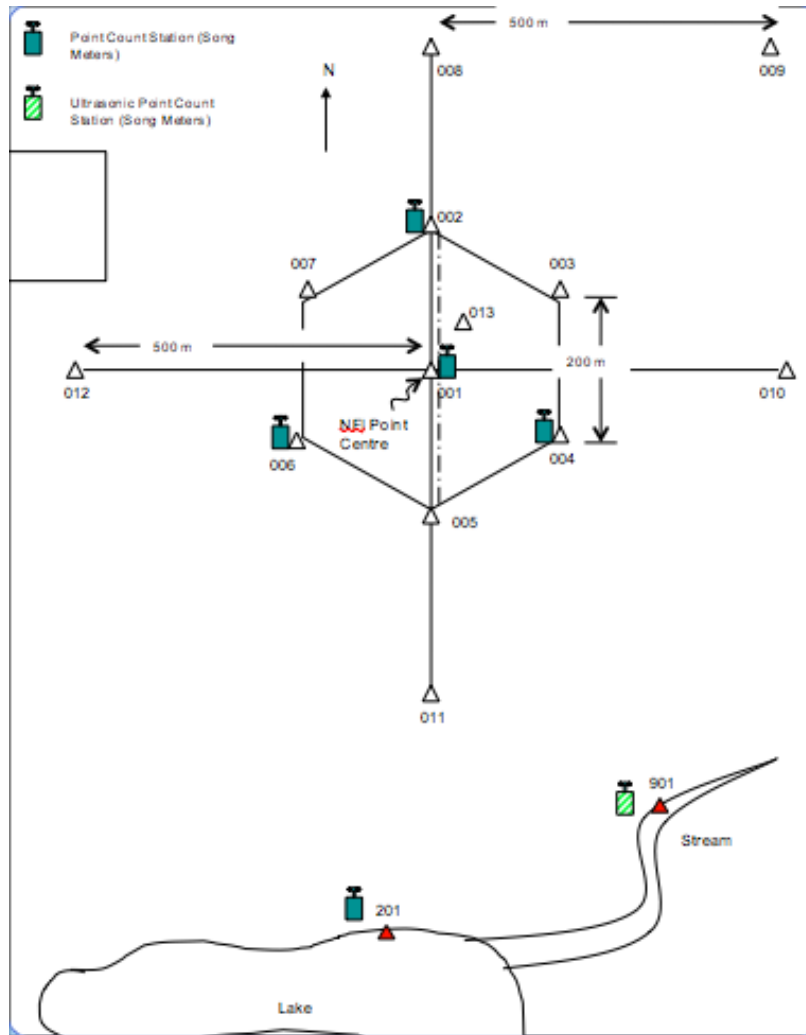


Figure 2.3. Short-term plot showing configuration used during the Far North Biodiversity Project in Ontario's far north showing SM2 and SM2BAT units at sampling stations.

The MSIM protocol specifies point counts at all seven hexagon stations. However, given the weight restrictions for helicopters and workload limitations of field crews, the FNBP used four ARUs as described above, plus the extra SM2BAT unit. Previous research has shown that recorders set up at all seven MSIM layout stations had a high degree sampling overlap among stations placed at 200 m intervals at each point of the hexagon (G. Holborn, personal communication, OMNR NW Region unpublished data 2010, 2011). Whereas ARU in each long-

term plot were active in one location for an entire sampling season, those in short-term plots were deployed for 6 days (2012) or 4 days (2014), and then relocated to sample a new area.

Interpretation of ARU recordings

The bird and anuran species vocalizations captured on each recording were identified aurally by experts and the results were then used in this study. The bat data were not used in this study. Selected recordings from all stations within long-term plots (001, 008, 009, 010, Figure 2.2) were interpreted and recordings from stations 002, 004, 006 and 901 for short-term plots were interpreted (Figure 2.3). The interpreter ranked the sound quality of recordings on a scale of 0-5, where 0 denoted recordings that were unusable because of wind, rain or other sound interference and 5 denoted excellent recording quality with no distracting noise. Only recordings with of sound quality 4 or better were analyzed. If a recording selected for interpretation was of poor quality, the next available high-quality recording was interpreted. Interpreters also rated their confidence in the identification of each species; only species identified with 80% confidence or better were used in the analysis. Recordings made at 05:30 were prioritized to capture the dawn chorus, and a smaller number of 22:00 recordings were interpreted to specifically target anurans and night-calling birds. For long-term plots, 05:30 recordings from each ARU were interpreted at five-day intervals; 22:00 recordings were interpreted at 10-day intervals. For each short-term plot, 05:30 recordings were interpreted for days 1, 3 and either day 4 (2014), or day 5 (2012); a 22:00 recording was interpreted for day 2. The number of interpreted recordings used in the analysis varied with the type of comparison.

Plot type comparisons (2012 data)

Since both plot types were deployed in Albany Ecodistrict over the same length of time, I can compare the efficacy of these two plot types in detecting bird and anuran richness within that year of the study. In 2012, 12 short-term plots were deployed in the Albany Ecodistrict (Crins et al., 2009) between June 7 to July 15. Two plots were established and monitored for six days, then two new plots were establishing for the next six days and so on. This strategy let us sample 12 distinct areas while collecting data across the ecodistrict for the core of the breeding season. Concurrently, long-term plots were deployed and left at 12 different locations for the duration of the breeding season.

In two cases where an SM2 unit failed at one of the point stations on a short-term plot, data from an extra SM2 unit at station 201 were used to keep the total count of SM units for each plot at four (total $n = 48$). Six SM2 units failed on long-term plots, but substitution was not an option for long-term plots which did not have the redundancy of extra ARUs, leaving a total of 42 ARUs to analyze for long-term plots compared with 48 for short-term plots. For short-term plots, two 05:30 (Days 1 and 3) and one 22:00 (Day 2) recordings were used for each of the 48 ARUs. For long-term plots, nine 10-minute recordings from 05:30 and five from 22:00 recordings were used for each of the 42 ARUs (at 5 and 10-day intervals, respectively) for a sampling effort (the number of interpreted recordings per richness estimate per station) of three recordings for short-term plots and 14 for long-term plots. This yielded a total of 144 recordings for short-term plots and 588 recordings for long-term plots (Table 2.1). In total, 528 recordings were from SM2 units

and 204 from SM2BAT units, for an average sampling effort of 8 versus 8.5 recordings for SM2 and SM2BAT units, respectively (Table 2.2).

Table 2.1. Bird species richness sample effort and yield by plot type in the Albany Ecodistrict of Ontario's far north in 2012.

| Plot Type | Plots established | Units analyzed | Total recordings interpreted | Sampling effort * |
|------------|-------------------|----------------|------------------------------|-------------------|
| Long-term | 12 | 42 | 588 | 14 |
| Short-term | 12 | 48 | 144 | 3 |

*number of recordings per richness estimate at a station

Table 2.2 Bird species richness sample effort, distribution among plot types and total recordings by autonomous recording unit type in the Albany Ecodistrict of Ontario's far north in 2012.

| Unit type | Units on long-term plots | Units on short-term plots | Total recordings analyzed | Sampling effort* |
|-----------|--------------------------|---------------------------|---------------------------|------------------|
| SM2BAT | 12 | 12 | 204 | 8.5 |
| SM2 | 30 | 36 | 528 | 8 |

*number of recordings per richness estimate per ARU

ARU type data comparisons using (2012 & 2014 data)

To more rigorously assess any sampling bias between ARU unit types (SM2 and SM2BAT), additional comparisons were made for long-term plots using a larger sample size that included data from three additional ecodistricts sampled in 2014 (Wood Creek, Winisk River and Dickey River). Short-term plots were excluded from this comparison since temporal coverage in 2014 for short-term plots was not comparable with long-term plots that year. As with the comparison of 2012 long-term and short-term plots, this analysis used 05:30 recordings interpreted at five-day intervals and 22:00 recordings interpreted at 10-day intervals. In the analysis, 738 recordings were included from SM2 and 261 recordings from SM2BAT units from all ecodistricts sampled

in 2012 and 2014 with an average sampling effort of 12 versus 10 for SM2 and SM2BAT units (Table 2.3).

Table 2.3. Bird species richness sample effort and total recordings by Automated Recording Unit type using 2012 and 2014 data from the Albany River, Winisk River, Wood Creek and Dickey River ecodistricts in Ontario's far north.

| Unit type | Units deployed | Failed units | Total recordings analyzed | Average sampling effort* |
|-----------|----------------|--------------|---------------------------|--------------------------|
| SM2 | 76 | 12 | 738 | 12 |
| SM2BAT | 27 | 1 | 261 | 10 |

*number of recordings per richness estimate per ARU

Statistical analysis

Using generalized linear mixed models and the “lme4” package in R version 3.3.1 (R Core Team, 2016), I tested whether plot types and ARU types detected species richness equally well, or if one plot type or ARU detected more species than the alternative. A Poisson link function was chosen *a priori*, as recommended for count data by Zuur et al. (2009). The predictors were plot type (long-term and short-term) and unit type (SM2 and SM2BAT). NFI plot was included as a random factor in all comparisons to account for any lack of independence caused by clustering of sampling units around individual NFI plots. The broader unit type comparison (SM2 vs SM2BAT) included 2012 and 2014 data, and models included Ecodistrict as an additive or interaction term. Using AICc model selection (Sugiura, 1978; Hurvich & Tsai, 1991), these models were compared against a base model containing only the unit type parameter. To assess model fit and the assumption of linearity and homoscedasticity for all models, I visually

inspected plots of residuals versus fitted values to ensure that there were no patterns in the residuals. R squared values were also considered to assess model fit.

2.3 Results

Bird species richness

Between 2010 and 2014, the ARUs from the FNBP detected 125 species of breeding birds (Table 1A, Appendix 1). In Albany River Ecodistrict in 2012, long-term plots captured an average of seven more bird species—or 1.5 times as many species—than short-term plots ($p < 0.001$) (Figure 2.5). There was no difference in the number of bird species detected between SM2 and SM2BAT unit types ($p = 0.359$, Figure 2.4, Table 2.4). When 2014 long-term plot data were combined with 2012 data to increase sample size, there was still no difference in the number of bird species detected between SM2 and SM2BAT units ($p = 0.17$, Figure 2.5, Table 2.4).

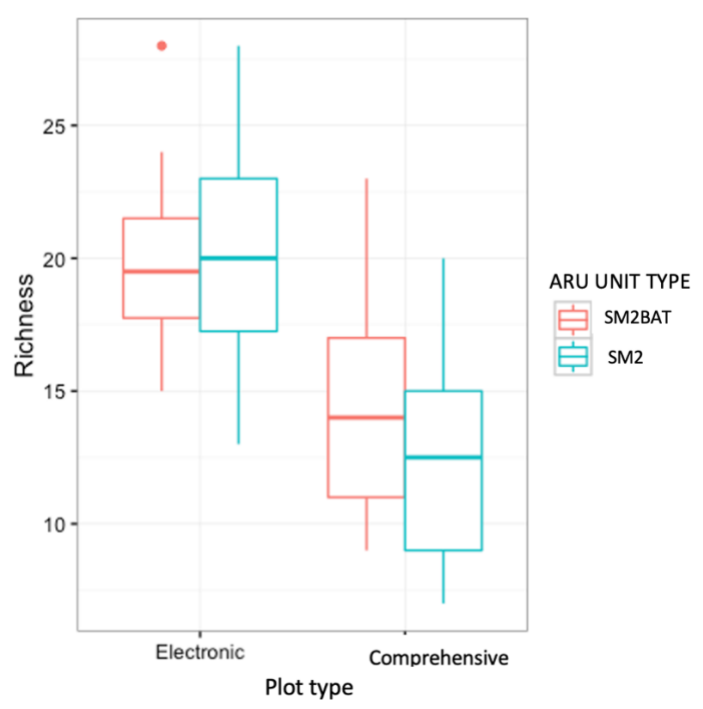


Figure 2.4. Median bird richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) by plot type and ARU unit type in the Albany river Ecodistrict of Ontario’s far north in 2012.

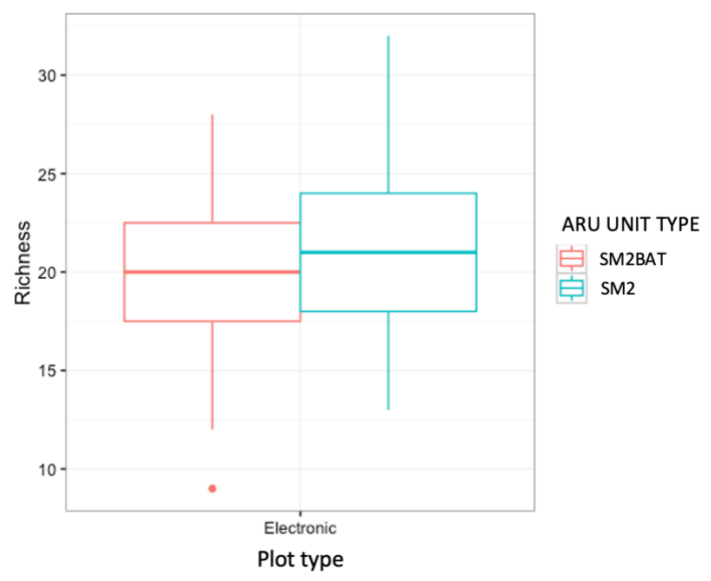


Figure 2.5. Median bird richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) by ARU unit type in Albany River Ecodistrict (2012) combined with Winisk River, Wood Creek and Dickey River Ecodistricts (2014) in Ontario's far north.

Table 2.4. Model results by A) plot type and ARU unit type in Albany River Ecodistrict of Ontario's far north in 2012 and B) ARU unit type in Albany Ecodistrict (2011) and Wood Creek, Dickey River, Winisk River Ecodistricts (2014).

| Response Variable | Predictor | Coefficient | Std Error | z- value | p-value |
|--|---------------------|--------------------|------------------|-----------------|----------------|
| A. Bird Richness (Albany River Ecodistrict - 2012) | Intercept | 3.02914 | 0.06253 | 0.06253 | <0.0001 |
| | SM2 Units | -0.05336 | 0.05821 | -0.92 | 0.359 |
| | Comprehensive plots | -0.42459 | 0.06997 | -6.07 | <0.0001 |
| B. Bird Richness (All Ecodistricts 2012 & 2014) | Intercept | 2.91839 | 0.05590 | 52.21 | <0.0001 |
| | Wood Cr | 0.07775 | 0.07658 | 1.02 | 0.3100 |
| | Dickey R | 0.14589 | 0.07187 | 2.03 | 0.0424 |
| | Winisk R | 0.14170 | 0.07547 | 1.88 | 0.0605 |
| | SM2 Units | 0.06966 | 0.05067 | 1.37 | 0.1692 |

For the overall unit type comparison using 2012 and 2014 data (Table 2.5), the base model containing only unit type with no term for Ecodistrict was the most parsimonious model; however, patterns in the residuals indicated unacceptable deviance from linearity. Although the residual plot for the additive model had a slight pattern not present in the interaction model, the increase in explained variance in the interaction model was negligible, and none of the interactions were significant. I report on the additive model since it was favored over the interaction model by AICc model selection and it was within 1.5 AICc points of the base model.

Table 2.5. AICc results for the base, additive and interaction models of bird species richness in Albany Ecodistrict (2012) and Dickey River, Winisk River and Wood Creek Ecodistricts (2014) in Ontario's far north.

| | AICc | ΔAICc | AICcWt | Cum.wt |
|--------------------|-------------|--------------------------------|---------------|---------------|
| Base | 560.78 | 0.00 | 0.64 | 0.64 |
| Additive | 562.26 | 1.48 | 0.30 | 0.94 |
| Interaction | 565.50 | 4.72 | 0.06 | 1.00 |

Anuran species richness

Six anuran species were detected in this study (*B. americanus*, American toad; *R. sylvatica*, wood frog; *R. clamitans*, green frog; *P. crucifer*, spring peeper; *L. septentrionalis*, mink frog; *P. maculate*, boreal chorus frog). In Albany Ecodistrict in 2012, an average of approximately 1.5 more species were detected in long-term plots than short-term plots ($p < 0.001$). As with the bird data, no difference was found in anuran detections between SM2 and SM2BAT units ($p = 0.78$, Figure 2.6, Table 2.6). No difference was found in the number of anurans detected between unit types when the sample size was increased by adding the long-term plot data from the 2014 Ecodistricts ($p = 0.43$, Figure 2.7, Table 2.6). For this comparison, plots of residuals versus fitted values indicated some lack of fit. However, examination of model predictions indicated that our model was conservative; a better fitting model would likely produce greater differences between treatments.

The difference in explained variance between the interaction and additive models was negligible, and both models had acceptable residual plots. The base model was within 2 AICc points of the

additive model, but the residual plot exhibited patterns not present in the additive model. Thus, I report on the additive model since it was favored by AICc as the most parsimonious (Table 2.7).

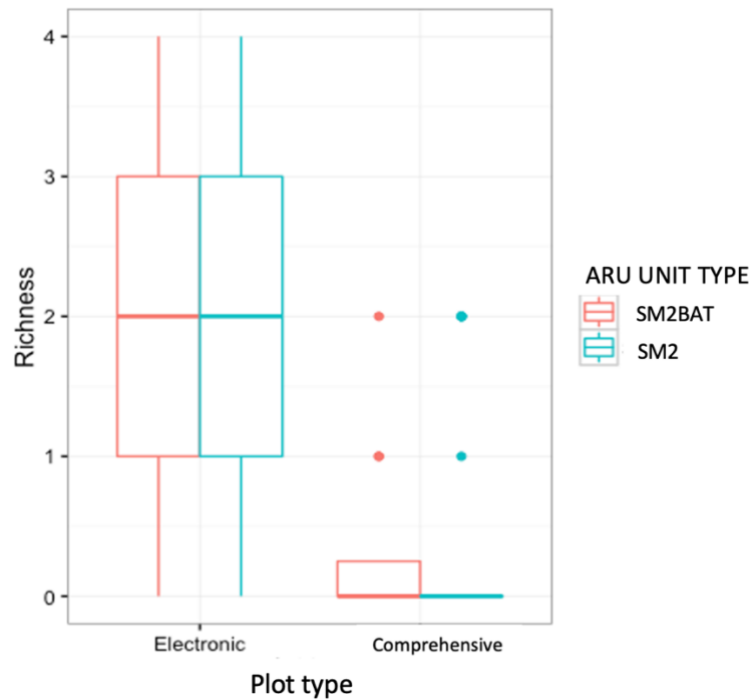


Figure 2.6. Median anuran richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) by plot type and ARU unit type in Albany River Ecodistrict (2012).

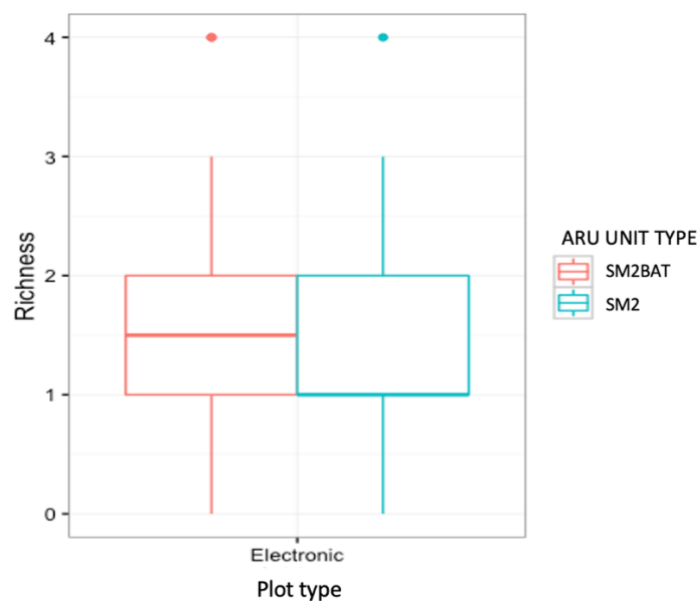


Figure 2.7. Median anuran richness (horizontal line), with the interquartile values (within box) and minimum and maximum range (vertical lines) for long-term plots by ARU unit type in Albany River Ecodistrict (2012) combined with Winisk River, Wood Creek and Dickey River Ecodistricts (2014).

Table 2.6. Model results by A). plot type and ARU unit type in Albany River Ecodistrict (2012) and B). ARU unit type in Albany Ecodistrict combined with Wood Creek, Dickey River, Winisk River Ecodistricts (2014).

| Response Variable | Predictor | Coefficient | Std Error | z- value | p-value |
|---|--------------------------|--------------------|------------------|-----------------|----------------|
| A. Anuran Species Richness (Albany River Ecodistrict 2012) | Intercept | 0.57227 | 0.32134 | 1.781 | 0.0749 |
| | SM2 Units | -0.06151 | 0.21835 | -0.282 | 0.7782 |
| | Comprehen- sive plots | -2.09266 | 0.52385 | -3.995 | 6.47e-05 |
| B. Anuran Species Richness (All Ecodistricts 2012 & 2014) | Intercept | 0.3859 | 0.2517 | 1.533 | 0.125 |
| | Dickey River | -0.2964 | 0.3210 | -0.924 | 0.356 |
| | Winisk River | 0.1044 | 0.3183 | 0.328 | 0.743 |
| | Albany River | 0.3911 | 0.2500 | 1.564 | 0.118 |
| | SM2 Units | -0.1414 | 0.1780 | -0.794 | 0.427 |

Table 2.7. AICc results for the base, additive and interaction models of anuran richness in Albany Ecodistrict (2012) combined with data from Dickey River, Winisk River and Wood Creek Ecodistricts (2014).

| | AICc | ΔAICc | AICcWt | Cum.wt |
|--------------------|-------------|--------------------------------|---------------|---------------|
| Additive | 261.58 | 0.00 | 0.58 | 0.58 |
| Base | 262.28 | 0.70 | 0.41 | 0.98 |
| Interaction | 268.63 | 7.05 | 0.02 | 1.00 |

2.4 Discussion

When using point counts, there have always been trade-offs made between how many sites to survey, how many visits to make to each site and budgetary constraints – especially in remote or difficult to access study sites (Carlson & Schmiegelow, 2002). Observer bias of biologists conducting point counts has also been a concern, especially when multiple observers are being used (Rempel et al., 2014; Shonfield & Bayne, 2017). With the advent of ARUs that are as good or better than biologists at detecting the sounds of singing or calling organisms in the field, it can be more efficient and cost-effective to use these devices rather than trained human observers (Rempel et al., 2014; Shonfield & Bayne, 2017). Using ARUs enables more repeat sampling of plots, reduces the time in the field and the associated risks of field activities, provides a permanent record of the data collected, and can reduce observer bias (Rempel et al. 2014; Shonfield & Bayne, 2017). As the choice of ARU makes and models has increased, considerable work has been done to explore the efficacy of different ARU units and optimal ways to use them in the field (Venier et al., 2012; Rempel et al., 2013; Rempel et al., 2014; Shonfield & Bayne, 2017). During the design of the FNBP, choices had to be made between prioritizing the use of

ARUs in short-term plots that could be moved regularly to sample more areas, versus using the ARUs in longer-term long-term plots, which reduced the total number of possible sites to be visited across the study area. My work makes a contribution to this research by quantifying the difference in bird and anuran species detection rates from two different types of ARUs and two differing plot designs in a large and remote study site.

ARU type comparison

Our results showed no significant difference in the effectiveness of SM2 versus SM2BAT meter in richness detections for anurans or birds. Although both ARU types performed equally well, SM2BAT units have the added capacity to collect bat data with no loss of bird and anuran data. This additional capacity could be useful in some biodiversity studies, however SM2BAT units are almost twice as expensive as SM2 units because they have both standard and ultrasonic circuitry. In addition to being more affordable, SM2s also have the built-in redundancy of an extra microphone should one of them get damaged by a bear, weather or other environmental factors. Since our study, Wildlife Acoustics Inc. has updated these ARUs to the SM4 and SM3BAT models. These updated versions should perform similarly to SM2 and SM2BAT units with respect to their ability to detect bird and anuran richness (Warren, C. Wildlife Acoustics, March 2019, personal communication). For any study not interested in bat data, I recommend the SM2-type units. Wildlife Acoustics Inc. now has more affordable models specifically for bats.

Avian plot type comparison

I found long-term plots were a more effective means of sampling bird species richness in Ontario's far north; on average long-term plots detected about seven more species than short-term plots—or about 1.5 times as many species. The obvious explanation for this substantial difference in richness detections is the difference in sampling effort (the number of interpreted recordings at each station) between long-term versus short-term plots. Although the number of long-term and short-term plots was the same (12 plots) and total the number of ARUs deployed for each plot type was very similar (42 on long-term plots and 48 on short-term plots), the total number of recordings—and thus the average number of recordings per richness estimate at a station—was much greater for long-term than short-term plots (14 versus 3 respectively). Given this difference in sampling effort, and the potential variability in the arrival of birds at their breeding territories, it is not surprising that more bird species were detected over the longer sampling periods of the long-term plots compared with the short-term plots (Shiu and Lee, 2003). However, it is valuable to understand the magnitude of the difference in species detection rates between these two plot protocols to inform future study design decisions.

To optimize future studies, it is also worth thinking about some more nuanced considerations for point count protocols. The breeding birds in our study lend themselves well to point count surveys because they are territorial, and their breeding seasons are relatively synchronous (Venier et al., 2012). Thus, repeated visits to a survey point over the breeding period should sample the same community, leading to more accurate species richness estimates (Venier et al., 2012). However, Rempel et al. (2014) suggest that when using audio recordings to estimate

occupancy, not all boreal bird species are equally detectable. They found that for birds with larger territories relative to the potential detection area of the ARU, detection rates were lower because there was a higher probability they would be outside the ARU detection range during their daily movements. These findings suggest that one reason long-term plots detected more species is that the higher number of recordings from each site provides a higher probability that species with large territories would be detected; the longer the ARU was operating, the higher the probability that a wide-ranging species would visit more parts of its large territory and end up being detected by an ARU within that territory. Additionally, Semli & Boulinier (2003) suggest that the frequency of vocalizations can also vary between the start and end of the breeding season, and Rempel et al. (2014) suggest that short term plots may also be influenced by immediate weather patterns; several cold or wet days in a row may lead to fewer vocalizations for some species. Thus, species detection rates during short-term plots may not be optimal for species with larger territories and are also much more sensitive to any seasonality in vocalizations and the influence of short-term weather patterns than long-term plots with their greater temporal coverage.

Anuran plot type comparison

Long-term plots detected an average of about 1.5 more species than short-term plots, a substantial difference given there were only six anuran species detected in total across our study site, and all but six plots detected 4 species or fewer.

Anurans can be classified into explosive and prolonged breeders. For explosive breeders, the entire breeding season is anywhere between 1 to 14 days, whereas the prolonged breeders may

breed over a period of one month or longer (McCauley et al., 2000). Of the six anuran species detected across all plots, two (wood frog and American toad) can be classified as explosive breeders (Oseen & Wassersug, 2002), whereas the other species are classified as prolonged breeders (Oseen & Wassersug, 2002; Whiting, 2010). As ectotherms, the timing and duration of anuran breeding behaviour, during which their vocalizations can be detected by ARUs, can be highly influenced by environmental factors, such as air and water temperature, rainfall, and humidity (Blair, 1961; Dorcas et al., 2009; Oseen & Wassersug, 2002). Explosive breeders are generally less responsive to environmental variables than prolonged breeders (Oseen & Wassersug, 2002). Thus, unlike the breeding birds in our study, anuran breeding may not be synchronous among species across the far north. Given the variable length and timing of breeding seasons for anurans—in addition to the differences in sampling effort between plot types—it is not surprising that more anurans were detected over the much longer sampling period of long-term plots than during the short six-day short-term plots. The longer sampling period of long-term plots provides more opportunity to capture vocalizations during the variable and potentially short anuran breeding periods.

Conclusions

When conducting auditory surveys, it is common practice to re-visit survey points more than once to generate a better estimate of species richness (Hutto et al., 1986; Ralph et al., 1995). In the case of territorial and actively breeding birds, any increase in richness detections with additional visits is assumed to be an improved richness estimate for the breeding birds at that survey plot, rather than the arrival of new species to the area (Venier et al., 2012). With anurans,

repeated visits to survey points may also improve species detections by overcoming the variability in breeding times and duration for different species and the impact of environmental conditions.

In our study, both SM2 and SM2BAT units from Wildlife Acoustics Inc. performed equally well at detecting birds and anurans. The extended temporal duration and greater number of recordings for each long-term plot compared to short-term plots appeared to provide better species richness estimates for bird and anurans.

The Far North Biodiversity Project was a multi-taxa survey and, thus, collecting ARU data during the short short-term plots was logical since biologists were already on the plot sites. These short-term plots allowed for sampling of several taxa in numerous parts of Ontario's far north while also gathering data via ARUs at each plot. However, future studies using ARUs for the detection of vocalizing bird and anuran species in large and remote landscapes such as Ontario's far north would benefit from deploying ARUs for the duration of the breeding season of their target species rather than deploying units for shorter duration and moving them regularly to sample more sites. While the latter approach may seem appealing, our results suggest that longer plots provide better species richness estimates.

Chapter 3 – Determinants of songbird diversity in Ontario’s far north

3.1 Introduction

Defining biodiversity

The term biodiversity is a contraction of *biological diversity* and a key concept in ecology that can be summarized as the total variation of living systems from genes to species and ecosystems (Purvis & Hector, 2000). MacArthur (1964, 1965), was the first ecologist to use the term *diversity*, and in the decades since, the concept has been expanded to include different notions for species (taxonomic), functional, genetic, phylogenetic and chemical diversity among numerous other groupings (Daly et al., 2018). Diversity has also been partitioned into different categories based on scale: *gamma* diversity is the total diversity across a landscape, *alpha* diversity is the diversity within a particular habitat or ecosystem, and *beta* diversity represents the difference in diversity between distinct habitats or ecosystems (Daly et al., 2018; Jost, 2006). In this study I am concerned with alpha diversity.

The multiple uses of the term *diversity* became problematic enough that Hulbert (1971) suggested it had become meaningless and the term should be abandoned. Two decades later, Delong (1996) unearthed 85 different definitions for biodiversity, and Ricotta (2005) described the concept as “extremely confusing.” Nonetheless, since many ecologists find the idea of biodiversity useful when thinking about ecological systems, a substantial literature has been published on the concept. For most ecologists, the term biodiversity reflects intuitive ideas about species and ecosystems, but when we try to quantify those things, it gets complicated.

Measuring diversity

In addition to, and perhaps partially because of, the difficulty of defining the concept of biodiversity is the challenge of measuring it. Dozens of mathematical indices have been created to tackle this problem—each with its own bias—and they often give contradictory results (Jost, 2006; Daly et al., 2018). Chao and Jost (2004) proclaimed that the array of diversity indices in the literature is “bewildering.”

In ecology, the most commonly used metric is species diversity, which is most commonly quantified using species richness, the Shannon index, and/or the Simpson Diversity index (Daly et al., 2018; Pallman et al., 2012; Roswell and Dushoff, 2021; Tuomisto, 2010). Species richness (i.e., the number of species present in an area) is often used in studies over large spatial extents and is intuitively easy to understand; a community with 8 species is twice as diverse as a community with 4 species. However, richness is also the simplest of species diversity measures, and can give unwarranted weights to rare species because it does not account for the relative abundance of species within a community (Jost, 2006; Tuomisto, 2010; Daly et al., 2018). By comparison, the Shannon index and the Simpson Diversity index are the two most popular compound indices that incorporate richness and abundance data into a single index, but they are not interchangeable. Shannon’s index weights each species exactly according to its frequency, whereas Simpson’s Diversity gives more weight to common or dominant species (Whittaker, 1965). Thus, the choice of the index must be made carefully as this choice can have serious implications when interpreting results (Morris et al., 2014).

The Shannon index has its origins in information theory and was originally proposed by Claude Shannon to quantify the uncertainty, or entropy, in strings of text (Shannon, 1948). It is also known as the Shannon-Weiner index, the Shannon-Weaver index and Shannon entropy (Daly et al., 2018). Shannon's diversity index is a measure of uncertainty when sampling a community (Shannon, 1948; Jost, 2006; Morris et al., 2014). As an ecological example, if a species is randomly selected from a highly diverse community, there will be relatively high uncertainty in its identity, leading to a higher index value. By comparison, in a non-diverse community, the identity of a randomly selected species will be less uncertain, and the index value will be lower.

By contrast, the Simpson Index (D) measures the probability that two individuals randomly selected from a sample will belong to the same species (Daly et al., 2018). Unlike Shannon's diversity index which has no upper limit, the Simpson Index is bound between 0 and 1, with 0 representing infinite diversity and 1 representing no diversity. That is, the bigger the value of D , the lower the diversity. This scaling is counter-intuitive, so in biology, D is often subtracted from 1 to give the Simpson Diversity Index (also referred to as the Gini-Simpson index, which I will use hereafter), where 0 is no diversity and 1 is very high diversity. Expressed this way, this index represents the probability that two individuals randomly selected from a sample will belong to different species. It places more emphasis on the dominant, or common, species in a community. These different permutations of Simpson's index are used in the literature, so it is important to ensure one understands which index an author is using (Daly et al., 2018).

In essence, species richness, the Shannon and the Gini-Simpson indices each measure different facets of a community's species composition and use different units to quantify diversity

(species, uncertainty, and probability, respectively), making comparisons among them difficult. A biologist may be able to calculate whether there is a statistical difference in raw index values between one community and another, but this explains very little about the magnitude—or the ecological significance—of that difference.

What does a Shannon Index value of 2.45 mean in biological terms? Does it represent a lot or a little diversity? How much more diverse is a community with a Shannon index value of 2.9, and how does this compare to a community with a Gini-Simpson value of 0.99? These are important questions.

Part of the problem in answering them is the non-linear nature of the Shannon and Simpson's indices. For perfectly even communities, both indices increase non-linearly; with increasing richness, communities appear more similar with respect to the magnitude of index values (Figure 3.1). This is more pronounced with the Gini-Simpson index since it is bound between 0 and 1. This non-linear response can lead to interpretation challenges, especially for ecologists accustomed to the linear and intuitive nature of species richness.

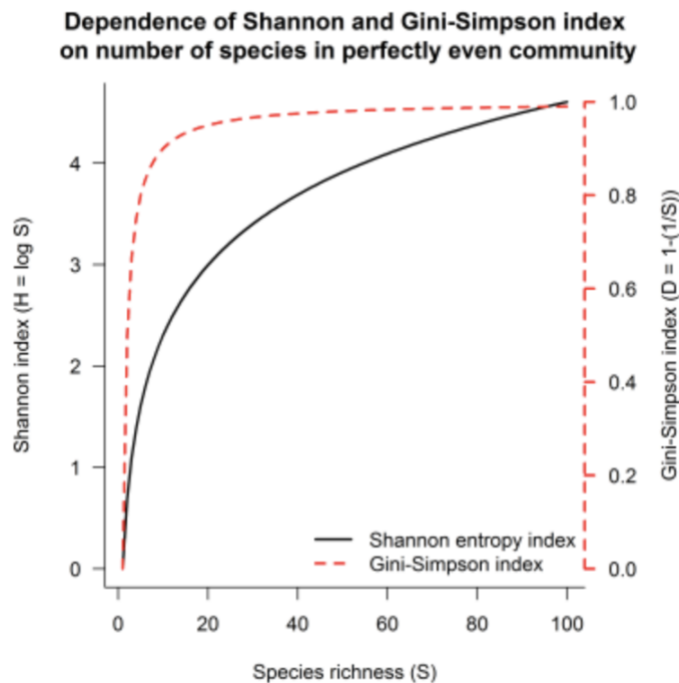


Figure 3.1. Dependence of Shannon and Gini-Simpson index on a number of species in a perfectly even community (Zeleny, n.d.).

To illustrate this problem, Jost (2009) used an example of a continent losing 999,900 of its one million species from a meteor impact. The raw Gini-Simpson index values change from 0.999999 before the strike to 0.99 afterwards. This is a change in the index value of just 1% even though there has been a catastrophic loss of diversity on the continent. This example illustrates how reporting the raw value of an index can make it difficult to interpret the magnitude of the results and can lead to misinterpretations of findings (Ricotta, 2003; Jost, 2006). This impact is more pronounced in the Gini-Simpson index than with Shannon's. Nonetheless, for any index, raw values are simply a proxy for the concept of diversity and should not be treated as a true measure of diversity as biologists understand it intuitively (Tuomisto, 2010). Jost (2019) contends that poor interpretation of indices arose, not from the indices themselves, but from biologists using these metrics as if they all shared the same intuitive and mathematical properties

as species richness, which they do not; different indices place more or less emphasis on different components of diversity.

Nonetheless, all these indices can be unified, subject to their sensitivity to relative abundance, or frequency of the species in the community (Daly et al., 2018; Jost, 2019). As a measure of diversity, species richness is not at all sensitive to abundance, treating rare and common species identically. The Shannon Index weights all species exactly by their frequency, without favoring either common or rare species, and the Gini-Simpson index gives common species more weight than rare species.

Using this approach, raw index values can be converted to Hill Diversity (Roswell et al., 2021). Hill (1973) was the first to recognize the utility of measuring diversity in units of effective numbers of species based how an index weights relative species abundance. After conversion, diversity is measured in units of *effective number of species*. This metric behaves in an intuitive and linear fashion that is easy to understand and allows for easy comparisons among communities and different studies regardless of what index is used (Jost, 2006; Daly et al., 2018). Amidst all the confusion in the literature regarding how to quantify diversity, Hill (1973) suggested that “the notion of diversity is little more than the notion of the effective number of species present,” a clarifying argument that was largely ignored for decades, until Jost (2006) re-introduced these ideas to ecologists (Roswell et al., 2021). There is now a growing consensus that using Hill Diversity is a preferred method for measuring community diversity (Roswell et al., 2021).

Converting raw index values into Hill Diversity, or the indices' number-equivalent, involves mathematically building a reference community of equally common species and calculating how many of those species correspond to a particular index value. For example, a community with a Shannon index value of 3.2, equates to 24.5 equally common species. Revisiting the questions posed earlier, Shannon Index values of 2.45 and 2.90 correspond to 11.6 and 18.2 effective species respectively, or a difference of about 7 species, which could be a lot or a little, depending on the species and community in question. The third community with a Gini-Simpson index of 0.99 represents 100 effective species, a substantial difference from the others that is very difficult for most people to recognize if they only reference the raw index values. However, after converting index values to their Hill Diversity equivalents, the magnitude of the differences in diversity between these communities is now in units that are easily understood: they behave in a linear fashion and are far less prone to misinterpretation than non-linear diversity indices (Daly et al., 2018).

The question then becomes which index to use, especially since different metrics may have different responses to scale (González-Megías et al., 2007). The answer depends on what you are interested in measuring. Authors interested in the most common species in a community may wish to use effective number of the Gini-Simpson index (HILL-GS), whereas the effective number of the Shannon index (HILL-SHAN), with its “middle-ground” sensitivity to rare species, may be a reasonable measure for most studies (Kempton, 1979; Roswell et al., 2021). Although it has been widely used, species richness (RICH) is not recommended as a single measure of diversity by many authors who have published on quantifying diversity (Magurran & McGill, 2011; Chase & Knight, 2013; Haegeman et al., 2013), because it places excessive

weight on rare species, is very sensitive to sample size and is difficult to estimate outside of controlled settings (González-Megías et al., 2007; Daly et al., 2018; Roswell et al., 2021). However, species richness still has its place, especially when combined with other metrics. For general diversity studies, many authors advocate using multiple diversity measures as this provides a more comprehensive picture of the shape of a community compared to any single measure (Stirling & Wilsey, 2001; Ma, 2005; González-Megías et al., 2007, Roswell et al., 2021). Here I use RICH, HILL-SHAN and HILL-GS as response variables because they provide readers with a thorough picture of avian diversity in the Ontario's far north, and because this comprehensive approach is consistent with emerging best practices in the field. (González-Megías et al., 2007; Daly et al., 2018, Roswell et al., 2021).

Biodiversity Distribution

Beyond the challenges of measuring diversity, a striking feature of Earth's biodiversity is its unequal distribution across the globe, with the number of species generally decreasing from the tropics to the poles, among many other well-documented gradients (Tittensor & Worm, 2016). Explanations for these patterns have challenged ecologists for more than 200 years, becoming a core theoretical question in ecology and evolutionary biology (Worm & Tittensor, 2016) and stimulating over 30 hypotheses. (Davies et al., 2007; Luo et al., 2012). With large-scale environmental deterioration from human activities, understanding foundations of global and regional variability in species diversity is no longer a matter of theoretical interest; it is critical for long-term biodiversity conservation planning (Kerr & Packer, 1999).

Two of the most recognized hypotheses to explain species diversity gradients are the species-energy hypothesis (Wright, 1983) and the habitat heterogeneity hypothesis (Méró et al., 2015) (Simpson, 1949; MacArthur & Wilson, 1967), both of which are recognized in shaping species distributions (Davies et al., 2007; Luo et al., 2012). The species-energy hypothesis suggests that higher species diversity arises in areas with higher productivity, ambient energy and water-energy dynamics (Carrara & Vázquez, 2010; Hawkins et al., 2003; Wang et al., 2009). In regions with more solar radiation and precipitation, higher primary productivity is expected to promote growth, reproduction, and species differentiation, leading to greater biodiversity (Carrara & Vázquez, 2010; Clarke & Gaston, 2006; Currie, 1991). The habitat heterogeneity hypothesis posits that variation in habitat features such as landscape, vegetation type, vegetation structure and elevation can produce a greater diversity of habitats for co-existing species, leading to higher biodiversity (Pianka, 1966; Kerr and Packer, 1997; Hugo & van Rensburg, 2008).

Variability in energy and habitats work in conjunction; energy variables are largely responsible for patterns in distribution and productivity of terrestrial plants across the globe (Holdridge, 1967), which then influence patterns of other taxa, including vertebrates (Hawkins et al., 2003; Currie et al., 2004). Temperature can directly limit animal distributions by excluding individuals from regions where physiological tolerances are exceeded (Root, 1988; Currie, 1991). Energy may also act indirectly on species distributions through energetic limitations on plant growth and food web development (Brown, 1981; Wright, 1983). Subsequently, vegetation composition and structure are well-documented drivers of local and regional abundance and community composition of bird populations (MacArthur, 1964; Rotenberry & Wiens, 1980; Cody, 1981; Davidowitz & Rosenzweig, 1998). Whereas energy variables typically influence the

continental distribution of species, vegetation affects the provision of shelter, food and other important aspects of habitat quality at the scales of the territory, patch and landscape (Johnson, 1980).

According to Johnson's (1980) hierarchical model of habitat selection, energy is viewed as controlling first-order selection, corresponding to the geographic range a species occupies, whereas vegetation influences second-order selection of home-ranges through individual choices such as specific foraging or nesting sites. In other words, climate and habitat variables tend to operate at different scales. Understanding the impact of scale on different variables is critical to understanding variation in biodiversity (Gaston, 2000; Hurlbert & Jetz, 2007; Whittaker et al., 2001). Scale consists of two important attributes: the unit of sampling, defined as "resolution" or "grain" and the geographical space, or "extent" covered by the study (Wiens, 1989; Scheiner, 2003; Rahbek, 2005). The choice of spatial extent and grain can directly affect the relative importance assigned to environmental variables, their hierarchical organization and the comparison of results from different studies (Rahbek & Graves, 2001; Johnson et al., 2004; Olivier & Wotherspoon, 2005; Rahbek, 2005; Luoto et al., 2007).

Jiménez-Valverde et al. (2011) found that avian distributions are well-described by energy characteristics at the large spatial extent of North America when modelling bird distributions using climate variables at a grain of 75 km. At a smaller geographical extent of the country of China, Luo et al. (2012) explored the predictive power of energy and habitat heterogeneity variables to model the distribution of vertebrate species richness. At a grain of 100 km, energy and habitat heterogeneity variables explained 67% and 25% of vertebrate richness, respectively.

Likewise, when modelling the abundance of 98 bird species across the boreal forest of northern Canada, Cumming et al. (2014) found climate variables (at 10 km resolution) explained 77% of variance in bird species abundance, and vegetation variables (mostly land cover type at 250m resolution and April leaf index at 1 km resolution) explained 23%. These results support Wright's (1983) assertion that determinants of bird species distributions are hierarchically structured with climate largely dictating broad patterns of species distributions (Currie, 1991; Huntley et al., 1995; Parmesan, 1996), and land cover and habitat variables playing smaller, but important roles (Venier et al., 2004; Pearson et al., 2004). Thuiller et al. (2004) suggest that including land cover data in bioclimatic models at a coarse grain of 50 km does not greatly improve the predictive power of models, whereas other studies have found that land cover at finer grains can significantly improve spatial predictions of bird, plant and butterfly species (Hill et al., 1999; Pearson et al., 2004; Luoto et al., 2007). In a study of boreal birds in Finland (300,000 km²), Luoto et al. (2007), explored the relative importance of climate and land cover variables in bird species distribution models at multiple resolutions. Using bird atlas data at a 10 km by 10 km grain, they re-sampled their dependent and explanatory variables at 20 km, 40 km, and 80 km grains, and found that the inclusion of land cover variables increased the performance of models at 10 km and 20 km grains, but not at the 40 km grain. Inclusion of land cover at the 80 km grain decreased the performance of models. Luoto et al. (2007) results show that habitat data can strengthen climate-based distribution models for boreal birds if the work is conducted at grains that are fine enough.

There is a well-documented positive relationship between habitat heterogeneity and species diversity, especially in the case of avian communities (MacArthur, 1961; Tews et al., 2004). The

habitat heterogeneity hypothesis predicts that with an increase in habitat types, resources and structural complexity, there should be a corresponding increase in the available niche space thereby allowing more species to coexist (e.g. Currie, 1991; Tews et al., 2004). However, more recent work (e.g. Allouche et al., 2012; Yang et al., 2015) provides evidence that the response in diversity to increasing habitat heterogeneity is not necessarily a continually increasing positive curve. Rather, increasing heterogeneity beyond a certain point can reduce the effective area available for individual species, reducing species richness and population sizes. A meta-analysis by Stein et al. (2014) suggests a positive relationship between diversity and habitat heterogeneity is the general rule, but the response can depend on the variables being used and the scale of the study. For conservation planning purposes at local or regional levels, understanding the finer-scale relationship between species diversity and habitat heterogeneity is important. For example, a bell-shaped response to heterogeneity would warrant prioritizing areas of intermediate heterogeneity for protection, whereas increasing positive responses suggest areas of high habitat heterogeneity should be prioritized. Moreover, it is difficult to predict *a priori* what diversity measure or spatial scale is most appropriate in any study (Stein, 2015). Thus, biodiversity studies should include multiple spatial scales and multiple diversity metrics (González-Megías et al., 2007).

Study area

This study was undertaken in the far north of Ontario, Canada. Defined by Ontario's Far North Act, 2010, S.O. 2010, c. 18 s.2, the far north of Ontario encompasses approximately 441,000 square kilometers of intact ecosystems composed predominantly of boreal forest, swamp, bogs and fens (Figure 1.1, Far North Science Advisory Panel, 2010) situated approximately north of

50.00 N. Unlike other parts of the province, this region has had very little industrial development (Far North Science Advisory Panel, 2010).

The region is comprised of two major ecozones: the Hudson Bay Lowlands and the Ontario Shield, which are further divided into 13 ecodistricts based on biogeoclimatic characteristics (Crins et al., 2009). The Hudson Bay Lowlands are the third largest wetland in the world (Abraham & Keddy, 2005). This region is also the world's second largest peatland and is a globally significant carbon sink (Packalen et al., 2014). In conjunction with neighbouring parts of Manitoba, Ontario's far north forms one of the largest pieces of intact forest in the world (World Resources Institute, 2010). The far north provides habitat for species at risk including woodland caribou (*Rangifer tarandus*), polar bears (*Ursus maritimus*), wolverines (*Gulo gulo*), olive-sided flycatchers (*Contopus cooperi*). Overall, 340 species of birds are known to be supported by Ontario's far north ecosystems during some point during their annual cycle (Abraham and McKinnon, 2011). Of those, 190 species have been documented breeding in the region (Far North Science Advisory Panel, 2010), making the far north an important nursery for North American boreal breeding birds, which live in low densities across the landscape (Stralberg et al., 2018).

In 2009, the Ontario Ministry of Natural Resources (OMNR) initiated the Far North Biodiversity Project (FNBP) – a five-year multi-species biological inventory project aimed at collecting baseline biodiversity data to help inform land use planning for the region. The project collected data on the distribution and abundance of numerous taxa including vertebrate, plant, insect and lichen species. Sampling of vocal species like bats, birds and anurans was done using long-term

bioacoustic monitoring devices (hereafter referred to as autonomous recording units, or ARUs, Chapter 2). Here, I use the bird data from the FNBP.

Objective and hypotheses

The objective of this study is to describe and better understand determinants of the distribution of breeding bird diversity in a large, remote and largely ecologically intact region of Ontario, Canada. I focus on birds that breed in the far north including landbirds, waterbirds, waterfowl and shorebirds that have recognizable calls used to defend territories and attract females during the breeding season. All breeding birds were included in my analysis because I deemed all species, whether common or rare, as important components of the breeding bird diversity of Ontario's far north. However, no playbacks were used, and thus secretive species may be underrepresented.

I used the FNBP bird data and a collection of energy and habitat predictor variables to (1) test the relative importance of the habitat heterogeneity and species-energy hypotheses with respect to breeding bird diversity at various grains of analysis, and (2) create distribution maps for breeding bird diversity across this region. I expected that at smaller grain sizes within our study I would find more support for the habitat heterogeneity hypothesis whereas at the larger grains the species-energy hypothesis would find greater support. I will compare the relative strength of these hypotheses through a model selection process in which a set of candidate general linear models will be ranked based on their explanatory power while accounting for model parsimony.

3.2 Methods

Avian data collection

Avian data were collected at sample plots across the far north of Ontario, located at the centre of randomly selected 20 km by 20 km grid cells from the National Forest Inventory (Gillis et al., 2005). Plots were stratified to ensure representative coverage for all ecoregions. Plots were accessed by helicopter and restricted to lie within a 150 km radius from the closest staging community which was the maximum one-way flight distance for a helicopter loaded with field crews and equipment. If the designated random point location was too wet, too forested or otherwise inaccessible for helicopter landings, plots were relocated to the nearest possible landing from which similar habitat could be accessed. FNBP staff collected data from 2009 to 2014. However, because of different sampling methods across years, and technical problems with equipment, I only use data from the five-year period 2010 to 2014 (Figure 3.2).

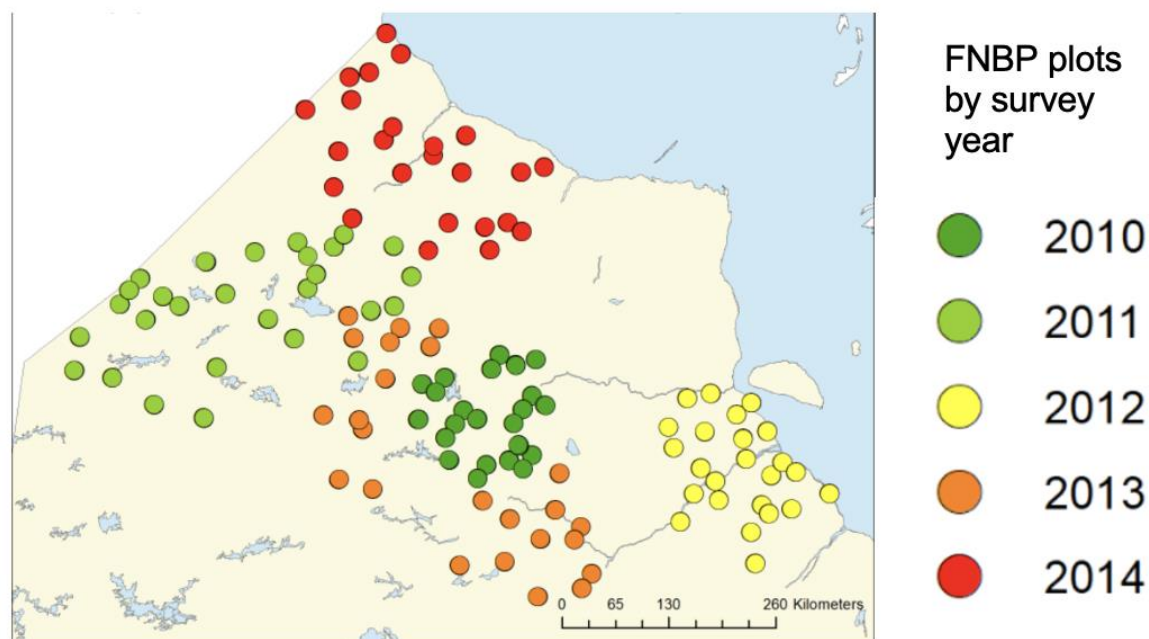


Figure 3.2. Far North Biodiversity Project plot locations in Ontario's far north 2010-2014

Two types of autonomous recording units (ARUs) were used to collect audio recordings of bird vocalizations: SM2 and SM2BAT units, both made by Wildlife Acoustics Inc. SM2 units have two microphones – one on each side of the device – to record bird vocalizations. SM2BAT units look identical but have one standard microphone for birds and one ultrasonic microphone to record bats. There are no significant differences in the detection rates for bird species between unit types (Chapter 2). All song meters were programmed to record 10-minute point counts daily at 05:30, 06:00, 06:30, 07:30 to capture the dawn chorus, and at 22:00 and 23:00, to specifically target birds that vocalize at night. Song meters were fixed to tree trunks or posts approximately 1.5 m above the ground. Care was taken to reduce sound interference by removing any vegetation within a one-meter radius of the microphones and to avoid setting up song meters near moving water.

Interpretation of ARU recordings

Bird species were identified aurally by experts listening to point count recordings following Rempel et al. (2014). The interpreter ranked the sound quality of bird recordings on a scale of 0-5, where 0 denoted recordings that were unusable because of wind, rain or other sound interference and 5 denoted excellent recording quality with no distracting noise. If a recording selected for interpretation was of poor quality, the next available high-quality recording was interpreted. Interpreters also rated their confidence in the identification of each species; only species identified with 80% confidence or better were used in the analysis. A small number of recordings were less than 10 minutes long. I only included recordings of 7.5 minutes or longer. Recordings made at 05:30 were prioritized to capture the dawn chorus, with a smaller number of 22:00 recordings interpreted to specifically target night-calling birds. For long-term plots, 05:30

recordings from each ARU were interpreted at five-day intervals; 22:00 recordings were interpreted at 10-day intervals. For each short-term plot 05:30 recordings were interpreted for days 1, 3 and either day 4 (2014), or day 5 (2012, 2013); a 22:00 recording was interpreted for day 2. Records that did not provide species-specific identification (e.g. woodpecker sp, duck sp, waterfowl taking off, insect chorus etc), and any blank records or species identified as unknown were filtered out.

Plot configurations – long-term

Songmeters were deployed in two different configurations: long-term and short-term plots. These configurations were adapted from the Multiple Species Inventory and Monitoring Protocol (MSIM) developed by the US Forest Service (Manley et al. 2006). On long-term plots, four songmeters (three SM2 and one SM2BAT) were deployed in a 500m square configuration with a songmeter at a sampling station at each corner (Figure 3.3). Whenever possible SM2BAT units were placed at an aquatic, or other ecological edge, to target aquatic birds and bats.

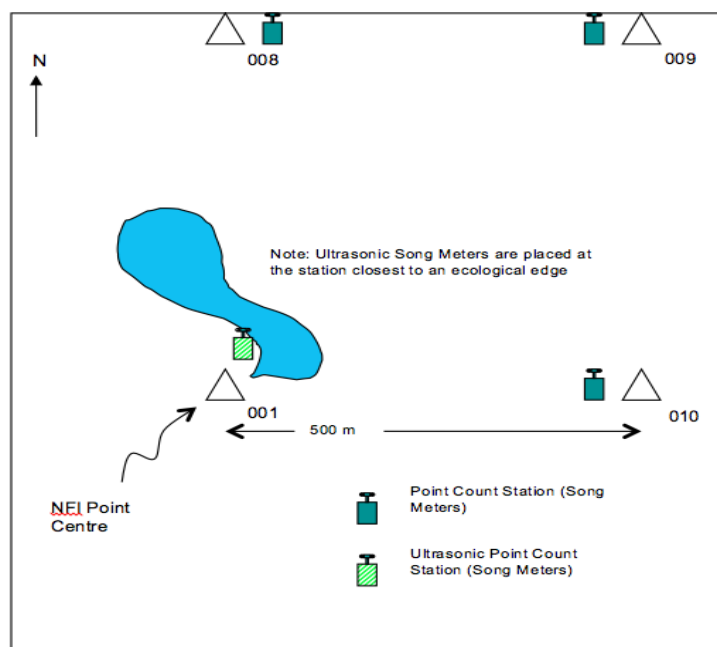


Figure 3.3. Configuration of long-term plots during the Far North Biodiversity Project in Ontario's far north showing SM2 and SM2BAT units

The MSIM protocol prescribed 1000 m by 1000 m squares. However, because of the large size of our study area and the expense of helicopter time, the FNBP opted for 500 m by 500 m squares. This arrangement allowed for faster plot set up and enabled the deployment of extra plots.

In 2010 and 2011 long-term plots were deployed for 10 days and three weeks respectively, before being moved to new locations where the deployment was repeated. In 2012, 2013 and 2014, long-term plots were deployed early in the spring at the beginning of the bird breeding season and left at the same location from approximately late May until mid-August, depending on the field season.

Plot configurations – short-term

On short-term plots, ARUs were deployed in a 400 m diameter hexagon. Hexagons were oriented towards north with SM2 units placed at stations at the north, southeast, southwest and center locations (Figure 3.4). The centre station was intended as backup in case other units failed and was offset 100 m from plot center to avoid disturbance by field crews conducting surveys of other taxa near plot center. Lastly, an SM2BAT meter was placed at least 200 meters away from the other units at an ecological edge (edge of stream, lake, pond or interface between bog and forest or fen and forest) at the discretion of field crews, to target aquatic birds.

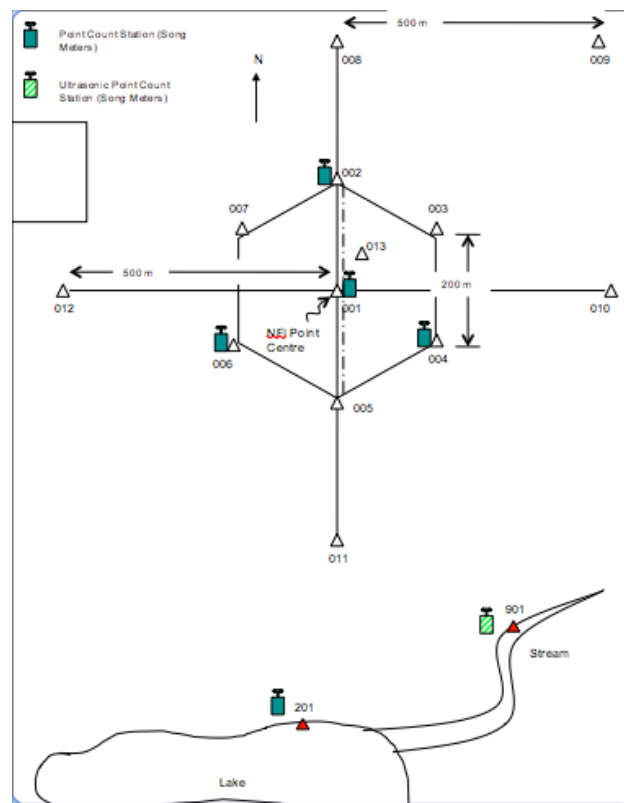


Figure 3.4. Configuration of short-term plots during the Far North Biodiversity Project in Ontario's far north showing configuration of SM2 and SM2BAT units.

The MSIM protocol specifies point counts at all seven hexagon stations. However, given the weight restrictions for helicopters and workload limitations of field crews, the FNBP used four songmeters as described above, plus the extra SM2BAT unit. Previous research has shown that recorders set up at all seven MSIM layout stations had a high degree of sampling overlap among stations placed at 200 m intervals at each point of the hexagon (G. Holborn, personal communication, OMNR NW Region unpublished data 2010, 2011). short-term plots were deployed for six days at each site between 2010-2013 and for four days in 2014.

Diversity Calculation

I explored diversity at the plot level using three forms of Hill Diversity representing different levels of sensitivity to common species: RICH, HILL-SHAN and HILL-GS. The analysis was conducted at the plot level, rather than station level because the resolution of our energy variables does not vary meaningfully among the stations within a plot, making the plot-level a much better match for the resolution of those variables. Also, the nature of the hypotheses I am testing has to do with more broad-scale impacts on species distributions across the landscape, rather than station-level differences.

To calculate diversity variables, bird richness and abundance data (Table 1A, Appendix 1) were pooled within each plot. These pooled data were used to calculate richness and the Shannon's and Gini-Simpson indices, which were transformed into their respective effective number equivalents (Table 3.1). I used three R packages to calculate the diversity indices. All three gave

identical results. Vegetarian v 1.2 (Charney & Record, 2012) was chosen because it calculates all indices of interest, and their Hill Diversity equivalents.

Table 3.1. Conversion of diversity indices to effective number of species, where S = number of species, P_i represents the relative abundance of the i_{th} species, the number of individual species i at the plot divided by the total number of individuals of all S species.

| Traditional index | Raw Index calculation | Effective number of species (Hill Diversity) |
|--------------------------|---------------------------------------|---|
| Richness | $x \equiv \sum_{i=1}^S p_i^0$ | x |
| Shannon Diversity | $x \equiv - \sum_{i=1}^S p_i \ln p_i$ | $\exp(x)$ |
| Gini-Simpson | $x \equiv 1 - \sum_{i=1}^S p_i^2$ | $1/(1-x)$ |

Covariates

Our independent variables can be grouped into two categories: environmental variables (divided into energy and habitat categories) and experimental variables (year, effort, and plot type).

Environmental variables - energy

To test the species-energy hypothesis, I focused on bioclimatic variables available to us that influence the growth, reproduction, and survival of plants – which, in turn, influences vertebrates like birds – and which are reasonable surrogates for energy in the environment. These variables

included latitude, average temperature during the warmest quarter (ATWQ) (McKenney et al., 2013) and the Normalized Difference Vegetation Index (NDVI) computed from MODIS remote sensing data averaged over 30 years (Tucker et al., 2005). None of these variables are energy in and of themselves but are useful and commonly used surrogates (Willig et al., 2003; Costello & Chaudhary, 2017; Clarke & Gaston, 2006; Pettorelli et al., 2005; Haedo et al., 2017; Gillespie et al., 2017).

Latitude is a proxy for direct solar energy, or photosynthetically available radiation, which influences primary plant productivity (Willig et al., 2003; Costello & Chaudhary, 2017) and thus the distribution and diversity of birds and other vertebrates (Hawkins et al., 2003; Currie et al., 2004; Carrara & Vázquez, 2010). ATWQ is an energy surrogate which also affects primary productivity and the rate at which organisms make use of photosynthetically available radiation (Clarke & Gaston, 2006) and is also correlated with vertebrate species distributions (Hawkins et al., 2003). Since most of the birds recorded on our ARUs are neo-tropical migrants and only present during breeding season, I decided the warmest quarter data is the most relevant temperature metric for our models.

While useful as energy surrogates, latitude and temperature alone do not dictate plant abundance and diversity (Clarke & Gaston, 2006), nor the vertebrate diversity that stems from them. As Clarke and Gaston (2006) point out, hot deserts with ample solar radiation have low plant diversity. Thus, latitude and ATWQ can be thought of as reflections of *ambient* energy (Davies et al., 2007). To strengthen our suite of energy variables, I included NDVI as an energy surrogate that represents what Davies et al. (2007) call *productive* energy. NDVI is a good indicator of

vegetation cover, primary productivity (Pettorelli et al., 2005; Haedo et al., 2017; Gillespie et al., 2017), and above ground plant biomass production (Lumbierres et al., 2017). Numerous studies have shown positive relationships between NDVI and bird diversity (Lee et al., 2004; Kennedy et al., 2014; Coetzee and Chown, 2016; Haedo et al., 2017; Leveau et al., 2020). Using these measures of ambient and productive energy in our models provides a comprehensive picture of the impact of energy variables on bird diversity in our study area. Both NDVI and ATWQ data in this study had a grain of 250m.

Environmental variables - habitat

To assess the impact of habitat heterogeneity on bird diversity, I used a suite of land cover types derived from the Far North Land Cover v.1.4 layer of the Ontario Land Cover Compilation v.2.0 (Ontario Ministry of Natural Resources 2014). The Far North Land Cover has a 30m grain and includes twenty-four land cover classes grouped under eight habitat categories (water, bog, fen, swamp, marsh, treed, non-treed and disturbance). Some of the 24 are not present in the far north (e.g., agriculture, alvar, plantations, hedge rows, etc.) and were excluded from our analysis. Of the 19 land classes present in the far north, shadow/cloud and unclassified types were also excluded leaving 17 land class types (Table 2A, Appendix 1).

I was less interested in the impact of any one of these variables than I was with creating estimates of habitat heterogeneity at each plot. Thus, for each plot, this suite of land cover types was used to calculate 1) a land cover richness value (LC-RICH) and 2) Shannon Diversity Index value for habitat diversity (LC-DIV). Using the proportions of different land cover types within

each plot, Shannon Diversity Index values were calculated using the Vegetarian package v 1.2 in R (Charney and Record, 2015).

Experimental variables – sampling effort

When conducting species surveys, the number of species detected is characteristically correlated with sampling effort (Ugland et al., 2003). However, the relationship between sampling effort and new species detections is not linear. Rather, species richness tends to increase with increasing sampling effort with declining slope to an asymptote, which would be the total species richness, in what is known as a species accumulation curve (Ugland et al., 2003).

In my study, sampling effort is reflected in the number of interpreted ARU recordings, which vary from 6 to 55 recordings per plot, depending on plot type, data interpretation limitations and ARU failures. To account for varying sampling effort, I used the number of interpreted recording sessions at a plot to account for the effect of effort on estimates of bird diversity. To model the positive, and curvilinear shape of the species accumulation curve, I included number of recording sessions (N_SESS), and the natural logarithm ($\log(N_SESS)$) and the square of this variable (N_SESS^2). We then relied on a preliminary model selection (Burnham and Anderson, 2001) to indicate the best combination of effort variables. This process indicated that natural log transformation of number of sessions was consistently selected as the best variable to account for sampling effort at the plot level and I included this variable in all our candidate models.

Experimental variables – year

Environmental variability across years such as timing of snowmelt, onset of green-up, varying insect productivity, bird mortality during migration and extreme weather events, can affect breeding birds from year to year. In addition, because of changes in field protocols arising from logistical challenges and expense over the course of this study, average total sampling effort was not consistent across years, nor was it, in any year, randomly distributed over the entire study area (Figure 3.2). Effort varied from a mean of 15 sessions (3 stations on 5 days) per plot in 2010 to a mean of 37 sessions in 2014 (Figure 3.5). Lastly, examining a correlation matrix of independent variables showed an r value of 0.39 for latitude and year, indicating the potential for a latitudinal gradient in bird diversity between years. To account for these potential sources of variability, Year was included as an independent variable in sets of candidate models.

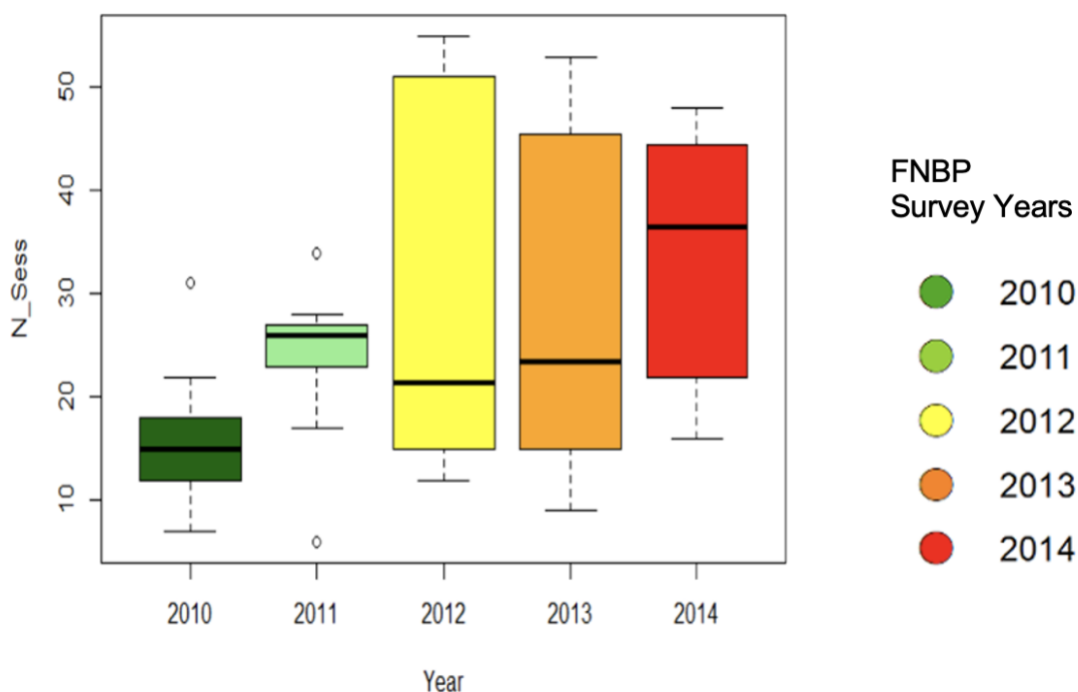


Figure 3.5. Sampling effort (number of interpreted ARU recordings of bird vocalizations per plot) versus sampling year, during the Far North Biodiversity Project in Ontario's far north.

Experimental variables - plot type

In Chapter 2, my results showed that long-term plots detected about 1.5 times as many species as short-term plots at the station level. Therefore, although in this chapter the analysis is being conducted at plot level, rather than station level, I included plot type (short-term versus long-term) in our model selection process to examine the influence it may have on our dependent variables.

Grain of analysis

To assess the impact of different grain of analysis on dependent variables, I created buffers around each plot for each of our independent variables. Minimum convex polygons were created from the stations for each plot and the distance between polygons was calculated. Four polygons were within 10km and 15km of one another, but none were closer than 10km. Thus, 10km was chosen as the maximum grain of analysis to minimize the overlap among polygons. Buffers around each plot were then calculated at 0m, 100m, 500m, 1000m, 2500m, 5000m, 7500m and 10,000m grains.

To explore the impact of grain size on the predictive power of our independent variables, I examined Pearson correlation coefficients (r values) of plot level diversity indices (RICH, HILL-SHAN, HILL-GS) with all independent variables across all spatial grains. For all dependent variables, r values for ATWQ and Latitude varied little across grain sizes. For RICH, r values for NDVI increased with grain, suggesting the collective explanatory power of energy variables is greatest at 10,000m. Although they varied more across grain sizes, overall r values for habitat

richness and Shannon’s Index of habitat diversity were greatest at smaller grains when compared to energy variables (Figure 3.6). Similar trends were seen for HILL-SHAN and HILL-GS.

I ran models across the full spectrum of grain sizes, holding grain constant for all variables within each set of candidate models. Doing so allowed exploration of the differing impacts of energy and habitat variables across differing grains of analysis while avoiding the potential for confounding the effect of varying grain size with the effect of the variables of interest.

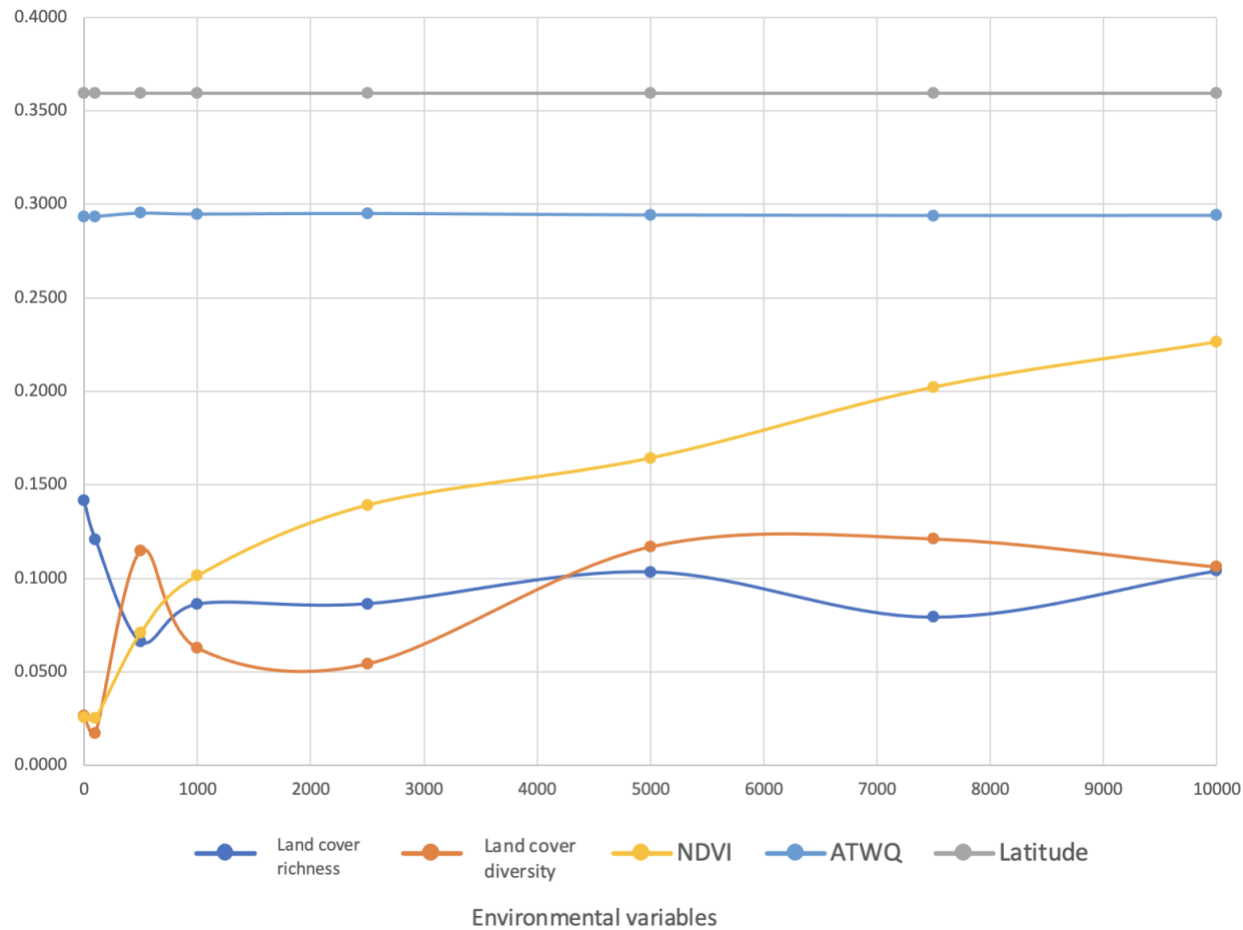


Figure 3.6. r values of Plot-level richness (RICH) with independent variables from 0m to 10,000m grains.

Assessing collinearity

I conducted a principal component analysis at the 500m and 10,000m spatial grains to assess collinearity between predictor variables at both ends of the spatial spectrum. The first three components cumulatively explain 46%, 73% and 86% of the variance in the dataset at 500m, and 43%, 70% and 86% at 10,000m (Table 3A and 3B, Appendix 1).

Examining the 500m grain bi-plot (Figure 3.7) showed that both land cover variables (LC-RICH and LC-DIV) are strongly correlated and appear to have a strong negative correlation with effort, although it is not clear why. Likewise, the energy variables NDVI and ATWQ are correlated and have strong negative correlations with latitude. Examination of the correlation coefficients showed values of -0.3573 between effort and land cover richness and -0.3736 between effort and Shannon's Index of land cover diversity (Table 4A, Appendix 1). Because correlations between predictor variables < 0.7 appear not to distort results (Dormann et al., 2013), I chose to retain all independent variables in my analyses.

The 10,000m grain bi-plot (Figure 3.8), showed similar relationships among the land cover variables and energy variables, but effort appeared to have even smaller correlations with the energy and land cover variables (Table 4B, Appendix 1).

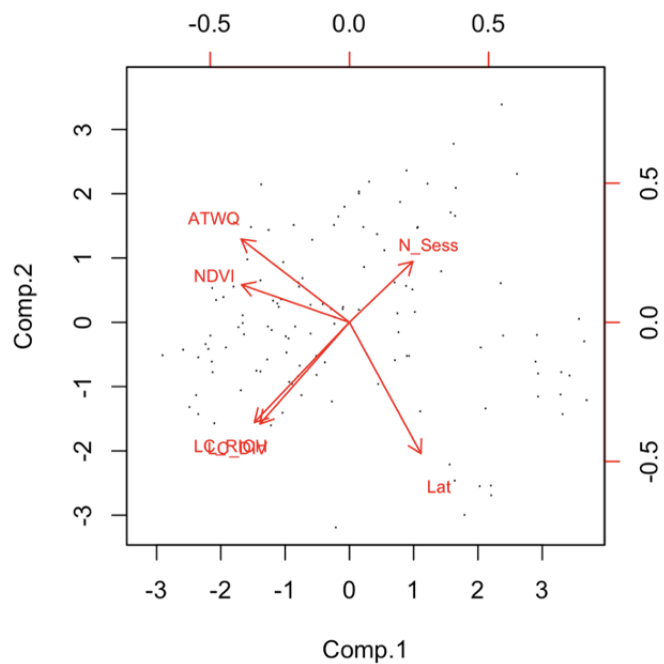


Figure 3.7. PCA Bi-plot of environmental variables and effort at 500m grain.

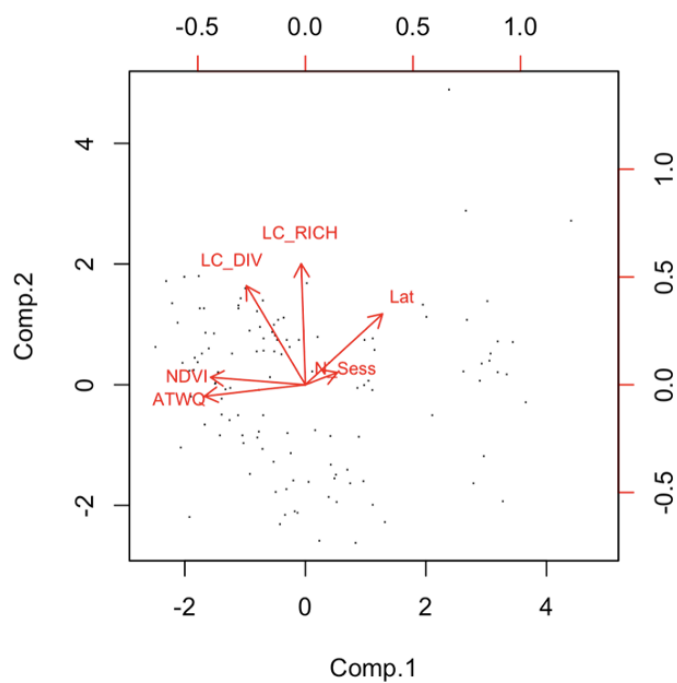


Figure 3.8. PCA Bi-plot of environmental variables and effort at 10,000m grain.

Candidate model specification

By visual inspection, I considered all three dependent variables to have a normal distribution for least squares linear modelling (Figure 3.9). Linear models were used to explore the impact on RICH, HILL-SHAN and HILL-SIM. R version 3.5.0 (2018) and the dredge and subset functions in the R package “MuMIn” (Barton, 2020) were used to prevent the inclusion of correlated variables within the same model.

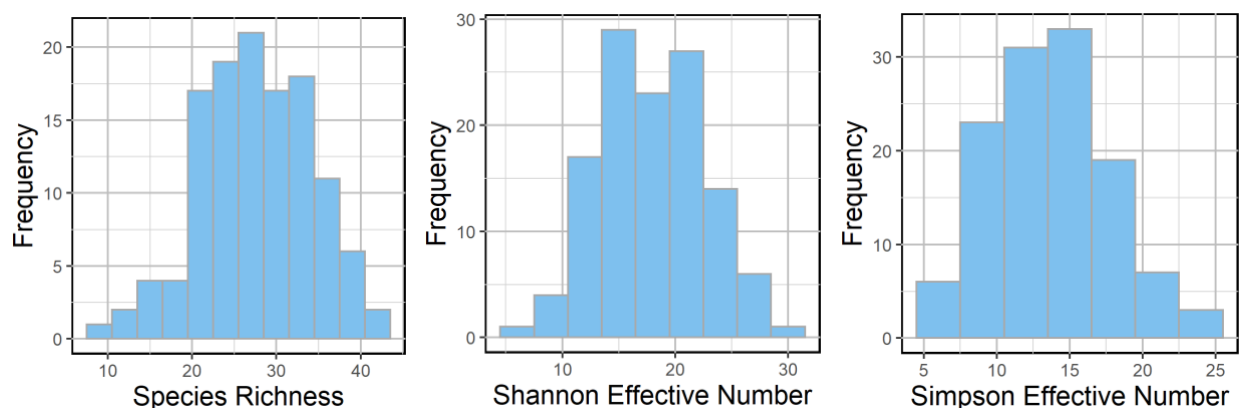


Figure 3.9. Histograms showing distribution of i) Species Richness, and the effective numbers derived from ii) Shannon diversity index and iii) the Gini-Simpson index

Including all energy and habitat variables, and all combinations of Year, Plot Type and effort variables, produced 384 candidate models. Examining the effect of covariates in this model selection process showed that $\log(N_{\text{Sess}})$ and Year were included in the top models when the energy and/or habitat variables were included. By contrast, models including N_{Sess} , N_{Sess}^2 and Plot Type with energy and habitat variables had higher ΔAIC values.

Since year and log of effort were identified as the best covariates to account for variation from year, effort, and plot type collectively, year and log of effort were forced into every model to ensure the variance accounted for by these two variables was constant. Accounting for this variance from experimental variables enabled exploration of the relative explanatory power of energy and habitat. Once collinearity among experimental variables was accounted for, the original 384 set of models was reduced to a set of 12 candidate models (Table 3.2).

Table 3.2. Candidate models for breeding bird species richness in Ontario's far north.

| Model No | log(N_Sess) | Year | Latitude | NDVI | ATWQ | Land cover richness (LC-RICH) | Shannon Index of Land cover diversity (LC-DIV) |
|----------|-------------|------|----------|------|------|-------------------------------|--|
| 1 | • | • | - | - | - | - | - |
| 2 | • | • | • | | | | |
| 3 | • | • | - | • | - | - | - |
| 4 | • | • | - | - | • | - | - |
| 5 | • | • | - | - | - | • | - |
| 6 | • | • | - | - | - | - | • |
| 7 | • | • | • | - | - | • | - |
| 8 | • | • | • | - | - | - | • |
| 9 | • | • | - | • | - | • | - |
| 10 | • | • | - | • | - | - | • |
| 11 | • | • | - | - | • | • | - |
| 12 | • | • | - | -- | • | - | • |

This candidate set in Table 3.2 was developed using RICH as the dependent variable. However, after doing model selection for all the dependent variables and examining coefficient significance, I discovered that for HILL-SHAN and HILL-GS, effort never had a coefficient significantly different from zero (at $p \leq 0.10$), and usually more than one year was significant. Therefore, I ran the model selection process for HILL-SHAN and HILL-GS, making ‘year only’ the base or null model. This left us with 12 slightly simplified candidate models for these dependent variables (Table 3.3). While I could have re-run the model selection process for the design variables, I felt the consistent lack of significance, and the tiny effect on R^2 values was sufficient evidence to drop the effort variable in the candidate models for the HILL-SHAN and HILL-GS selection process.

Table 3.3. Candidate models for the effective number of species derived from the Shannon index and the effective number of species from the Gini-Simpson index.

| Model No | Year | Latitude | NDVI | ATWQ | Land cover richness (LC-RICH) | Shannon Index of Land cover diversity (LC-DIV) |
|----------|------|----------|------|------|-------------------------------|--|
| 1 | • | - | - | - | - | - |
| 2 | • | • | | | | |
| 3 | • | - | • | - | - | - |
| 4 | • | - | - | • | - | - |
| 5 | • | - | - | - | • | - |
| 6 | • | - | - | - | - | • |
| 7 | • | • | - | - | • | - |
| 8 | • | • | - | - | - | • |
| 9 | • | - | • | - | • | - |
| 10 | • | - | • | - | - | • |
| 11 | • | - | - | • | • | - |
| 12 | • | - | -- | • | - | • |

Model selection process

Models for each of these configurations were estimated and Akaike's model selection (Sugiura, 1978; Hurvich & Tsai, 1991) was used to identify the best models which contained: A) effort and year only, or year only), B) effort and year, or year only plus an energy variable, C) effort and

year, or year only + a habitat variable, and D) effort and year, or year only + an energy variable + a habitat variable. R^2 values for the top models at each grain were used to partition and plot the specific variance accounted for by a) experimental design variables (the base model of year + effort, or year only), b) energy, c) habitat and d) the explained variance shared by the energy and habitat variables following Bowman et al., 2001. Although ΔAIC values are our preferred measure of model fit, plotting R^2 values as described was useful to help visualize the relative explanatory contribution of the energy and habitat variables. For predictive purposes for mapping of bird diversity I used the equation estimated for the top model (lowest ΔAIC) within each grain size, with the highest explanatory power (R^2) across grains.

Predictive diversity mapping

For creating a predictive map of the diversity measures, I selected the model from each model set with the highest R^2 that was also among the top models, aiming for a consistent set of predictive variables across the three diversity indices. For HILL-SHAN and HILL-GS models the highest R^2 values were at the 100m grain, while for RICH, the highest R^2 was at 0m (Tables 3.4, 3.5 and 3.6). However, the difference in R^2 between 0 and 100m grains for RICH was only 0.3%, so for consistency I used the 100m grain model. For all three diversity measures the environmental variables with the highest R^2 values at the 100m grain were NDVI and LC-RICH.

To generate a predictive equation, 2012 was used as the “standard year” since the mean diversity values from 2012 were either the centre-ranked value (RICH) or not substantially different from it (HILL-SHAN, HILL-GS). This created the following predictive equations:

Equation 1: $RICH = 6.876579696 + 0.002276 \times NDVI_{100m} + 0.903460 \times LC_RICH_{100m}$

Equation 2: $HILL-SHAN = 1.8343323 + 0.0016466 \times NDVI_{100m} + 0.6894137 \times LC_RICH_{100m}$

Equation 3: $HILL-GS = 3.7131399 + 0.0008572 \times NDVI_{100m} + 0.5874838 \times LC_RICH_{100m}$

500m was chosen as the pixel size for the output as a compromise of grain and computation capability; a 500m pixel is a reasonable approximation of the size of the plot buffered by 100m. Land cover richness (LC-RICH) was estimated for each 15m pixel using a 500m focal area (approx. size of plot), then resampled to 500m pixels for prediction. ArcGIS tool Spatial Analyst/Raster Calculator used the prediction equations and the independent variables to create maps for each diversity measure for year 2012. For RICH, average effort (the average of the log number of sessions) was applied.

3.3 Results

Species richness

Of all the energy and habitat variables, NDVI and LC-RICH most frequently had the greatest explanatory power with respect to bird richness estimates (Table 3.4). At 0 and 100 m grains, the top models included both NDVI and LC-RICH as the preferred energy and habitat variables. However, in the second-ranked models the single variables NDVI or LC-RICH appeared as the best environmental predictors at 0 and 100m grains, respectively. At the 500m, 1000m, 2500m and 5000m grains the top models all selected LC-RICH as the top explanatory variable. Neither

habitat nor energy variables were included in the top models at the 7500 and 10,000m grains, but at both grains NDVI was the only environmental variable in the secondarily ranked models.

Overall, R^2 values for all environmental variables diminished with increasing grain size. Year and effort were forced into all models as a constant, and the R^2 for the base models containing only these variables was 36.4% for all grains. With respect to the contributions of environmental variables, habitat (LC-RICH) contributed greater additional explanatory power, over the base model, than did energy for grains ranging from 100m to 5000m, whereas energy made a greater additional explanatory contribution than habitat at 0m, 7500m and 10,000m grains.

Table 3.4. Model Selection Results for Bird Species Richness (RICH): Top model selected for each hypothesis, at each grain size, Hypothesis abbreviations: H&E: Energy and Habitat heterogeneity; E: Energy only; H: Habitat heterogeneity only; E&Y: Null model of only Effort and Year effects. Frequentist coefficient significance: $p < 0.001$ as ***; $p < 0.01$ as **; $p < 0.05$ as *; and $p < 0.10$ as °

| Model Specification | | Model Selection Criteria | | | | Model Coefficients | | | | |
|---------------------|------------|--------------------------|---------------|--------|--------------------|--------------------|--------|-----------|----------|--------|
| Grain size (m) | Hypothesis | AIC Rank | Δ AICc | Weight | R ² (%) | ATWQ | Lat | NDVI | LC-RICH | LC-DIV |
| 0 | H&E | 1 | 0.00 | 0.740 | 44.5 | | | 0.00284** | 0.895* | |
| 0 | E | 2 | 3.66 | 0.119 | 41.7 | | | 0.00342** | | |
| 0 | H | 3 | 5.13 | 0.057 | 41.0 | | | | 1.122** | |
| 0 | E&Y | 7 | 12.05 | 0.002 | 36.4 | | | | | |
| 100 | H&E | 1 | 0.00 | 0.517 | 44.2 | | | 0.00228° | 0.903* | |
| 100 | H | 2 | 1.71 | 0.220 | 42.3 | | | | 1.146*** | |
| 100 | E | 5 | 4.59 | 0.052 | 41.0 | | | 0.00333** | | |
| 100 | E&Y | 9 | 11.47 | 0.002 | 36.4 | | | | | |
| 500 | H | 1 | 0.00 | 0.351 | 42.0 | | | | 0.979** | |
| 500 | H&E | 2 | 0.27 | 0.306 | 42.9 | | | 0.00194 | 0.777* | |
| 500 | E | 5 | 3.88 | 0.051 | 40.1 | | | 0.00342** | | |
| 500 | E&Y | 7 | 8.99 | 0.004 | 36.4 | | | | | |
| 1000 | H | 1 | 0.00 | 0.465 | 42.9 | | | | 1.029*** | |
| 1000 | H&E | 2 | 1.90 | 0.179 | 43.1 | | -0.443 | | 1.047*** | |
| 1000 | E | 5 | 8.99 | 0.005 | 38.5 | | | 0.00268* | | |
| 1000 | E&Y | 9 | 10.92 | 0.002 | 36.4 | | | | | |
| 2500 | H | 1 | 0.00 | 0.316 | 39.0 | | | | 0.649* | |
| 2500 | H&E | 2 | 2.18 | 0.106 | 39.1 | -0.286 | | | 0.678* | |
| 2500 | E&Y | 6 | 2.93 | 0.073 | 36.4 | | | | | |
| 2500 | E | 7 | 3.84 | 0.046 | 37.1 | | | 0.00159 | | |
| 5000 | H | 1 | 0.00 | 0.270 | 38.1 | | | | 0.571° | |
| 5000 | E&Y | 2 | 1.19 | 0.149 | 36.4 | | | | | |
| 5000 | H&E | 3 | 1.99 | 0.100 | 38.3 | | | 0.00087 | 0.525 | |
| 5000 | E | 6 | 2.43 | 0.080 | 36.9 | | | 0.00150 | | |
| 7500 | E&Y | 1 | 0.00 | 0.269 | 36.4 | | | | | |
| 7500 | E | 2 | 1.33 | 0.138 | 36.9 | | | 0.00152 | | |
| 7500 | H | 3 | 1.93 | 0.102 | 36.5 | | | | 0.190 | |
| 7500 | H&E | 7 | 3.51 | 0.046 | 36.9 | | | 0.00137 | 0.124 | |
| 10000 | E&Y | 1 | 0.00 | 0.292 | 36.4 | | | | | |
| 10000 | E | 2 | 1.75 | 0.122 | 36.6 | | | 0.00113 | | |
| 10000 | H | 5 | 2.25 | 0.095 | 36.4 | | | | | 0.400 |
| 10000 | H&E | 7 | 4.06 | 0.038 | 36.6 | | | 0.00118 | -0.054 | |

At the 100m grain, the habitat model (LC-RICH) contributed 5.9% of additional explanatory power over the base model of effort and year, whereas the energy model (NDVI) added 4.6% more explanatory power. Thus, these two models collectively explained 10.5% of the variance in species richness. However, when habitat and energy variables were in the same model, they added 7.8% in additional explanation. Subtracting this value from the collective explanatory power of habitat and energy models shows that 2.7% of the explanatory power is shared between habitat and energy models at the 100m grain. Shared explanation between habitat and energy was observed at all grains (Figure 3.10A).

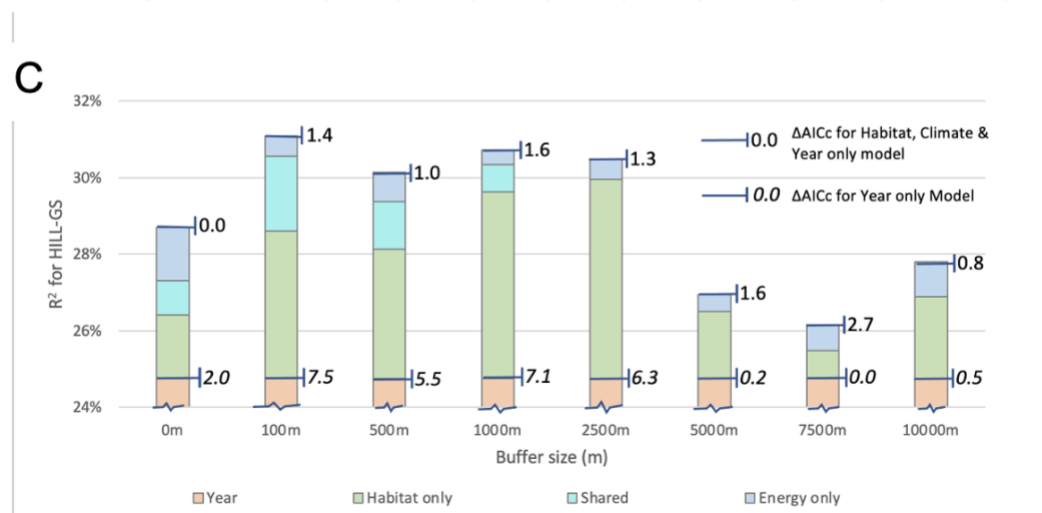
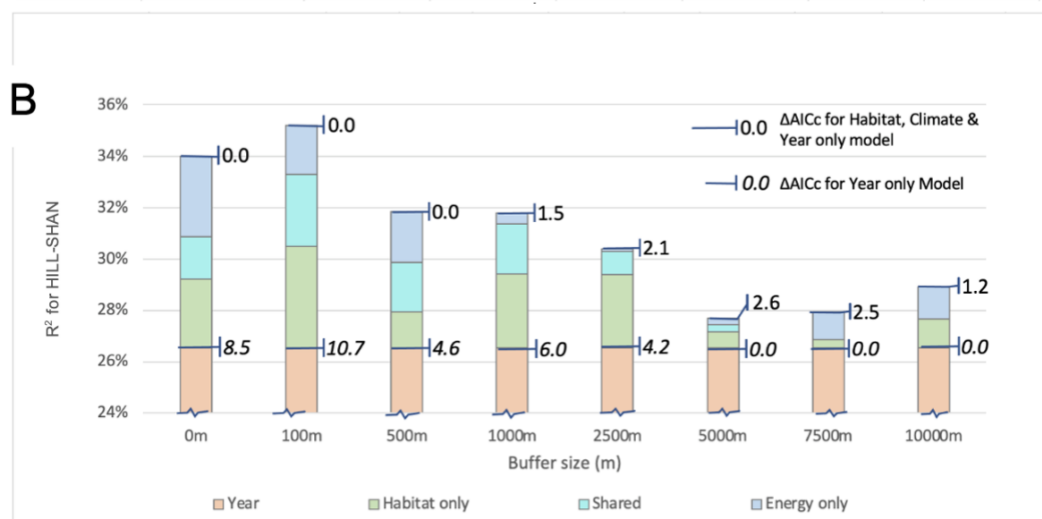
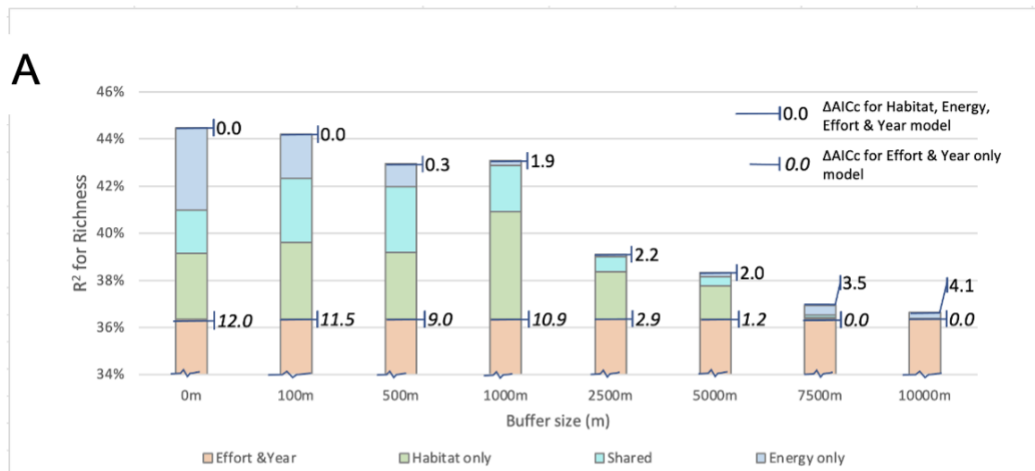


Figure 3.10. R^2 partitioning of habitat, energy, year, and effort contributions for A). breeding bird richness and habitat, energy, and year contributions for B). HILL-Shannon diversity and C). Hill-Gini-Simpson diversity in Ontario's far north, showing ΔAIC values at 0 to 10,000m grains

Hill-Shannon diversity

With only one exception at the 2500m grain, where Latitude was selected, NDVI had the greatest explanatory power of any of the energy variables (Table 3.5). As with the results for RICH, the top models for HILL-SHAN at 0 and 100m included both NDVI and LC-RICH as the preferred energy and habitat variables, with NDVI and LC-RICH being the best environmental predictor in the second-best models at 0 and 100m respectively. Unlike RICH, the top model at the 500m grain for HILL-SHAN included NDVI and LC-DIV with NDVI as the only experimental variable in the second-best model. At the 1000 and 2500m grains the top models were habitat-only models, but unlike with RICH, where LC-RICH was the only habitat variable selected, LC-DIV was in the top model at the 2500m grain and was also selected in models at the 500, 5000 and 7500m grain sizes. Like RICH, where environmental variables were not included in top models at the two largest grains, Year was the only variable in the top model at the 5000, 7500 and 10,000 grains for HILL-SHAN. However, LC-DIV was the only experimental variable selected in the second-ranked model at 5000m and as found with RICH, NDVI was the only environmental variable in the second-best models at the 7500 and the 10,000m grains.

Table 3.5. Model Selection Results for Hill-Shannon Index of Bird Species Diversity (HILL-SHAN): Top model selected for each hypothesis, at each grain size, Hypothesis abbreviations: H&E: Energy and Habitat heterogeneity; E: Energy only; H: Habitat heterogeneity only; Y: Null model of only Year effects. Frequentist coefficient significance: $p < 0.001$ as ***; $p < 0.01$ as **; $p < 0.05$ as *; and $p < 0.10$ as °

| Model Specification | | Model Selection Criteria | | | | Model Coefficients | | | | |
|---------------------|------------|--------------------------|---------------|--------|--------------------|--------------------|--------|-----------|----------|--------|
| Grain size (m) | Hypothesis | AIC Rank | Δ AICc | Weight | R ² (%) | ATWQ | Lat | NDVI | LC-RICH | LC-DIV |
| 0 | H&E | 1 | 0 | 0.571 | 34.0 | | | 0.00194* | 0.632* | |
| 0 | E | 2 | 2.56 | 0.159 | 31.3 | | | 0.00234** | | |
| 0 | H | 3 | 3.34 | 0.108 | 30.9 | | | | 0.784** | |
| 0 | Y | 7 | 8.52 | 0.008 | 26.5 | | | | | |
| 100 | H&E | 1 | 0 | 0.409 | 35.2 | | | 0.00165° | 0.689** | |
| 100 | H | 2 | 1.25 | 0.219 | 33.2 | | | | 0.849*** | |
| 100 | E | 6 | 4.94 | 0.035 | 31.2 | | | 0.00244** | | |
| 100 | Y | 10 | 10.75 | 0.002 | 26.5 | | | | | |
| 500 | H&E | 1 | 0 | 0.225 | 31.8 | | | 0.00210* | | 1.696 |
| 500 | E | 2 | 0.20 | 0.203 | 30.4 | | | 0.00252* | | |
| 500 | H | 4 | 1.18 | 0.125 | 29.9 | | | | 0.514* | |
| 500 | Y | 10 | 4.58 | 0.023 | 26.5 | | | | | |
| 1000 | H | 1 | 0 | 0.260 | 31.3 | | | | 0.618** | |
| 1000 | H&E | 3 | 1.50 | 0.123 | 31.8 | | | 0.000969 | 0.529* | |
| 1000 | E | 9 | 4.26 | 0.031 | 28.9 | | | 0.00203° | | |
| 1000 | Y | 10 | 6.02 | 0.013 | 26.5 | | | | | |
| 2500 | H | 1 | 0 | 0.366 | 30.3 | | | | | 3.012* |
| 2500 | H&E | 3 | 2.14 | 0.125 | 30.4 | | -0.208 | | | 3.065* |
| 2500 | Y | 6 | 4.16 | 0.046 | 26.5 | | | | | |
| 2500 | E | 7 | 4.75 | 0.034 | 27.5 | | | 0.00135 | | |
| 5000 | Y | 1 | 0 | 0.212 | 26.5 | | | | | |
| 5000 | H | 2 | 0.76 | 0.145 | 27.4 | | | | | 1.610 |
| 5000 | E | 4 | 1.39 | 0.106 | 27.0 | | | 0.00105 | | |
| 5000 | H&E | 7 | 2.62 | 0.057 | 27.7 | | | 0.000758 | | 1.395 |
| 7500 | Y | 1 | 0 | 0.247 | 26.5 | | | | | |
| 7500 | E | 2 | 0.74 | 0.171 | 27.4 | | | 0.00147 | | |
| 7500 | H | 3 | 2.00 | 0.091 | 26.7 | | | | | 0.713 |
| 7500 | H&E | 7 | 2.49 | 0.071 | 27.8 | | | 0.00168 | -0.184 | |
| 10000 | Y | 1 | 0 | 0.215 | 26.5 | | | | | |
| 10000 | E | 2 | 0.77 | 0.146 | 27.4 | | | 0.00145 | | |
| 10000 | H | 3 | 0.99 | 0.131 | 27.3 | | | | -0.298 | |
| 10000 | H&E | 4 | 1.17 | 0.120 | 28.5 | | | 0.00175 | -0.369 | |

Overall, R^2 for all environmental variables diminished with grain size. The null model, for which year was the only independent variable, had an R^2 value of 26.5% for all grains. Consistent with findings from RICH, habitat variables (LC-RICH and LC-DIV) explained more of the overall variance than energy variables at 100m and between 1000 and 5000m grains, and energy (NDVI) had greater explanatory power at the 0, 7500 and 10,000m grains. At the 100m grain, habitat variables offered 6.7% more explanatory power over the base model of year, whereas energy variables offered 4.7% more explanation. As with RICH, 2.7% of this explanatory power was shared between energy and habitat models. One anomaly compared with RICH was that energy had greater explanatory power than habitat variables at the 500m grain (3.9% versus 3.4% respectively, including 2% shared explanation between energy and habitat models) (Figure 3.10B).

Hill-Gini-Simpson diversity

The R^2 value for year was constant in all models at 24.8%. As with the other diversity indices, the top model at 0m was NDVI and LA-RICH. However, for HILL-GS, LA-DIV had far more influence than it did for the other indices, with LC-DIV included in the top models between the 100 and 5000m grains. At the 100m grain, the habitat and energy models added 5.8% and 2.4% of additional explanation respectively over the base model of year, including 1.9% shared explanation between habitat and energy models (Table 3.6, Figure 3.10C).

Table 3.6. Model Selection Results for Hill-Gini-Simpson Index of Bird Species Diversity (HILL-GS): Top model selected for each hypothesis, at each grain size, Hypothesis abbreviations: H&E: Energy and Habitat heterogeneity; E: Energy only; H: Habitat heterogeneity only; Y: Null model of only Year effects. Frequentist coefficient significance: $p < 0.001$ as ***; $p < 0.01$ as **; $p < 0.05$ as *; and $p < 0.10$ as °

| Model Specification | | Model Selection Criteria | | | | Model Coefficients | | | | |
|---------------------|------------|--------------------------|---------------|--------|--------------------|--------------------|-----|----------|---------|---------|
| Grain size (m) | Hypothesis | AIC Rank | Δ AICc | Weight | R ² (%) | ATWQ | Lat | NDVI | LC-RICH | LC-DIV |
| 0 | H&E | 1 | 0 | 0.198 | 28.7 | | | 0.00112 | 0.430 | |
| 0 | H | 2 | 0.081 | 0.190 | 27.3 | | | | 0.519* | |
| 0 | E | 3 | 0.522 | 0.153 | 27.0 | | | 0.00140° | | |
| 0 | Y | 6 | 2.02 | 0.072 | 24.8 | | | | | |
| 100 | H | 1 | 0 | 0.214 | 30.6 | | | | | 2.863** |
| 100 | H&E | 4 | 1.36 | 0.108 | 31.1 | | | 0.000857 | 0.587* | |
| 100 | E | 9 | 5.71 | 0.012 | 27.2 | | | 0.00152* | | |
| 100 | Y | 10 | 7.54 | 0.005 | 24.8 | | | | | |
| 500 | H | 1 | 0 | 0.358 | 29.4 | | | | | 2.55** |
| 500 | H&E | 2 | 0.97 | 0.221 | 30.1 | | | 0.001 | | 2.267* |
| 500 | E | 5 | 4.43 | 0.039 | 26.8 | | | 0.00156° | | |
| 500 | Y | 7 | 5.46 | 0.023 | 24.8 | | | | | |
| 1000 | H | 1 | 0 | 0.405 | 30.3 | | | | | 2.905** |
| 1000 | H&E | 2 | 1.60 | 0.182 | 30.7 | -0.400 | | | | 2.978** |
| 1000 | Y | 9 | 7.14 | 0.011 | 24.8 | | | | | |
| 1000 | E | 10 | 7.58 | 0.009 | 25.9 | | | 0.001 | | |
| 2500 | H | 1 | 0 | 0.431 | 29.8 | | | | | 3.021** |
| 2500 | H&E | 2 | 1.35 | 0.220 | 30.4 | -0.471 | | | | 3.165** |
| 2500 | Y | 5 | 6.26 | 0.019 | 24.8 | | | | | |
| 2500 | E | 7 | 7.83 | 0.009 | 25.2 | | | 0.0008 | | |
| 5000 | H | 1 | 0 | 0.206 | 26.2 | | | | | 1.783 |
| 5000 | Y | 2 | 0.15 | 0.191 | 24.8 | | | | | |
| 5000 | H&E | 3 | 1.57 | 0.094 | 26.7 | -0.428 | | | | 1.991 |
| 5000 | E | 5 | 2.15 | 0.070 | 24.9 | -0.249 | | | | |
| 7500 | Y | 1 | 0 | 0.247 | 24.8 | | | | | |
| 7500 | H | 2 | 1.49 | 0.117 | 25.2 | | | | -0.187 | |
| 7500 | E | 3 | 1.57 | 0.113 | 25.2 | | | 0.001 | | |
| 7500 | H&E | 7 | 2.67 | 0.065 | 25.9 | | | 0.001 | -0.239 | |
| 10000 | H | 1 | 0 | 0.218 | 26.5 | | | | -0.386 | |
| 10000 | Y | 2 | 0.54 | 0.166 | 24.8 | | | | | |
| 10000 | H&E | 3 | 0.76 | 0.149 | 27.4 | | | 0.001 | -0.439° | |
| 10000 | E | 4 | 1.98 | 0.081 | 25.3 | | | 0.001 | | |

Overall, the decreasing trend in the impact of environmental variables with increasing grain size is consistent across all our diversity measures. For top models, the R^2 values are almost always higher with the Hill numbers compared to the raw Shannon or Gini-Simpson indices, indicating that the Hill numbers are a better fit for the data than the raw indices.

Predictive diversity maps

Predictive maps for all three diversity measures show similar patterns in the distribution of bird diversity across Ontario's far north for all three diversity indices. Distinct differences in bird diversity are visible between Ecozones with the highest diversity seen in the more southerly and westerly Ontario Shield Ecozone compared with the Hudson Bay Lowlands Ecozone.

Nonetheless, within the Lowlands there are some concentrated areas of higher diversity associated with large waterways and some coastal formations. Although the predicted patterns of diversity are similar for all three indices, the magnitude of those index values differ considerably. The highest predicted values for richness were 32.1 to 36 species, versus 20.1 to 22 effective species for Hill-Shannon and 15.1 to 17.8 effective species for Hill-Simpson (Figures 3.11, 3.12 and 2.13).

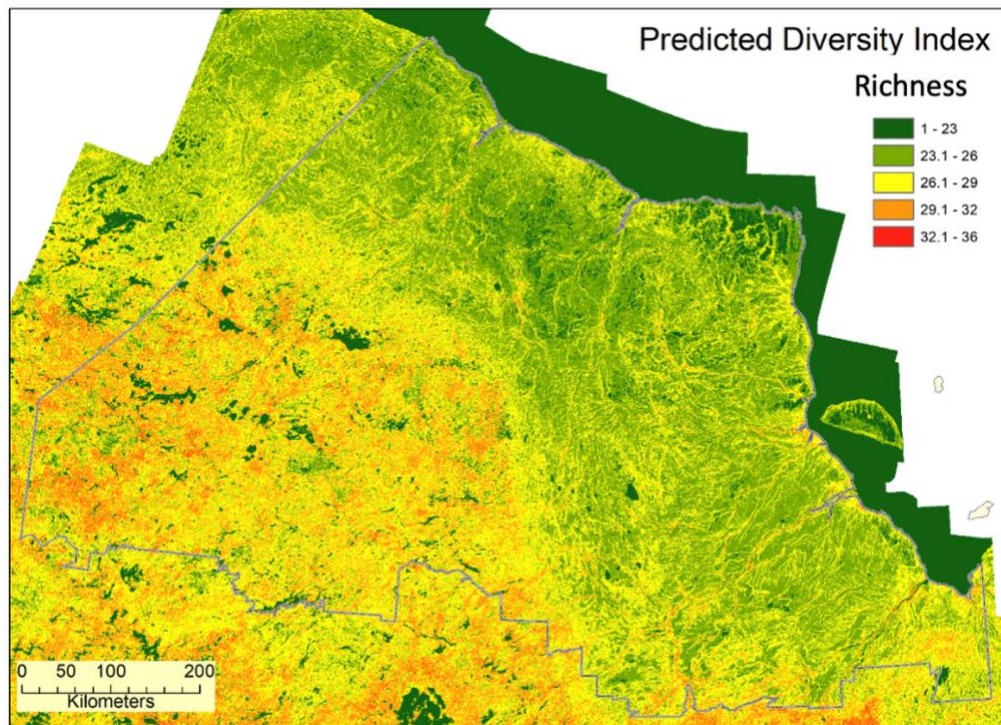


Figure 3.11. Breeding bird species richness detected between 2010-2014 by autonomous recording units across Ontario's far north at 500m grain.

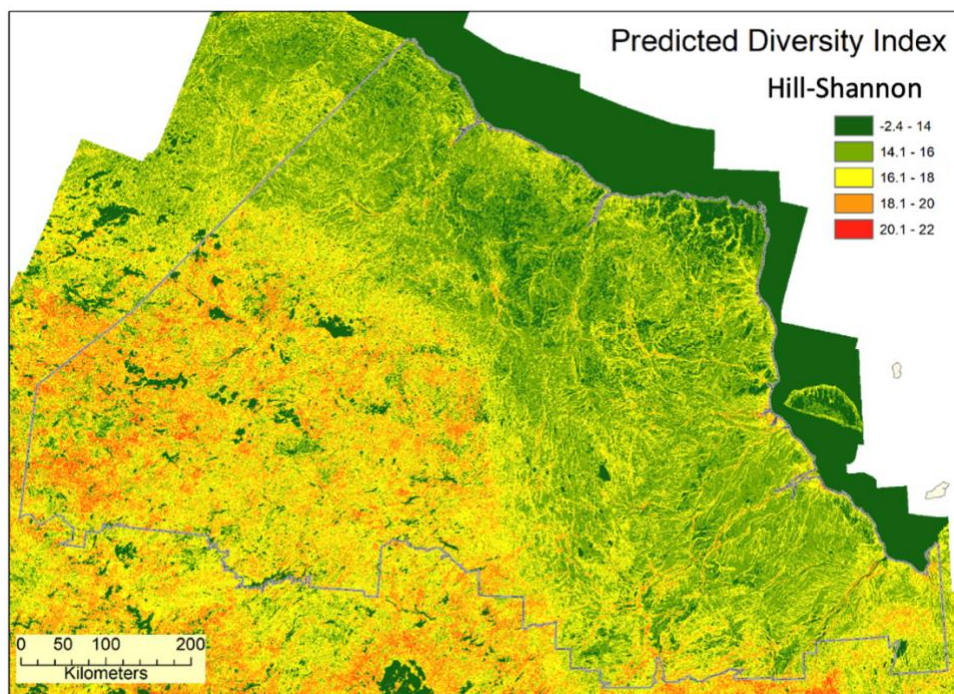


Figure 3.12. Hill-Shannon diversity for breeding birds detected between 2010-2014 by autonomous recording units across Ontario's far north at 500m grain.

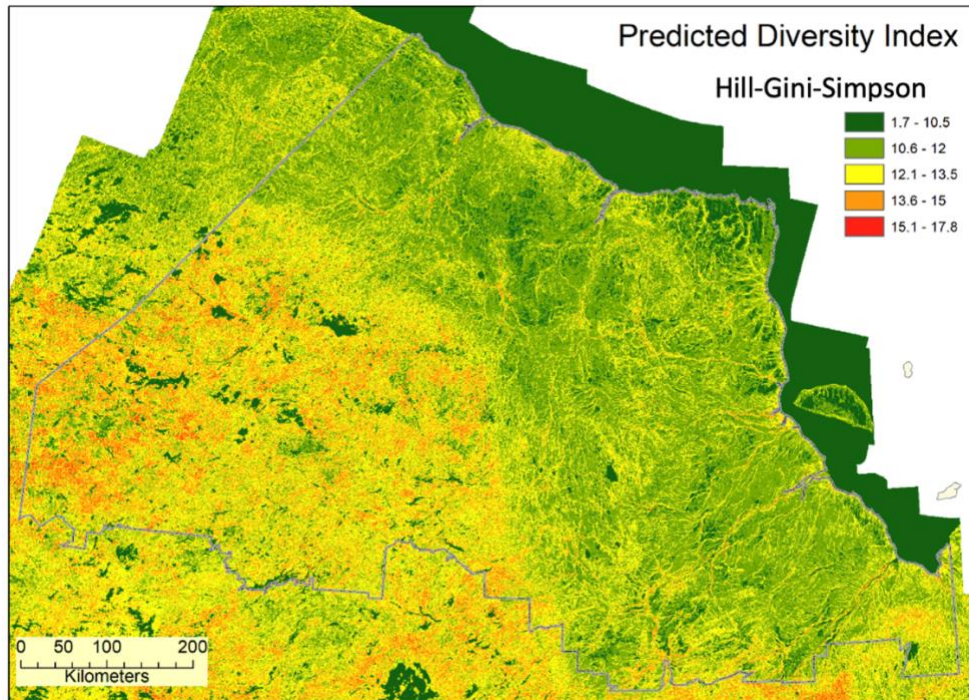


Figure 3.13. Hill-Gini-Simpson diversity for breeding birds detected between 2010-2014 by autonomous recording units across Ontario's far north at 500m grain.

3.4 Discussion

I tested the relative impact of the species-energy and habitat heterogeneity hypotheses to predict breeding bird diversity at various grains of analysis using multiple diversity measures in the far north of Ontario. Our top models supported both hypotheses, however, as expected, the influence of each hypothesis varied with the grain of analysis. Overall habitat heterogeneity explained more of the variance in bird diversity at grains between 0m and 2500m, whereas energy variables were better predictors from 5000m to 10,000m, although there was little additional explanation of diversity at the larger grains.

Species Richness

From the 100m to 5000m grains, the habitat heterogeneity hypothesis found more support than the energy hypothesis. However, at the larger grain of 7500m and 10,000m, the energy variables had more explanatory power. These results support the general findings from the literature that the determinants of bird distribution are hierarchically structured with energy and habitat variables acting as useful correlates for diversity at different scales (Altamirano et al., 2010; Gaston, 2000; González-Megías et al., 2007; Hurlbert & Jetz, 2007; Luoto et al., 2007).

An exception to this trend in our results was at the 0m grain where energy variables had greater explanatory power. I expect this irregularity in the pattern of our data is explained by our microphones sampling bird song from beyond the boundaries of the grain for which I had associated habitat data, thus under-emphasizing the impact of habitat at that grain size due to the mismatch of the area sampled.

Overall, the experimental variables of year and effort explained most of the variance in bird species richness (36.4%). This impact of effort was not unexpected as species diversity detections are clearly linked to sampling effort (Daly et al., 2018). A significant year effect is also understandable given the variability in weather across years within the study area, and the within-year, geographically clustered sample plot pattern necessitated by economic constraints.

The greatest explanatory power from the environmental variables was at the 0 and 100m grains, where those variables in the top models explained about 8% of the variance in bird diversity, diminishing to 0.3% at 10,000m. Some of this variance was shared between habitat and energy variables, with the amount of shared variance ranging from 2.78% at the 500 m grain to 0.11% at

7500 m. The general decrease in explained variance with increasing grain size is likely a function of a mismatch between the grain size and the resolution of our dependent variables which was constant at the grain of the plot. It is reasonable to assume that bird diversity within the plots is more closely related to the environmental variables in the immediate vicinity than to those that are perhaps 1 to 10 km away, which are well outside the average territory sizes and acoustic ranges of boreal birds (Toms et al., 2005). Thus, it is not surprising that the highest R^2 values in our study were at grains where the resolution of environmental variables was the closest match to the resolution of the plot and the dependent variables. Nonetheless, even with the mismatch of resolutions, and the shared variance between environmental variables, the relative and scale-dependent impacts of habitat heterogeneity and energy on bird diversity are still visible in our results.

Land cover richness was favoured over Land cover diversity in all models where a habitat heterogeneity variable was selected in the top two models, suggesting that the richness of land cover types is a better predictor of bird richness in our study site than land cover diversity. This might be a result of patterning on the ground. Higher habitat richness may be a better indication of accessibility for multiple functions in bird breeding. Higher habitat diversity may relate to the number of edges or edge habitats, which may not be as important to the species that occur in my study site. Of the three energy variables I used, NDVI was the one most commonly selected by our models, suggesting the impact of energy on bird richness at the extent and grain of our study is mediated more by energy impacts on vegetation than it is by surrogate measures of solar radiation like temperature or latitude. The exception was at the 1000 m and 2500m grains where latitude and ATWQ were the top energy variables, but at all larger grains NDVI was the top

energy variable. At larger extents scales other studies have found temperature variables to be good predictors of bird distributions in North America (e.g. Jiménez-Valverde et al., 2011).

Hill-Shannon diversity

As with RICH, the habitat heterogeneity hypothesis generally had greater support than the energy hypothesis at smaller grains, but not at the 0m grain where energy had more explanatory power, likely because of the sampling-area and grain-size mismatch. Another anomaly in this pattern was found at the 500m grain where energy variables explained slightly more variance than habitat variables (1.97% versus 1.41% respectively). However, our results for HILL-SHAN generally reflect our findings from RICH, suggesting that even with this compound measure of diversity, the habitat heterogeneity hypothesis has more support at smaller grains and the energy hypothesis has relatively more support at larger grains.

As with RICH, NDVI was almost always the preferred energy variable in all models. However, unlike RICH where Land cover richness was the preferred land cover variable in all top models, Land cover diversity was selected almost as often in the preferred models for HILL-SHAN, suggesting that land cover diversity, and not just land cover richness is an important predictor for Hill-Shannon bird diversity in Ontario's far north.

Hill-Gini-Simpson diversity

As with RICH and HILL-SHAN, the habitat heterogeneity hypothesis was well-supported over the energy hypothesis from the 100m to 5000m grains, where this variable had consistently greater explanatory power than it did for the other two diversity measures.

Unlike the other bird diversity models, habitat heterogeneity explained more variance than energy at the 0m grain, but the relative explanatory power of energy at 0m was still much greater than was found from 100m to 5000m, suggesting the impact of the mismatch of sampling-area to grain at 0m was consistent with results for the other dependent variables.

Land cover diversity was the land cover variable most commonly selected. As with richness and Hill-Shannon, the relative contribution of energy increased at the 7500 and 10,000m grains compared with smaller grains. However, at 7500 and 10,000m where land cover richness was the top land cover variable, there was no significant relationship between habitat heterogeneity and bird diversity. This runs contrary to the established literature where a positive relationship is generally found between land cover richness and bird diversity (Stein et al., 2014; Tews et al., 2004). Although these results are counterintuitive, the coefficient values at these resolutions were not significantly different from zero (Table 3.6).

NDVI was still the energy variable that was most commonly selected, but as with RICH where different energy variables were in the second-best models at the 1000m and 2500m grains, ATWQ was the top energy variable for HILL-GS at those grains. It is not clear why energy variables other than NDVI are preferred at these two grains, but a similar pattern also emerged with HILL-SHAN where Latitude was selected at 2500m.

Nonetheless, it is well documented in the literature that biotic drivers of species diversity, such as habitat heterogeneity, are generally more important at smaller grains, whereas abiotic drivers, such as temperature, latitude, and NDVI pre-dominate at larger grains (Götzenberger et al., 2012; Schweiger and Beierkuhnlein, 2016). These patterns were visible in our results for all three diversity indices used.

Implications of scale

Because of the impact of scale, many authors have suggested that single-scale studies may have limited explanatory power or could produce misleading results (Altamirano et al., 2010; González-Megías et al., 2007; Luoto et al., 2007; Stein, 2015). For example, at the extent of the country of China and at a single 100km grain of analysis, Luo et al. (2012) found support for the species-energy hypothesis, which explained more than 60% of vertebrate species richness, whereas in their study the habitat heterogeneity hypothesis found considerably less support, explaining 26% of vertebrate richness. However, the relative lack of support for the habitat heterogeneity hypothesis in their study may be an artifact of the grain of their analysis. Our work, and others (e.g., Stefanescu et al., 2004; Vernier et al., 2004) illustrate that the inclusion of land cover data is important for models at local and regional scales. This suggests that if Luo et al. (2012) had also tested the hypotheses at finer grains, they may have found greater support for the habitat heterogeneity hypothesis and additional and complementary information about the factors governing biodiversity distribution in China which could be useful for local conservation planning.

Nonetheless, at the grain and extent used by Luo et al. (2012), it is worth noting that habitat heterogeneity still explained about 26% of the distribution of vertebrate species richness.

Although Cumming et al. (2014) were studying individual boreal bird species distributions and not vertebrate diversity, they found that at a single grain of 100m at the extent of Canada's boreal forest, the explanatory power of their climate-based models was improved by about 25% with the inclusion of habitat data. Similarly, when modelling bird species distributions in Finland at

multiple scales (10,000 to 80,000m) Luoto et al. (2007) improved the explanatory power of bioclimatic models by 25% with the inclusion of land cover data. These studies illustrate that although energy variables tend to be better predictors of species distributions at large spatial extents and grains, habitat predictors can add useful predictive power to species-energy models even at large scales (Stein et al., 2014). Our results for all three diversity (richness, Hill-Shannon and Hill-Gini-Simpson) measures are consistent with other studies showing energy-based variables as the best descriptors of bird distributions at larger grains of analysis (Cumming et al., 2014; Gaudreau et al., 2018; Luoto et al., 2007; Venier, 2004) with habitat heterogeneity exerting greater influence than energy predictors at finer scales (Pearson & Dawson, 2003; Pearson et al., 2004). Our results for these three diversity measures also reinforce the scale-dependence of species diversity predictors and the importance of conducting diversity studies at multiple scales to glean a comprehensive picture of the factors that govern biodiversity distribution to ensure that results—and any ecological inferences made from them—are meaningful (Lawler et al., 2004; Pearson et al., 2004; Rahbek, 2005).

Choice of diversity metrics and predictive maps

I used our best models to create predictive maps of bird diversity across the far north for three different diversity metrics. Visual examination of the maps (Figures 3.11, 3.12 and 3.13) shows very similar patterns of predicted bird diversity for all three diversity indices, which is to be expected as all three predictive equations are linear combinations of the same two explanatory variables. The greatest diversity is generally estimated on the Ontario Shield and less diversity predicted for the Hudson Bay Lowlands. However, within the Lowlands, discrete areas of higher diversity are noticeable along sections of large rivers such as the Sutton, Winisk, Ekwan, Albany,

Attawapiskat and the Moose. Higher diversity is also noted along coastal reaches in proximity to mouths of these large rivers and that of the Harricana river at the southern end of James Bay.

These results are consistent with my observations of greater habitat heterogeneity in riparian areas during helicopter flights over the study area and also consistent with other published work (e.g. Crins et al., 2009). It is possible that these clusters of avian diversity reflect higher levels of habitat heterogeneity associated with riparian vegetation, and also the transitional habitats of the freshwater-marine interface that creates edges analogous to riparian habitats further inland.

These results are an example of the importance of including habitat variables in diversity modelling and conducting studies at multiple grains; species-energy models at the 10,000 or 7500m grains would fail to recognize these important clusters of localized diversity, which should be prioritized for any bird conservation efforts in the Hudson Bay Lowlands.

While the patterns in the predicted diversity maps are similar for all three indices, the magnitude of the predicted diversity values (richness and the effective number of species derived from the Shannon and Gini-Simpson indices) vary considerably with the highest richness values being almost double those for Hill-Gini-Simpson. Since richness gives rare and common species equal weight it is logical that it will always have a greater value than Hill-Gini Simpson which puts more weight on common species. However, the substantial difference in diversity estimates between these two metrics suggests there is a considerable degree of dominance within this community of breeding birds, and a sizable number of rare species. Nonetheless, whether one is interested in the distribution of common or rare species in the far north, the maps illustrate that the broad patterns of diversity are similar, while the use of multiple diversity metrics, including Hill-Diversity equivalents, provides further insight into the shape of the community beyond what

a single diversity metric would provide. Many other authors have argued persuasively that using multiple diversity metrics, including Hill-diversity equivalents, should be a best-practice in diversity studies because results become more intuitive, informative and less prone to misinterpretation (e.g. Daly et al., 2018; Jost, 2006; González-Megías et al., 2007; Roswell & Dushoff, 2021).

Conservation implications

Numerous recent papers have documented a decline in global biodiversity (Sage, 2020), and in North American birds specifically (Rosenberg et al., 2019). There have also been explorations of avian conservation and the related implications of climate change at large spatial extents in Canada's boreal forest (Cumming et al., 2014; Stralberg et al., 2015; Stralberg et al., 2018). Canada's boreal forest supports billions of birds from over 300 species (Stralberg et al., 2018). While the distribution of avian species has been explored across the boreal forest in other studies (e.g., Cumming et al., 2010; Cumming et al., 2014; Stralberg et al., 2018; Stralberg et al., 2019), our work provides more detailed information on the determinants and distribution of breeding bird diversity at finer grains within Ontario's far north that could be applied to conservation planning in this region.

Generally, my results show that the Ontario Shield Ecozone in the study area has greater breeding bird diversity than the HBL and should be a key component in any conservation planning related breeding bird diversity in the region. However, whereas the Ontario Shield is contiguous with a continent-wide band of boreal forest underlain by Precambrian shield, the HBL are a unique landform that representing a globally significant wetland (Abraham and

Keddy 2005). The lowlands and its coastline host a distinctive assemblage of breeding bird species that do not breed elsewhere in Ontario and are particularly important for numerous shorebird, waterbird and waterfowl species normally associated with the arctic (Abraham and Keddy, 2005; Cadman et al., 2007). Given these unique attributes, the HBL should not be overlooked with respect to breeding bird conservation in Ontario's far north even though my results indicate that, overall, there is greater breeding bird diversity on the Ontario Shield.

At fine grains my work suggests that habitat heterogeneity is an important predictor of bird diversity in Ontario's far north and, as such, any conservation planning at finer grains should include habitat models rather than those strictly driven by energy predictors. Our study provides the best available dataset of boreal breeding bird diversity across this large and remote area and thus, our models contribute to predicting bird diversity for parts of the far north where there are few or no observations.

In their work to identify priority areas for bird conservation across Canada's boreal forest, Stralberg et al. (2018), identified parts of the far north as high value areas.

According to their study, the areas ranked as highest conservation priority included parts of the Hudson Bay Lowlands north of the Ontario Shield. Although this is not perfectly aligned with our findings of greater diversity on the Shield rather than the Lowlands, it is a reflection that the competing constraints of conservation planning produce differing results. Whereas our predictive maps create the most detailed picture of bird diversity available for the far north, Stralberg et al. (2018) illustrate that this is just one criterion of conservation planning.

All this information is important as interest in industrial development, including mineral extraction in the far north's "Ring of Fire," continues to increase. Despite resistance from some First Nations in the far north, the current Ontario government is actively supportive of moving forward with building permanent roads for mine development in the region (Crawley, 2021). Although the Far North Act (2010) committed to protecting at least 225,000 square kilometres of the region in a network of protected areas, no action has been taken in the last decade and this commitment is currently under revision (Far North Act proposed amendments, 2020).

The intact nature of the boreal forest, and Ontario's far north specifically, still provide a rare opportunity for proactive conservation planning at a large extent. Given the broad distribution patterns of boreal birds, small and distinct protected areas will not be sufficient to protect boreal bird populations in Ontario's far north over the long term. In keeping with the scale of the landscape and the nature of its avian community, large areas that are off limits to development are necessary to maintain the biodiversity of breeding birds in the region over the long term.

Chapter 4 – General discussion

Canada's boreal forest comprises some of the most intact ecosystems in the world today (Stralberg et al., 2018), providing seasonal habitat for an estimated 1 to 3 billion migratory birds represented by 300 species (Stralberg et al., 2019; Wells et al., 2020). Within that vast landscape, the boreal forests of Ontario's far north and the adjacent forests of Manitoba, comprise the largest block of undeveloped boreal forest in the world (Far North Science Advisory Panel, 2010). Ontario's far north also includes the Hudson Bay Lowlands, which represent the third largest wetland in the world (Abraham & Keddy, 2005). Three hundred and forty species of birds are supported by the far north during some point in their annual cycle. Of those, 190 species breed in the region, making it an important nursery for migratory boreal birds, and also implying a responsibility for Ontario to protect their nesting grounds (Far North Science Advisory Panel, 2010).

During field research between 2009 and 2014, the Far North Biodiversity Project (FNBP) compiled the most comprehensive dataset on biodiversity ever compiled for this remote region. For this thesis, I used the 2010-2014 breeding bird data from the FNBP to explore and refine field methods for sampling breeding birds in a large and remote study area, while testing the habitat heterogeneity and species-energy hypotheses and producing predictive maps of breeding bird diversity across the study site.

In Chapter 2, I explored the efficacy of two different autonomous recording unit (ARU) models manufactured by Wildlife Acoustics Inc. to detect bird and anuran species richness. SM2 units are equipped with two microphones to detect and record bird and anuran vocalizations, whereas

the SM2BAT units have one microphone to detect and record birds and anurans, and a second ultrasonic microphone to detect bats. To maximize the opportunity to sample the widest variety of taxa possible, the FNBP utilized both types of units. My analysis showed that there was no significant difference in the detection rates of birds or anurans between these unit types.

These results suggest that using either unit type is acceptable for bird or anuran studies, as only one regular microphone can adequately sample these taxa, while the ultrasonic microphone on the SM2BAT units provides the added advantage of simultaneously collecting bat data.

However, the second microphone on SM2 units provides redundancy should one microphone malfunction or become damaged by a bear or other environmental factors while deployed in the field for extended periods of time. Thus, although both unit types will collect avian and anuran data equally well, researchers need to decide whether the double-microphone redundancy of the SM2 units is more useful than the ability to gather bat data simultaneously.

Sampling a large and remote study area is logistically complicated and expensive. Maximizing data collection and minimizing costs are important considerations for study design. The FNBP utilized two different plot configurations (long-term and short-term) adapted from the Multiple Species Inventory and Monitoring Protocol (MSIM) developed by the US Forest Service (Manley et al., 1997). Four ARUs were deployed (three SM2 and one SM2BAT) on each long-term plot in a square configuration. short-term plots consisted of three SM2 units in a triangular configuration with an SM2BAT unit deployed at a nearby water or habitat edge to target bats. Long-term plots were deployed for the duration of the nesting season, whereas short-term plots were deployed for four to six days at a series of locations and a shorter total proportion of a

nesting season. However, the short duration of short-term plots enabled crews to sample more locations within the targeted ecozone in a season, which was important for the overall FNBP study.

The question was whether there was a difference in the species detection rates between these two plot types and, if so, what was the magnitude of that difference. My analysis showed that long-term plots detected considerably more species for both birds and anurans compared with short-term plots. On average, long-term plots detected about 7 more species, or 1.5 times as many bird species. For anurans the relative difference between plot types was even more substantial. Most plots only detected 4 or fewer anuran species. Nonetheless, on average, long-term plots detected 1.5 more species than short-term plots.

Since the sampling effort (number of recording sessions) over a longer portion of the breeding season was much greater with long-term plots, thus covering a greater range of species arrivals and breeding seasons, it is not surprising that this plot type detected more species of birds and anurans. However, my results quantified that difference giving an idea of how much the short-term plots may have underestimated the bird and anuran richness. Based on these results, I recommend that future studies of birds alone forgo the use of ARUs in short duration plots such as the FNBP short-term plots in favour of deploying those units for longer periods of time - preferably for the entire breeding season. Although moving the ARUs to new plots every several days allows for sampling more widely across a study area, it also under-samples bird and particularly anuran richness. Depending on study objectives, some researchers may wish to sample more areas and sacrifice plot duration. But in doing so, they should clearly understand

the trade-offs between greater sampling area and decreased unique species richness estimates. Future studies may consider exploring whether shorter plots of 3-weeks could be a reasonable compromise between increased sampling area and species detections. However, the associated costs of helicopter and crew time required to move plots must also be considered.

I explored the relative impact of the habitat heterogeneity versus the species-energy hypotheses to predict bird diversity at different grains of analysis using multiple diversity measures. During this analysis, I found that the impact of plot type on diversity was reflected not in plot type specifically but in effort, since the impact of effort on the diversity metrics was always substantially greater than from plot type.

Depending on the grain of analysis, I found a difference in the relative support for the habitat heterogeneity and species-energy hypotheses. The habitat heterogeneity hypothesis was a better predictor of bird diversity at grains from 100m to 5000m, whereas the species-energy hypothesis was a better predictor at larger grains from 7500 to 10,000m. These results highlight the importance of conducting diversity studies at multiple grains since the impact of independent variables varies with the extent and grain of analysis. Studies conducted at a single grain run the risk of drawing conclusions of limited applicability relating to the best predictors of bird diversity, which could be especially troublesome if results are being used to inform land use planning and recommendations for protected areas (Roswell & Dushoff, 2021). In other words, when being used to inform land use planning decisions, the grain of diversity studies should be well matched with the extent and grain of the area in question. Otherwise, in the worst-case scenarios, this could lead to high priority conservation lands being slated for development, or the

creation of protected areas that are poorly matched with actual conservation priorities (Jenkins et al., 2015).

My maps of predicted bird diversity showed that the Ontario Shield Ecozone is home to a greater diversity of breeding birds than the Hudson Bay Lowlands Ecozone. However, given the unique attributes of the Hudson Bay Lowlands and the distinct assemblage of birds that breed in this region, it is also important for breeding bird conservation in the far north (Abraham and Keddy, 2005). Although boreal birds tend to be widely dispersed across the landscape, rather than clustered in hot spots of diversity (Slattery et al., 2011; Stralberg et al., 2018), our maps show that in the Hudson Bay Lowlands the greatest diversity tends to be concentrated around waterways, specifically large river system and the shorelines associated with the mouths of these rivers, presumably because of the greater habitat heterogeneity found in the riparian and edge habitat in those areas. Thus, if trying to protect avian diversity in the Hudson Bay Lowlands, these specific areas should be prioritized.

When identifying priority areas for songbird conservation across Canada's boreal forest using a framework of multiple conservation constraints, Stralberg et al. (2018) found that Ontario's far north was among the regions containing some of the highest ranked areas in the country.

According to their work, the areas ranked as highest conservation priority in the far north included parts of the Hudson Bay Lowlands north of the Ontario Shield. Although this is not perfectly aligned with our findings of greater diversity on the Shield rather than the Lowlands, our results simply report on the predicted diversity values, whereas the models Stralberg et al.

(2018) used included six competing conservation constraints in their work that our models did not address.

In our study, I did not see substantial differences in the results based on the diversity metric used when testing the habitat heterogeneity and species-energy hypotheses. Nor did I see noticeable differences in the patterns of our predictive diversity maps for each of our three diversity indices. However, models based on the Hill-diversity metrics had greater predictive power than models based on raw index values, and the use of Hill numbers – or effective number of species – allowed for intuitive comparisons of the differences between indices on our maps of predicted bird diversity.

For diversity studies, I recommend the use of multiple diversity measures especially when studying communities with uneven or unknown community structures since multiple measures can reveal more about the shape, or structure, of a community. Taking this comprehensive approach is not onerous analytically, provides greater certainty in results and, thus, is more defensible. Moreover, the use of Hill diversity metrics is also recommended because they simplify the interpretation of compound indices and allow for intuitive comparisons between studies using different indices.

Over the next century, the North American boreal forest is likely to undergo substantial climate-related changes with increased incidences of drought, insect-caused tree mortality, wetland drying, and wildfires (Allen et al., 2010; Balling et al., 1998; Klein et al., 2005; Michaelian et al., 2010; Peng et al., 2011). Some North American breeding birds have already expanded their

ranges northward in response to climate change (Hitch & Leberg, 2007). In Ontario's far north, interest in developing the considerable mineral deposits is also increasing (Crawly, 2021; Tencer, 2013), and the Far North Act is being revised to exclude the provision to protect 50 percent of the region (Far North Act proposed amendments, 2020). Collectively, these changes lend urgency to the need to comprehensively describe the region's biodiversity to ensure that the land use planning processes underway are well-informed by the best science and to provide a baseline against which to measure future changes in the biodiversity of Ontario's far north.

Literature Cited

- Abraham, K. F., and Keddy, C. J. (2005). "The Hudson Bay Lowland." In L. H. Fraser and P. A. Keddy (eds), *The World's Largest Wetlands*, (Cambridge: Cambridge University Press), 118–148.
- Abraham, K.F. and McKinnon, L.M. (2011). Hudson Plains Ecozone+ evidence for key findings summary. Canadian Biodiversity: Ecosystem Status and Trends 2010, Evidence for Key Findings Summary Report No. 2. Canadian Councils of Resource Ministers. Ottawa, ON. vi + 98 p.
- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660– 684
- Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., & Kadmon, R. (2012). Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, 109(43), 17495–17500.
<https://doi.org/10.1073/pnas.1208652109>
- Altamirano, A., Field, R., Cayuela, L., Aplin Paul., P., Lara, A., & Rey-Benayas, J. M. (2010). Woody species diversity in temperate Andean forests: The need for new conservation strategies. *Biological Conservation*, 143(9), 2080–2091.
<https://doi.org/10.1016/j.biocon.2010.05.016>
- Badiou, P., Orians, G., Pimm, S., Possingham, H., Raven, P., & Reid, F. (2013). *Conserving the World's Last Great Forest Is Possible: Here's How*. A science / policy briefing note issued under the auspices. October.
- Berlanga, H., J. A. Kennedy, T. D. Rich, M. C. Arizmendi, C. J. Beardmore, P. J. Blancher, G. S. Butcher, A. R. Couturier, A. A. Dayer, D. W. Demarest, W. E. Easton, M. Gustafson, E. Iñigo-Elias, E. A. Krebs, A. O. Panjabi, V. Rodriguez Contreras, K. V. Rosenberg, J. M. Ruth, E. Santana Castellón, R. Ma. Vidal, and T. Will. 2010. Saving our shared birds: partners in flight tri- national vision for landbird conservation. Cornell Lab of Ornithology, Ithaca, New York, USA. [online] URL: http://www.savingoursharedbirds.org/final_reports_pdfs/PIF2010_English_Final.pdf
- Blancher, P. Importance of Canada's boreal forest to landbirds. The Canadian Boreal Initiative and Bird Studies Canada. 48 p
- Bowman, J., Forbes, G. J., & Dilworth, T. G. (2001). The spatial component of variation in small- mammal abundance measured at three scales. *Canadian Journal of Zoology*, 79, 137–144.
- Bryant, D., Nielsen, D., & Tanglely, L. (1997). The last frontier Forests. In *Cités* (Vol. 31, Issue 3).
- Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. a, Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., ... Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science (New York, N.Y.)*, 328(5982), 1164–1168. <https://doi.org/10.1126/science.1187512>
- Caro, T., Darwin, J., Forrester, T., Ledoux-Bloom, C., & Wells, C. (2012). Conservation in the Anthropocene. *Conservation Biology*, 26(1), 185–188. <https://doi.org/10.1111/j.1523-1739.2011.01752.x>
- Carrara, R., & Vázquez, D. P. (2010). The species-energy theory: A role for energy variability.

- Ecography*, 33(5), 942–948. <https://doi.org/10.1111/j.1600-0587.2009.05756.x>
- Chao, Anne and Jost, L. (2004). Diversity analysis : a fresh approach. In *Diversity* (p. 9p).
- Chetkiewicz, C., & Lintner, A. (2014). *Getting It Right in Ontario's Far North*. 136.
- Clarke, A., & Gaston, K. J. (2006). Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, 273(1599), 2257–2266.
<https://doi.org/10.1098/rspb.2006.3545>
- Crins, W. W. J., Gray, P. A. A., Uhlig, P. W. C. W. C., & Wester, M. C. C. (2009). The ecosystems of Ontario, Part 1: Ecozones and Ecoregions. Inventory, Monitoring and Assessment, SIB TER IMA TR-01, 77.
- Cumming, S. G., Stralberg, D., Lefevre, K. L., Sólymos, P., Bayne, E. M., Fang, S., Fontaine, T., Mazerolle, D., Schmiegelow, F. K. A. a., & Song, S. J. (2014). Climate and vegetation hierarchically structure patterns of songbird distribution in the Canadian boreal region. *Ecography*, 37(May 2013), no-no. <https://doi.org/10.1111/j.1600-0587.2013.00299.x>
- Currie, D. J. (1991). Energy and Large-Scale Patterns of Animal and Plant-Species Richness. *The American Naturalist*, 137(1), 27–49. <https://doi.org/10.1086/285144>
- Daly, A. J., Baetens, J. M., & De Baets, B. (2018). Ecological diversity: Measuring the unmeasurable. *Mathematics*, 6(7). <https://doi.org/10.3390/math6070119>
- Darras, K., Batáry, P., Furnas, B., Celis-Murillo, A., Van Wilgenburg, S. L., Mulyani, Y. A., & Tschardtke, T. (2018). Comparing the sampling performance of sound recorders versus point counts in bird surveys: A meta-analysis. *Journal of Applied Ecology*, 55(6), 2575–2586. <https://doi.org/10.1111/1365-2664.13229>
- Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., Ding, T. S., Rasmussen, P. C., Bennett, P. M., Owens, I. P. F., Blackburn, T. M., & Gaston, K. J. (2007). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, 274(1614), 1189–1197.
<https://doi.org/10.1098/rspb.2006.0061>
- Dorcas, M. E., Price, S. J., Walls, S. C., & Barichivich, W. J. (2009). Auditory monitoring of anuran populations. In *Amphibian ecology and conservation: A Handbook of Techniques* (Issue January, pp. 281–298).
- Field, R., Hawkins, B. A., Cornell, H. V, Currie, D. J., Diniz-filho, J. A. F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., Brien, E. M. O., & Turner, J. R. G. (2008). Spatial species-richness gradients across scales : a meta-analysis. *Journal of Biogeography*.
<https://doi.org/10.1111/j.1365-2699.2008.01963.x>
- Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, 405(6783), 220–227.
<https://doi.org/10.1038/35012228>
- Gaudreau, J., Perez, L., & Harati, S. (2018). Towards modelling future trends of Quebec's boreal birds' species distribution under climate change. *ISPRS International Journal of Geo-Information*, 7(9). <https://doi.org/10.3390/ijgi7090335>
- Gauthier, A. S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., Gauthier, S., & Bernier, P. (2021). Linked references are available on JSTOR for this article : Boreal forest health and global change. *Boreal global change*. 349(6250), 819–822.
- Gillis, M. D., Omule, A. Y., & Brierley, T. (2005). Monitoring Canada's forests: The national forest inventory. *Forestry Chronicle*, 81(2), 214–221. <https://doi.org/10.5558/tfc81214-2>
- González-Megías, A., María Gómez, J., & Sánchez-Piñero, F. (2007). Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography*, 30(1), 31–41.
<https://doi.org/10.1111/j.2006.0906-7590.04867.x>

- Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. (2012). Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews*, *87*(1), 111–127. <https://doi.org/10.1111/j.1469-185X.2011.00187.x>
- Hawkins, B. A., Richard Field, Cornell, H. V., Currie, D. J., Gan, J.-F. G., Kaufman, D. M., Jeremy T. Kerr, 4, Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., & Eric E. Porter, A. J. R. G. T. (2003). Energy, water and broad-scale geographic patterns of species richness. *Ecology*, *84*(12), 3105–3117. <https://doi.org/10.1890/03-8024>
- Hill, M. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, *54*(2), 427–432. <https://doi.org/10.2307/1934352>
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(33), 13384–13389. <https://doi.org/10.1073/pnas.0704469104>
- Hurvich, C. M., & Tsai, C. L. (1991). Bias of the corrected aic criterion for underfitted regression and time series models. *Biometrika*, *78*(3), 499–509. <https://doi.org/10.1093/biomet/78.3.499>
- Jenkins, C. N., Houtan, K. S. Van, Pimm, S. L., & Sexton, J. O. (2015). US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences*, 1–6. <https://doi.org/10.1073/pnas.1418034112>
- Jiménez-Valverde, A., Barve, N., Lira-Noriega, A., Maher, S. P., Nakazawa, Y., Papeş, M., Soberón, J., Sukumaran, J., & Peterson, A. T. (2011). Dominant climate influences on North American bird distributions. *Global Ecology and Biogeography*, *20*(1), 114–118. <https://doi.org/10.1111/j.1466-8238.2010.00574.x>
- Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., & Wilmshurst, J. M. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science*, *356*(6335), 270–275. <https://doi.org/10.1126/science.aam9317>
- Jost, L. (2006). Entropy and diversity. *Oikos*, *113*, 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Jost, L. (2009). Mismeasuring biological diversity: Response to Hoffmann and Hoffmann (2008). *Ecological Economics*, *68*(4), 925–928. <https://doi.org/10.1016/j.ecolecon.2008.10.015>
- Jost, L. (2019). What do we mean by diversity?: The path towards quantification. *Metode*, *2019*(9), 55–61. <https://doi.org/10.7203/metode.9.11472>
- Kerr, J. T., & Packer, L. (1999). The environmental basis of North American species richness patterns among *Epicauta* (Coleoptera: Meloidae). *Biodiversity and Conservation*, *8*(5), 617–628. <https://doi.org/10.1023/A:1008846131749>
- Kirk, D. a., Diamond, A. W., Hobson, K. a., & Smith, A. R. (1996). Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Canadian Journal of Zoology*, *74*(9), 1749–1770. <https://doi.org/10.1139/z96-193>
- Leveau, L. M., Isla, F. I., & Isabel Bellocq, M. (2020). From town to town: Predicting the taxonomic, functional and phylogenetic diversity of birds using NDVI. *Ecological Indicators*, *119*(August), 106703. <https://doi.org/10.1016/j.ecolind.2020.106703>
- Locke, H. (2013). Nature needs half: A necessary and hopeful new Agenda for protected areas. *Parks*, *19*(2), 13–22. <https://doi.org/10.2305/IUCN.CH.2013.PARKS-19-2.HL.en>
- Lumbierres, M., Méndez, P. F., Bustamante, J., Soriguer, R., & Santamaría, L. (2017). Modeling

- biomass production in seasonal wetlands using MODIS NDVI land surface phenology. *Remote Sensing*, 9(4), 1–18. <https://doi.org/10.3390/rs9040392>
- Luo, Z., Tang, S., Li, C., Fang, H., Hu, H., Yang, J., Ding, J., & Jiang, Z. (2012). Environmental effects on vertebrate species richness: Testing the energy, environmental stability and habitat heterogeneity hypotheses. *PLoS ONE*, 7(4), 23–26. <https://doi.org/10.1371/journal.pone.0035514>
- Luoto, M., Virkkala, R., & Heikkinen, R. K. (2007). The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography*, 16(1), 34–42. <https://doi.org/10.1111/j.1466-8238.2006.00262.x>
- MacArthur, R. H. & MacArthur, J. (1961). On Bird Species Diversity. *Ecology*, 42(3), 594–598.
- Magurran, Anne E. and McGill, B. J. (2011). *Biological Diversity: Frontiers in Measurement and Assessment* (B. J. Magurran, Anne E. and McGill (ed.)). Oxford University Press Inc.
- Manley, P. N., Service, U. S. F., Horne, B. Van, Wildlife, N., & Service, U. S. F. (1997). The Multiple Species Inventory and Monitoring Protocol : A Population , Community , and Biodiversity Monitoring Solution for National Forest System Lands. *USDA Forest Service Proceedings RMRS-P-42CD.*, 1, 671–680.
- McCauley, S. J., Bouchard, S. S., Farina, B. J., Isvaran, K., Quader, S., Wood, D. W., & St. Mary, C. M. (2000). Energetic dynamics and anuran breeding phenology: Insights from a dynamic game. *Behavioral Ecology*, 11(4), 429–436. <https://doi.org/10.1093/beheco/11.4.429>
- McKenney, D., Pedlar, J., Hutchinson, M., Papadopol, P., Lawrence, K., Campbell, K., Milewska, E., Hopkinson, R. F., & Price, D. (2013). Spatial climate models for Canada’s forestry community. *Forestry Chronicle*, 89(5), 659–663. <https://doi.org/10.5558/tfc2013-118>
- Méró, T. O., Lontay, L., & Lengyel, S. (2015). Habitat management varying in space and time: the effects of grazing and fire management on marshland birds. *Journal of Ornithology*. <https://doi.org/10.1007/s10336-015-1202-9>
- Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S. a., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., & Rillig, M. C. (2014). Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, 4(18), 3514–3524. <https://doi.org/10.1002/ece3.1155>
- Noss, R. F., Dobson, A. P., Baldwin, R., Beier, P., Davis, C. R., Dellasala, D. A., Francis, J., Locke, H., Nowak, K., Lopez, R., Reining, C., Trombulak, S. C., & Tabor, G. (2011). Bolder Thinking for Conservation. *Conservation Biology*, 26(1), 1–4. <https://doi.org/10.1111/j.1523-1739.2011.01738.x>
- Oseen, K. L., & Wassersug, R. J. (2002). Environmental factors influencing calling in sympatric anurans. *Oecologia*, 133(4), 616–625. <https://doi.org/10.1007/s00442-002-1067-5>
- P.Lee, D.Aksenov, L. Laestadius, R. Nogueron, W. S. (2007). Canada’s Large Intact Forest Landscapes. In *Canada’s Large Intact Forest Landscapes*.
- Packalen, M. S., Finkelstein, S. A., & McLaughlin, J. W. (2014). Carbon storage and potential methane production in the Hudson Bay Lowlands since mid-Holocene peat initiation. *Nature Communications*, 5(May), 1–8. <https://doi.org/10.1038/ncomms5078>
- Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. In *Nature* (Vol. 405, Issue 6783, pp. 212–219). <https://doi.org/10.1038/35012221>
- R.S. Rempel, J.M. Jackson, and J. N. R. (2014). *Acoustic Monitoring and Assessment of Forest*

Songbirds : Sample Design , Analysis Methods , and.

- Rempel, R. (2014). *Effectiveness monitoring of forest management guides. Acoustic monitoring objectives, sample design, analysis methods, and observation error* (Issue 80).
- Rempel, R. S., Francis, C. M., Robinson, J. N., & Campbell, M. (2013). Comparison of audio recording system performance for detecting and monitoring songbirds. *Journal of Field Ornithology*, *84*(1), 86–97. <https://doi.org/10.1111/jfo.12008>
- Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. <https://doi.org/10.1126/science.aaw1313>
- Roswell, M; Dushoff, Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*, 321–338. <https://doi.org/10.1111/oik.05876>
- Sage, R. F. (2020). Global change biology: A primer. *Global Change Biology*, *26*(1), 3–30. <https://doi.org/10.1111/gcb.14893>
- Shiu, H. J., & Lee, P. F. (2003). Assessing avian point-count duration and sample size using species accumulation functions. *Zoological Studies*, *42*(2), 357–367.
- Shonfield, J., & Bayne, E. M. (2017). Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, *12*(1). <https://doi.org/10.5751/ace-00974-120114>
- Stein, A. (2015). Environmental heterogeneity–species richness relationships from a global perspective. *Frontiers of Biogeography*, *7*(4), 168–173. <https://doi.org/10.21425/f5fbg27952>
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866–880. <https://doi.org/10.1111/ele.12277>
- Stralberg, D., Berteaux, D., Drever, C. R., Drever, M., Lewis, I. N., Schmiegelow, F. K. A., & Tremblay, J. A. (2019). Conservation planning for boreal birds in a changing climate: A framework for action. *Avian Conservation and Ecology*, *14*(1). <https://doi.org/10.5751/ACE-01363-140113>
- Stralberg, D., Camfield, A. F., Carlson, M., Lauzon, C., Westwood, A., Barker, N. K. S., Song, S. J., & Schmiegelow, F. K. A. (2018). Strategies for identifying priority areas for songbird conservation in Canada’s boreal forest. *Avian Conservation and Ecology*, *13*(2). <https://doi.org/10.5751/ACE-01303-130212>
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- The Far North Science Advisory Panel. (2010). *Science for a Changing Far North* (Issue April).
- Tittensor, D. P., & Worm, B. (2016). A neutral-metabolic theory of latitudinal biodiversity. *Global Ecology and Biogeography*, *25*(6), 630–641. <https://doi.org/10.1111/geb.12451>
- Toms, J. D., Hannon, S. J., & Schmiegelow, F. K. A. (2005). Population dynamics of songbirds in the boreal mixedwood forests of Alberta, Canada: Estimating minimum and maximum extents of spatial population synchrony. *Landscape Ecology*, *20*(5), 543–553. <https://doi.org/10.1007/s10980-004-5038-6>
- Tucker, C. J., Pinzon, J. E., Brown, M. E., Slayback, D. A., Pak, E. W., Mahoney, R., Vermote, E. F., & El Saleous, N. (2005). An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *International Journal of Remote Sensing*, *26*(20),

- 4485–4498. <https://doi.org/10.1080/01431160500168686>
- Ugland, K. I., Gray, J. S., & Ellingsen, K. E. (2003). The species – accumulation curve and estimation of species richness. *British Ecological Society, Rosenzweig 1995*, 888–897.
- Venier, L. A., Holmes, Stephen, B., Holborn, George, W., McIlwrick, Kenneth, A., & Brown, G. (2012). Evaluation of an Automated Recording Device for Monitoring Forest Birds. *Wildlife Society Bulletin*, 36(1), 30–39. <https://doi.org/10.1002/wsb.88>
- Venier, L. a., McKenney, D. W., Wang, Y., & McKee, J. (1999). Models of large-scale breeding-bird distribution as a function of macro-climate in Ontario, Canada. *Journal of Biogeography*, 26(2), 315–328. <https://doi.org/10.1046/j.1365-2699.1999.00273.x>
- Venier, L. a., Pearce, J., McKee, J. E., McKenney, D. W., & Niemi, G. J. (2004). Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. *Journal of Biogeography*, 31(2), 315–331. <https://doi.org/10.1046/j.0305-0270.2003.01014.x>
- Wang, K., Franklin, S. E., Guo, X., He, Y., & McDermid, G. J. (2009). Problems in remote sensing of landscapes and habitats. *Progress in Physical Geography*, 33(6), 747–768. <https://doi.org/10.1177/0309133309350121>
- Watson, J. E. M., Evans, T., Venter, O., & Williams, B. (2018). The exceptional value of intact forest ecosystems | Nature Ecology & Evolution. *Nature Ecology and Evolution*, 2(4), 599–610. <https://www.nature.com/articles/s41559-018-0490-x#Sec15>
- Watson, J. E. M., & Venter, O. (2017). A global plan for nature conservation. *Nature*, 550(7674), 48–49. <https://doi.org/10.1038/nature24144>
- Wells, J., D., Childs, D., Reid, F., Ph, D., & Smith, K. (2014). *Boreal Birds Need Half: Maintaining North America's Bird Nursery and Why it Matters*.
- Wells, J. V., Dawson, N., Culver, N., Reid, F. A., & Morgan Siegers, S. (2020). The State of Conservation in North America's Boreal Forest: Issues and Opportunities. *Frontiers in Forests and Global Change*, 3(July), 1–18. <https://doi.org/10.3389/ffgc.2020.00090>
- Wester, M. C., Henson, B. L., Crins, W. J., Uhlig, P. W. C., & Gray, P. A. (2018). The Ecosystems of Ontario, Part 2: Ecodistricts. *Ontario Ministry of Natural Resources and Forestry, Science and Research Branch*, 516. <https://files.ontario.ca/ecosystems-ontario-part2-03262019.pdf>
- Whiting, A. V. (2010). Factors affecting larval growth and development of the boreal chorus frog *Pseudacris maculata*. In *Dept of Biological science - U Alberta*.
- Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness : towards a general , theory of species diversity hierarchical. *Journal of Biogeography*, 28(4), 453–470. <https://doi.org/10.1046/j.1365-2699.2001.00563.x>
- Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34(Hawkins 2001), 273–309. <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>
- Yang, Z., Liu, X., Zhou, M., Ai, D., Wang, G., Wang, Y., Chu, C., & Lundholm, J. T. (2015). The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. *Scientific Reports*, 5(October), 1–7. <https://doi.org/10.1038/srep15723>

Appendix 1

Table 1A. Breeding birds in taxonomic order as detected on autonomous recording units during the Far North Biodiversity Project between 2010-2014, showing the number of individuals of each species for long-term and short-term plots. Species at risk in Ontario are shaded in grey.

| Taxonomic Groups | Species Common Name | Scientific Name | Taxa Code | Number of individual detections of ARUs | | |
|-----------------------------------|------------------------|-----------------------------------|-------------------------------------|---|------------------|-------------|
| | | | | Long-term plots | Short-term plots | Grand Total |
| Ducks, geese and waterfowl | Snow Goose | <i>Chen caerulescens</i> | SNGO | | 1 | 1 |
| | Canada Goose | <i>Branta canadensis</i> | CAGO | 724 | 84 | 808 |
| | Northern Shoveler | <i>Anas clypeata</i> | NSHO | 1 | | 1 |
| | Green-winged Teal | <i>Anas crecca</i> | GWTE | 1 | | 1 |
| | Mallard | <i>Anas platyrhynchos</i> | MALL | 12 | 4 | 16 |
| | Black Scoter | <i>Melanitta nigra</i> | BLSC | 2 | | 2 |
| | Common Merganser | <i>Mergus merganser</i> | COME | | 9 | 9 |
| Grouse and Allies | Ruffed Grouse | <i>Bonasa umbellus</i> | RUGR | 11 | 9 | 20 |
| | Spruce Grouse | <i>Falcapennis canadensis</i> | SPGR | 1 | 4 | 5 |
| | Willow Ptarmigan | <i>Lagopus lagopus</i> | WIPT | 38 | 3 | 41 |
| | Sharp-tailed Grouse | <i>Tympanuchus phasianellus</i> | STGR | 26 | 5 | 31 |
| Nightjars | Common Nighthawk | <i>Chordeiles minor</i> | CONI | 140 | 160 | 300 |
| Rails | Yellow Rail | <i>Coturnicops noveboracensis</i> | YERA | 20 | | 20 |
| | Sora | <i>Porzana Carolina</i> | SORA | 54 | 5 | 59 |
| Cranes | Sandhill Crane | <i>Grus canadensis</i> | SACR | 518 | 150 | 668 |
| Plovers | Black-bellied Plover | <i>Pluvialis squatarola</i> | BBPL | | 12 | 12 |
| | Semipalmated Plover | <i>Charadrius semipalmatus</i> | SEPL | 1 | 2 | 3 |
| Sandpipers and Allies | Stilt Sandpiper | <i>Calidris himantopus</i> | STSA | 11 | | 11 |
| | Least Sandpiper | <i>Calidris minutilla</i> | LESA | 104 | 13 | 117 |
| | Semipalmated Sandpiper | <i>Calidris pusilla</i> | SESA | 1 | | 1 |
| | Short-billed Dowitcher | <i>Limnodromus griseus</i> | SBDO | 58 | 12 | 70 |
| | Wilson's Snipe | <i>Gallinago gallinago</i> | WISN | 650 | 159 | 809 |
| | Spotted Sandpiper | <i>Actitis macularius</i> | SPSA | 55 | 72 | 127 |
| | Solitary Sandpiper | <i>Tringa solitaria</i> | SOSA | 103 | 34 | 137 |
| | Lesser Yellowlegs | <i>Tringa flavipes</i> | LEYE | 230 | 86 | 316 |
| | Greater Yellowlegs | <i>Tringa melanoleuca</i> | GRYE | 491 | 133 | 624 |
| | Gulls and terns | Bonaparte's Gull | <i>Chroicocephalus philadelphia</i> | BOGU | 129 | 57 |
| | Ring-billed Gull | <i>Larus delawarensis</i> | RBGU | | 10 | 10 |

| | | | | | | |
|----------------------------|--------------------------------|---------------------------------|------|-----|-----|-----|
| | Herring Gull | <i>Larus argentatus</i> | HERG | 11 | 5 | 16 |
| | Common Tern | <i>Sterna hirundo</i> | COTE | 1 | | 1 |
| | Arctic Tern | <i>Sterna paradisaea</i> | ARTE | 2 | | 2 |
| Loons | Common Loon | <i>Gavia immer</i> | COLO | 369 | 269 | 638 |
| Hérons and bitterns | American Bittern | <i>Botaurus lentiginosus</i> | AMBI | 73 | 12 | 85 |
| Hawks and eagles | Bald Eagle | <i>Haliaeetus leucocephalus</i> | BAEA | 4 | 6 | 10 |
| Owls | Great Horned Owl | <i>Bubo virginianus</i> | GHOW | | 1 | 1 |
| | Great Gray Owl | <i>Strix nebulosa</i> | GGOW | 12 | 3 | 15 |
| | Long-eared Owl | <i>Asio otus</i> | LEOW | 1 | 1 | 2 |
| | Boreal Owl | <i>Aegolius funereus</i> | BOOW | 1 | 1 | 2 |
| Kingfishers | Belted Kingfisher | <i>Megaceryle alcyon</i> | BEKI | 1 | 4 | 5 |
| Woodpeckers | Yellow-bellied Sapsucker | <i>Sphyrapicus varius</i> | YBSA | 9 | 7 | 16 |
| | American Three-toed Woodpecker | <i>Picoides dorsalis</i> | TTWO | 63 | 20 | 83 |
| | Black-backed Woodpecker | <i>Picoides arcticus</i> | BBWO | 6 | 6 | 12 |
| | Downy Woodpecker | <i>Picoides pubescens</i> | DOWO | | 2 | 2 |
| | Hairy Woodpecker | <i>Picoides villosus</i> | HAWO | 3 | 8 | 11 |
| | Northern Flicker | <i>Colaptes auratus</i> | NOFL | 17 | 8 | 25 |
| | Pileated Woodpecker | <i>Dryocopus pileatus</i> | PIWO | 1 | | 1 |
| | Woodpecker Species | Woodpecker Species | WOOD | 22 | | 22 |
| Tryant flycatchers | Olive-sided Flycatcher | <i>Contopus cooperi</i> | OSFL | 174 | 74 | 248 |
| | Eastern Wood-Pewee | <i>Contopus virens</i> | EAWP | | 1 | 1 |
| | Yellow-bellied Flycatcher | <i>Empidonax flaviventris</i> | YBFL | 223 | 154 | 377 |
| | Alder Flycatcher | <i>Empidonax alnorum</i> | ALFL | 401 | 214 | 615 |
| | Least Flycatcher | <i>Empidonax minimus</i> | LEFL | 12 | 18 | 30 |
| Vireos | Blue-headed Vireo | <i>Vireo solitaries</i> | BHVI | 11 | 25 | 36 |
| | Philadelphia Vireo | <i>Vireo philadelphicus</i> | PHVI | 7 | 28 | 35 |
| | Red-eyed Vireo | <i>Vireo olivaceus</i> | REVI | 24 | 30 | 54 |
| Crows and Jays | Gray Jay | <i>Perisoreus canadensis</i> | GRAJ | 359 | 269 | 628 |
| | American Crow | <i>Corvus brachyrhynchos</i> | AMCR | 22 | 6 | 28 |
| | Common Raven | <i>Corvus corax</i> | CORA | 67 | 28 | 95 |
| Larks | Horned Lark | <i>Eremophila alpestris</i> | HOLA | 14 | | 14 |
| Swallows | Tree Swallow | <i>Tachycineta bicolor</i> | TRES | 12 | 9 | 21 |
| Chickadees | Black-capped Chickadee | <i>Poecile atricapillus</i> | BCCH | 1 | 2 | 3 |
| | Boreal Chickadee | <i>Poecile hudsonicus</i> | BOCH | 36 | 29 | 65 |

| | | | | | | |
|---------------------|------------------------|--|------|------|-----|------|
| Nuthatches | Red-breasted Nuthatch | <i>Sitta canadensis</i> | RBNU | 8 | 17 | 25 |
| Treecreepers | Brown Creeper | <i>Certhia americana</i> | BRCR | 12 | 19 | 31 |
| Wrens | Winter Wren | <i>Troglodytes</i> [<i>troglodytes</i>] <i>hiemalis</i> | WIWR | 117 | 227 | 344 |
| Kinglets | Golden-crowned Kinglet | <i>Regulus satrapa</i> | GCKI | 46 | 41 | 87 |
| | Ruby-crowned Kinglet | <i>Regulus calendula</i> | RCKI | 432 | 220 | 652 |
| Thrushes | Veery | <i>Catharus fuscescens</i> | VEER | 1 | | 1 |
| | Gray-cheeked Thrush | <i>Catharus minimus</i> | GCTH | 37 | 12 | 49 |
| | Swainson's Thrush | <i>Catharus ustulatus</i> | SWTH | 387 | 458 | 845 |
| | Hermit Thrush | <i>Catharus guttatus</i> | HETH | 1485 | 579 | 2064 |
| | American Robin | <i>Turdus migratorius</i> | AMRO | 308 | 184 | 492 |
| Waxwings | Bohemian Waxwing | <i>Bombycilla garrulus</i> | BOWA | 1 | 5 | 6 |
| | Cedar Waxwing | <i>Bombycilla cedrorum</i> | CEDW | 7 | 45 | 52 |
| Pipits | American Pipit | <i>Anthus rubescens</i> | AMPI | | 1 | 1 |
| Finches | Evening Grosbeak | <i>Coccothraustes vespertinus</i> | EVGR | | 1 | 1 |
| | Pine Grosbeak | <i>Pinicola enucleator</i> | PIGR | 23 | 9 | 32 |
| | Purple Finch | <i>Haemorhous purpureus</i> | PUFI | 1 | | 1 |
| | Common Redpoll | <i>Acanthis flammea</i> | CORE | 143 | 34 | 177 |
| | Red Crossbill | <i>Loxia curvirostra</i> | RECR | | 1 | 1 |
| | White-winged Crossbill | <i>Loxia leucoptera</i> | WWCR | 177 | 165 | 342 |
| | Pine Siskin | <i>Spinus pinus</i> | PISI | 6 | 5 | 11 |
| | American Goldfinch | <i>Spinus tristis</i> | AMGO | 3 | 1 | 4 |
| Longspurs | Lapland Longspur | <i>Calcarius lapponicus</i> | LALO | 1 | | 1 |
| | Smith's Longspur | <i>Calcarius pictus</i> | SMLO | 29 | | 29 |
| Sparrows | Chipping Sparrow | <i>Spizella passerina</i> | CHSP | 152 | 67 | 219 |
| | Clay-colored Sparrow | <i>Spizella pallida</i> | CCSP | 2 | 5 | 7 |
| | Fox Sparrow | <i>Passerella iliaca</i> | FOSP | 663 | 318 | 981 |
| | American Tree Sparrow | <i>Spizella arborea</i> | ATSP | 108 | 36 | 144 |
| | Dark-eyed Junco | <i>Junco hyemalis</i> | DEJU | 748 | 291 | 1039 |
| | White-crowned Sparrow | <i>Zonotrichia leucophrys</i> | WCSP | 260 | 107 | 367 |
| | White-throated Sparrow | <i>Zonotrichia albicollis</i> | WTSP | 1896 | 802 | 2698 |
| | Le Conte's Sparrow | <i>Ammodramus leconteii</i> | LCSP | 13 | 22 | 35 |
| | Nelson's Sparrow | <i>Ammodramus nelsoni</i> | NSTS | 23 | 13 | 36 |
| | Savannah Sparrow | <i>Passerculus sandwichensis</i> | SAVS | 621 | 95 | 716 |
| | Song Sparrow | <i>Melospiza melodia</i> | SOSP | | 6 | 6 |
| | Lincoln's Sparrow | <i>Melospiza lincolni</i> | LISP | 961 | 211 | 1172 |
| | Swamp Sparrow | <i>Melospiza georgiana</i> | SWSP | 295 | 57 | 352 |

| | | | | | | |
|---------------------------|-------------------------|--------------------------------|------|-----|-----|-----|
| Troupials | Red-winged Blackbird | <i>Agelaius phoeniceus</i> | RWBL | 35 | 4 | 39 |
| | Rusty Blackbird | <i>Euphagus carolinus</i> | RUBL | 143 | 53 | 196 |
| New World Warblers | Ovenbird | <i>Seiurus aurocapilla</i> | OVEN | 4 | 16 | 20 |
| | Northern Waterthrush | <i>Seiurus noveboracensis</i> | NOWA | 378 | 219 | 597 |
| | Black-and-white Warbler | <i>Mniotilta varia</i> | BAWW | 7 | 15 | 22 |
| | Tennessee Warbler | <i>Oreothlypis peregrina</i> | TEWA | 183 | 173 | 356 |
| | Orange-crowned Warbler | <i>Oreothlypis celata</i> | OCWA | 215 | 99 | 314 |
| | Nashville Warbler | <i>Oreothlypis ruficapilla</i> | NAWA | 40 | 55 | 95 |
| | Connecticut Warbler | <i>Oporornis agilis</i> | CONW | 62 | 46 | 108 |
| | Mourning Warbler | <i>Oporornis philadelphia</i> | MOWA | 3 | 1 | 4 |
| | Common Yellowthroat | <i>Geothlypis trichas</i> | COYE | 272 | 119 | 391 |
| | American Redstart | <i>Setophaga ruticilla</i> | AMRE | 7 | 29 | 36 |
| | Cape May Warbler | <i>Setophaga tigrina</i> | CMWA | | 8 | 8 |
| | Magnolia Warbler | <i>Dendroica magnolia</i> | MAWA | 61 | 109 | 170 |
| | Bay-breasted Warbler | <i>Dendroica castanea</i> | BBWA | 2 | 7 | 9 |
| | Blackburnian Warbler | <i>Setophaga fusca</i> | BLBW | 2 | 3 | 5 |
| | Yellow Warbler | <i>Dendroica petechia</i> | YWAR | 78 | 51 | 129 |
| | Chestnut-sided Warbler | <i>Setophaga pensylvanica</i> | CSWA | 15 | 21 | 36 |
| | Blackpoll Warbler | <i>Setophaga striata</i> | BPWA | | 7 | 7 |
| | Palm Warbler | <i>Dendroica palmarum</i> | PAWA | 718 | 187 | 905 |
| | Yellow-rumped Warbler | <i>Dendroica coronata</i> | YRWA | 457 | 244 | 701 |
| | Wilson's Warbler | <i>Wilsonia pusilla</i> | WIWA | 189 | 130 | 319 |

Table 2A. Anurans detected on autonomous recording units during the Far North Biodiversity Project between 2010-2014, showing the number of individuals of each species for long-term and short-term plots.

| Common name | Scientific name | Taxa Code | Number of individual detections of ARUs | | |
|----------------------|-----------------------------------|-----------|---|------------------|-------|
| | | | Long-term plots | Short-term plots | Total |
| Spring Peeper | <i>Pseudacris crucifer</i> | SPPE | 193 | 29 | 222 |
| Chorus Frog (Boreal) | <i>Pseudacris maculata</i> | BOCF | 186 | 32 | 218 |
| Wood Frog | <i>Lithobates sylvaticus</i> | WOFR | 94 | 8 | 102 |
| American Toad | <i>Anaxyrus americanus</i> | AMTO | 71 | 25 | 96 |
| Mink Frog | <i>Lithobates septentrionalis</i> | MIFR | 9 | 0 | 9 |
| Green Frog | <i>Lithobates clamitans</i> | GRFR | 4 | 0 | 4 |

Table 3A. The 17 land cover names and codes derived from the Ontario Land Cover Compilation v.2.0 used to calculate Number of Land classes and Effective Number for Shannon Diversity as indices for habitat heterogeneity*

| Land-class Code | Original Ontario Land cover Compilation classifications | Land classes present in the Far North* | Pct of 10km buffered Plots |
|------------------------|--|---|-----------------------------------|
| 1 | Clear open water | ✓ | 11.10% |
| 2 | Turbid water | ✓ | 1.11% |
| 3 | Shoreline | | |
| 4 | Mudflats | ✓ | 0.37% |
| 5 | Marsh | ✓ | 0.80% |
| 6 | Swamp | ✓ | 11.3% |
| 7 | Fen | ✓ | 22.3% |
| 8 | Bog | ✓ | 27.8% |
| 9 | Shadow/cloud | ✓** | 0.02% |
| 10 | Heath | ✓ | 0.13% |
| 11 | Sparse treed | ✓ | 2.41% |
| 12 | Treed upland | ✓ | |
| 13 | Deciduous treed | ✓ | 1.21% |
| 14 | Mixed Treed | ✓ | 2.17% |
| 15 | Coniferous treed | ✓ | 10.12% |
| 16 | Plantations (treed cultivated) | | |
| 17 | Hedge rows | | |
| 18 | Disturbance | ✓ | 8.75% |
| 19 | Cliff and Talus | | |
| 20 | Alvar | | |
| 21 | Sand barren & Dune | | |
| 22 | Open tallgrass prairie | | |
| 23 | Tallgrass savannah | | |
| 24 | Tallgrass woodland | | |
| 25 | Sand/gravel/mine tailings/extraction | ✓ | 0.04% |
| 26 | Bedrock | ✓ | 0.06% |
| 27 | Community/infrastructure | ✓ | 0.00% |
| 28 | Agriculture | | |
| 99 | Unclassified types | ✓** | 0.02% |

*Far North Land Cover Data Specifications, version 1.4, 2014

**Not included in habitat diversity calculations

Table 4A. Variance explained and component loadings from principal component analysis at 500m grain size.

Importance of components:

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 |
|------------------------|-----------|-----------|-----------|------------|------------|------------|
| Standard deviation | 1.6703070 | 1.2571563 | 0.9051132 | 0.63063577 | 0.51944173 | 0.37799690 |
| Proportion of Variance | 0.4649876 | 0.2634070 | 0.1365383 | 0.06628358 | 0.04496995 | 0.02381361 |
| Cumulative Proportion | 0.4649876 | 0.7283945 | 0.8649329 | 0.93121644 | 0.97618639 | 1.00000000 |

Loadings:

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 |
|---------|--------|--------|--------|--------|--------|--------|
| N_Sess | 0.285 | 0.273 | 0.874 | 0.270 | 0.021 | 0.087 |
| LC_RICH | -0.427 | -0.449 | 0.247 | -0.089 | 0.571 | 0.470 |
| LC_DIV | -0.402 | -0.456 | 0.116 | 0.606 | -0.466 | -0.180 |
| NDVI | -0.485 | 0.169 | 0.305 | -0.624 | -0.501 | 0.052 |
| ATWQ | -0.486 | 0.374 | 0.064 | 0.098 | 0.446 | -0.642 |
| Lat | 0.322 | -0.589 | 0.256 | -0.392 | 0.074 | -0.570 |

Table 4B. Variance explained and component loadings from principal component analysis at 10,000m grain size.

Importance of components:

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 |
|------------------------|-----------|-----------|-----------|------------|------------|------------|
| Standard deviation | 1.6143285 | 1.2658326 | 0.9751252 | 0.65469563 | 0.54114428 | 0.34536738 |
| Proportion of Variance | 0.4343428 | 0.2670554 | 0.1584782 | 0.07143773 | 0.04880619 | 0.01987977 |
| Cumulative Proportion | 0.4343428 | 0.7013981 | 0.8598763 | 0.93131404 | 0.98012023 | 1.00000000 |

Loadings:

| | Comp.1 | Comp.2 | Comp.3 | Comp.4 | Comp.5 | Comp.6 |
|---------|--------|--------|--------|--------|--------|--------|
| N_Sess | 0.186 | 0.071 | 0.969 | 0.139 | 0.039 | 0.025 |
| LC_RICH | -0.024 | 0.701 | 0.060 | -0.671 | -0.219 | -0.075 |
| LC_DIV | -0.342 | 0.573 | -0.063 | 0.392 | 0.544 | 0.317 |
| NDVI | -0.550 | 0.043 | 0.085 | 0.284 | -0.735 | 0.258 |
| ATWQ | -0.586 | -0.067 | 0.132 | -0.007 | 0.174 | -0.777 |
| Lat | 0.449 | 0.411 | -0.171 | 0.544 | -0.288 | -0.472 |

Table 5A. Correlation coefficients for all independent variables at 500m grain.

| | Land cover richness | Land cover diversity | NDVI | ATWQ | Latitude | Effort |
|-----------------------------|----------------------------|-----------------------------|-------------|-------------|-----------------|---------------|
| Land cover richness | 1.0 | 0.7207 | 0.4676 | 0.3490 | 0.0740 | -0.3573 |
| Land cover diversity | 0.7207 | 1.0 | 0.3627 | 0.2663 | -0.0007 | -0.3736 |
| NDVI | 0.4676 | 0.3627 | 1.0 | 0.6839 | -0.4453 | -0.1633 |
| ATWQ | 0.3490 | 0.2663 | 0.6839 | 1.0 | -0.7251 | -0.1739 |
| Latitude | 0.0740 | -0.0007 | -0.4453 | -0.7251 | 1.0 | 0.1352 |
| Effort | -0.3573 | -0.3736 | -0.1633 | -0.1739 | 0.1352 | 1.0 |

Table 5B. Correlation coefficients for all independent variables at 10,000m grain.

| | Land cover richness | Land cover diversity | NDVI | ATWQ | Latitude | Effort |
|-----------------------------|----------------------------|-----------------------------|-------------|-------------|-----------------|---------------|
| Land cover richness | 1.0 | 0.5112 | 0.0509 | -0.0326 | 0.2894 | 0.0814 |
| Land cover diversity | 0.5112 | 1.0 | 0.4649 | 0.4507 | 0.0155 | -0.1281 |
| NDVI | 0.0509 | 0.4649 | 1.0 | 0.7845 | -0.5156 | -0.1747 |
| ATWQ | -0.0326 | 0.4507 | 0.7845 | 1.0 | -0.7229 | -0.1718 |
| Latitude | 0.2894 | 0.0155 | -0.5156 | -0.7229 | 1.0 | 0.1352 |
| Effort | 0.0814 | -0.1281 | -0.1747 | -0.1718 | 0.1352 | 1.0 |