Avian species richness elevational patterns in mountain peatlands

by

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Author's declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Statement of Contributions

While I am the sole author of this thesis, I acknowledge that Dr. Rebecca Rooney assisted with editing my thesis and Dr. Heidi Swanson assisted in statistical analysis. I will invite both to be co-authors on when publishing Chapter 2 and invite Dr. Rebecca Rooney to be a co-author when publishing Chapter 3.

Abstract

Avian research and elevation gradients have been studied extensively in the last century but there is a lack of understanding of the patterns and underlying mechanisms that drive avian species richness in mountain peatlands. This project examined the richness-elevation pattern and possible underlying mechanisms driving this pattern and the accuracy of avian species richness observed when collecting richness estimates from ARUs. Avian species richness was recorded using ARUs at 24 mountain peatland sites in the Upper Bow Basin for one hour during the dawn chorus on four days spread out between May 22nd and June 12th during the breeding season. Avian species richness in mountain peatlands displayed a plateauing pattern, cubic model, much like the plateauing patterns described by McCain in 2009 and it was determined that this pattern was a result of the effect of area on richness and the effect of Natural Subregion, a proxy variable for climate, temperature, soil and vegetation community, on richness. Also, the methods chosen to survey avian species richness provided accurate estimates of avian species richness but to get accurate estimates each survey required a larger survey effort than suggested by the literature.

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Table of contents

List of figures

Chapter 1

Chapter 2

Chapter 3

Appendix B

List of tables

Chapter 1

Chapter 2

Chapter 3

Appendix A

Appendix C

Appendix D

List of Symbols and Abbreviations

AIC	Aikake Information Criteria
AICc	Aikake Information Criteria corrected for small sample sizes
ARU	Autonomous Recording Unit
ICE	Incidence-based coverage estimator
Jack 1	First order Jackknife
Jack 2	Second order Jackknife
m a.s.l.	Meters above sea level
MDE	Mid-Domain Effect
R^2	Coefficient of determination
R^2 adj	Adjusted Coefficient of determination
S	Species richness
$\chi 2$	Chi-squared statistic
95% CI	95% Confidence Interval

1. Thesis Context and General Introduction

Describing spatial and temporal patterns in species richness and attempting to discern the processes responsible is a major area of enquiry in the discipline of ecology. Tremendous theoretical and empirical work has focused on the relationship between species richness and latitude (Rohde, 1992; Stevens, 1992), productivity (White & Running, 1994; Brown & Lomolino, 1998; Kessler et al., 2001; Mittelbach et al., 2001; Graham & Duda, 2011), habitat area (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Rahbek, 1997), and elevation (Rahbek, 1995; Lomolino, 2001; McCain, 2009; McCain & Grytnes, 2010). Given the current biodiversity crisis we face, understanding the drivers of patterns of species occurrence and coexistence has taken on practical significance and an urgency that demands more research attention. Studying these patterns in species richness is critical for conservation and for understanding trends in global species diversity (Lomolino, 2001; McCain & Grytnes, 2010). Mountain peatlands are relatively understudied ecosystems, but they can provide important habitat for birds, particularly as mountainous areas provide some of the last remaining wilderness on earth. Mountain peatland birds also provide an excellent model system for studying general patterns in species richness with elevation (e.g., Rahbek, 1997; McCain & Grytnes, 2010). The overall goal of my thesis is to evaluate the nature of the relationship between avian richness and elevation, using mountain peatland habitat in the Upper Bow Basin of Alberta, Canada.

1.1 Alberta mountain peatlands

Peatlands are high value ecosystems sensitive to change (Erwin, 2009) that may take thousands of years to form (Squeo et al., 2006). Peatlands in mountain ranges are formed in glaciated areas that made depressions over time (Squeo et al., 2006). When the ice melted in the depressions, water accumulated and began the process of forming a peatland ecosystem (Squeo et al., 2006). First, vegetation colonizes the mineral substrate, and this determines what type of peatland develops, because to become a peatland, accumulation of organic matter must be faster than the rate of decomposition (Squeo et al., 2006).

Peatlands can be classified as either bogs or fens (Gorham & Janssens, 1990). Fens are typically fed by groundwater and nutrient levels can vary from rich to poor, depending on the water source. Poor fens have low concentrations of dissolved minerals in water and a pH below 5.5, moderate rich fens have water with slightly higher concentrations of dissolved minerals and a pH between 5.5 and 7.0, and rich fens have the highest concentration of dissolved minerals, and a pH above 7.0 (Zoltai & Vitt, 1995). Bogs are more acidic than fens (pH <5.5) and are nutrient poor because their water originates exclusively from precipitation, which has low levels of dissolved minerals or nutrients (Gorham & Janssens, 1990; Zoltai & Vitt, 1995).

In contrast with our expansive boreal peatlands, mountain peatlands are understudied in Canada due to their remoteness, isolation, and lack of mapping. For example, in Alberta, they are excluded from wetland inventories, meaning they are unmapped and not characterized (Alberta Goverment, 2017). Due to their isolation, public access to sites is mainly restricted to summer and fall months.

Although species that occupy boreal peatlands are well documented (Calmé & Desrochers, 1999; Calme & Desrochers, 2000; Calmé et al., 2002; Austin & Cooper, 2016), uncertainty exists surrounding species occupancy of Alberta's mountain peatlands. For example, many gaps exist in our understanding of habitat use by avian species and the role of elevation in determining which species are present (e.g., Squeo et al., 2006; McCain, 2009; Randin et al., 2009). Without studying species richness in Alberta's mountain peatlands, we cannot know for certain which species are present, what ecological processes are acting on them and what disturbances, natural or anthropogenic, could be detrimental to the communities present.

1.2 Peatland services & human disturbance

Mountain peatlands play an important role in the environment (Kimmel & Mander, 2010). Three of their primary ecosystem services include support for biodiversity (Squeo et al., 2006; Warner & Asada, 2006), are carbon reservoirs (Austin & Cooper, 2016), and manage water quality and levels (Laine et al., 1995). Peatlands support high biodiversity and rare species from multiple taxa (Squeo et al., 2006), such as mammals, birds, reptiles, vascular plants and bryophytes. Peatland communities support both peatland specialist species that occupy territories restricted to peatlands (e.g., sundew and pitcher plants) and generalist species that occupy territories that overlap with neighboring ecosystems (Warner & Asada, 2006). Example taxa with large territories that make use of peatlands, but are not restricted to them, include birds and mammals (Warner & Asada, 2006). Peatlands are also large carbon reservoirs where carbon is part of the organic matter locked within the peat (Turetsky et al., 2002). Peatlands can absorb pollutants (e.g., Sulphur dioxide) from the atmosphere and from run-off, taking pollutants out of the available water (Winner et al., 1978). Another example of peatlands removing pollutants is the uptake of mecury into plant tissues especially moss species (Moore et al., 1995) while water can pass in and out of moss cells (Clymo & Hayward, 1982). As long as mountain peatlands are undisturbed, they can continue to support high biodiversity (Austin & Cooper, 2016), carbon reservoirs (Kimmel & Mander, 2010; Austin & Cooper, 2016), and water purifiers (Moore et al., 1995).

Disturbed peatlands can become major sources of greenhouse gas emissions (Turetsky et al., 2002), particularly if the peat dries out and becomes oxic. Drainage of peatlands degrades the quality of water, transports pollutants downstream (Laine et al., 1995), and affects aquatic species (Blann et al., 2009). The removal of water from peatlands increases fire frequency which can cause even more damage to surrounding ecosystems (e.g., mixed forests; Takakai et al., 2006). Peatland drainage degrades land quality (Laine et al., 1995), and increases the risk of flooding and drought downstream (Erwin, 2009a). Natural disturbances (i.e. forest fire or mudslide) can cause a loss of biodiversity and primary production (Wilsey & Potvin, 2000) and can increase the release of greenhouse gas emissions from the stored carbon in the accumulated peat. In summary, peatlands are important ecosystems that provide vital functions and services for the environment and society, but the degradation of this system can cause a multitude of detrimental effects.

1.3 Determinants of avian species richness

Elevation can be a major determinant of which species are able to persist in an environment (Randin et al., 2009) because several limiting environmental factors change predictably with increasing elevation (McCain & Grytnes, 2010). Factors such as water availability and climate (i.e. temperature and precipitation rates) change with elevation (Table 1.1) and influence the species that can persist in an area (McCain, 2009). The interactions between elevation and climate (i.e. temperature, solar radiation and precipitation) can influence productivity in the environment and varies among mountains (Table 1.1; Barry, 2008). Outside of climatic factors, other abiotic factors (i.e. soil quality and pH, water availability, cloud cover, habitat area) also vary with elevation (McCain & Grytnes, 2010). Abiotic and climatic factors that vary along elevation gradients can strongly influence the species that reside in different areas on mountains.

Table 1.1 Environmental conditions that vary with elevation, adapted from Barry (2008).

Increasing elevation correlates with	**Correlation**
Temperature	Decreases by an average of 0.6 C° with a 100 m increase in elevation
Air pressure	Decreases with an increase in elevation
Solar radiation	Increases with an increase in elevation
Precipitation (i.e. rain, snow and condensation)	Increases with elevation, but is variable between mountain ranges and proximity to large bodies of water and weather patterns

Factors that vary along elevation gradients such as productivity, temperature, moisture, and soil types are collectively what differentiates Natural Subregions (Downing & Pettapiece, 2006). The Upper Foothills covers 3.3% of the province, that ranges in elevation from 950 – 1750 m a.s.l. (Downing & Pettapiece, 2006). The temperature ranges from -11.6º C and 13.4º C (mean annual temperature = 1.3º C) and has 632 mm of mean annual precipitation (Downing & Pettapiece, 2006). Soils types found in this Natural Subregion are brunisolic gray luvisols, orthic gray luvisols, mesisols and gleysols (Downing & Pettapiece, 2006). The habitat contains closed coniferous forests made up of lodgepole pine (*Pinus contorta*), black spruce (*Picea Mariana*), and white spruce (*Picea glauca*; Downing & Pettapiece, 2006).

The Montane Natural Subregion covers 1.3% of the province that ranges in elevation from 825 – 1850 m a.s.l. (Downing & Pettapiece, 2006). The temperature ranges from -10.0º C and 13.9º C (mean annual temperature = 2.3º C) and has 589 mm of mean annual precipitation (Downing & Pettapiece, 2006). Soil types found in this Natural Subregion are black to dark gray chernozems and occurrences of brunisols, and luvisols (Downing & Pettapiece, 2006). The habitat contains grasslands and mixed or aspen (*Populus* species), lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and white spruce forests (*Picea glauca*) (Downing & Pettapiece, 2006).

The Subalpine Natural Subregion covers 3.8% of the province that ranges in elevation from 1300 – 2300 m a.s.l. (Downing & Pettapiece, 2006). In the study area, the Upper Bow River Basin, this Natural Subregion occurs above the Montane or Upper Foothills Natural

Subregion depending on the location (Downing & Pettapiece, 2006). North of the Bow River, the Subalpine is above the Upper Foothills Natural Subregion and south of the Bow River, the Subalpine is above the Montane Natural Subregion (Figure 2.4). The temperature ranges from -11.7º C and 11.3º C (mean annual temperature = -0.1º C) and has 755 mm of mean annual precipitation (Downing & Pettapiece, 2006). Soil types found in this Natural Subregion are eutric and brunisols soils (Downing & Pettapiece, 2006). The habitat contains mixed conifer forests (lodgepole pine; *Pinus contorta*, and Engelmann spruce; *Picea engelmannii*; Downing & Pettapiece, 2006).

The Natural Subregions then may serve as a proxy or surrogate for a suite of relevant variables that may influence species richness since the factors listed above remain somewhat homogenous within a Natural Subregion along with characteristic vegetation assemblages (Downing & Pettapiece, 2006). Therefore, there is an expected difference in species richness between Natural Subregions and since elevation ranges can overlap between Natural Subregions (Downing & Pettapiece, 2006), the composite of variables may better predict species richness than elevation alone.

Prior to Rahbek's 1995 study on species richness trends along elevation gradients, research suggested that with increasing elevation, species richness declined monotonically for all taxa (Terborgh, 1977; Rohde, 1992; Stevens, 1992). Rahbek (1995) found different patterns associated with different taxa along elevation gradients. McCain and Grytnes (2010) compiled data on the relationship between non-flying small mammals (McCain, 2005), bats (McCain, 2007), avian (McCain, 2009), reptile (McCain, 2010) and plant (Rahbek, 2005) species richness and elevation. They identified four different patterns in species richness that occur along elevation gradients (McCain & Grytnes, 2010). Either there should be a) a near linear decline in species richness as elevation increases; b) a negative quadratic relationship with the peak in species richness at the middle of the elevation range; c) a low elevation plateau in species richness, followed by a decline; or d) a low elevation plateau, followed by a mid-elevation peak in species richness (Figure 1.1; McCain & Grytnes, 2010). There is some tendency for different taxa to evidence different forms of the richness-elevation relationship. For example, reptiles tended to follow a near linear decline in richness with elevation in most studies reviewed by McCain and Grytnes (2010), whereas plants more commonly exhibited a mid-elevation peak in richness (Rahbek, 2005). Yet McCain and Grytnes (2010) found that studies of avian species richness were near equally split in terms of which richness-elevation pattern was reported (Figure 1.1), making birds of particular interest in richness-elevation studies. By examining what covariates might influence the nature of the relationship between richness and elevation, it may be possible to identify important mechanisms responsible for these conflicting patterns. Though they did not review evidence from the Canadian Rocky Mountains, avian species richness should exhibit one of the four patterns with elevation in this mountain range as McCain (2009) identified in other mountain ranges.

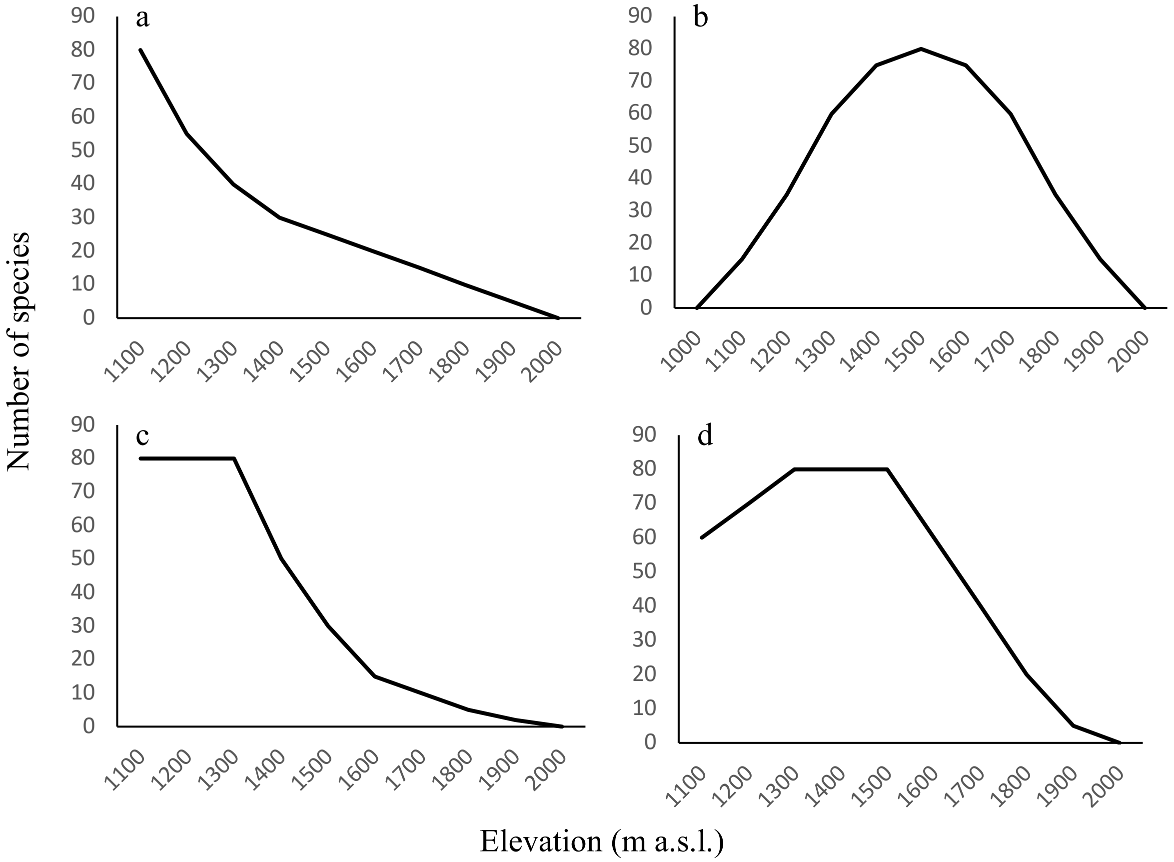

Figure 1.1 McCain's four general species richness patterns with increasing elevation where species richness exhibits a) a near linear decline as elevation increases; b) a negative quadratic relationship; c) a low-elevation plateau, followed by monotonic decline as elevation increases; and d) plateaus at low elevations with a mid-elevation peak in species richness, followed by a monotonic decline. Figure adapted from McCain and Grytnes 2010.

1.4 Avian use of peatlands and response to elevation

Aves (birds) are a vocal class of species with many conspicuous members (Rahbek & Graves, 2001). I identified them as an ideal class for my study on the richness-elevation relationship and assessment of richness estimate accuracy in mountain peatlands for five main reasons. First, avian taxonomy is widely understood, making identifications based on visual and auditory surveys reliable. Second, there exist standardized methods to survey avian species that include recording devices that enable remote monitoring in difficult to access locations such as mountain peatlands. Third, Aves is a diverse class that occupies a broad range of ecological niches (Montaño-Centellas et al., 2020), and so I anticipate species richness will vary detectably among my study sites. Fourth, several migratory avian species may occupy these mountain peatlands during their breeding season, at which time vocalizations become more frequent. Thus, I will be able to use recording units to determine cumulative species richness for all sites and find when no new species were added to the species pool. Lastly, bird watching is a very popular economic activity and an excellent motivator for people who care for habitat protection (U.S. Fish and Wildlife Service, 2018), if a flagship species approach to conservation is adopted.

Certain avian species require a specific habitat for foraging and nesting, while other species can thrive in a variety of different habitats (i.e. specialist vs. generalist species). Specialist species require specific biotic and abiotic factors to populate a certain habitat whereas generalist species can inhabit various habitats due to their lack of specific requirements to colonize (Kassen, 2002). Although, few birds are specialists to Canada's peatlands there are many species that occur in high densities there (Locky, 2003). Species that are likely to be found at higher elevations (i.e. Subalpine/Alpine Natural Subregion) include: larks (i.e. horned lark, *Eremophila alpestris*), and the American pipit (*Anthus rubescens*), based on previous study of avian species distributions in the Anatolian mountain range (Ambarli & Bilgin, 2014). Species common to bogs across Canada include passerine species such as the Northern Waterthrush (*Parkesia noveboracensis*) and Lincoln's Sparrow (*Melospiza lincolnii*; Breining, 1992; Calmé et al., 2002). Species with territories that tend to overlap with peatlands include Kinglets, Thrushes, Warblers and Sparrow species (Calmé et al., 2002). In Alberta, some waterbirds prefer to nest and breed in peatlands such as ring-neck ducks (*Aythya collaris*; Locky, 2003), and other waterbirds that prefer open peatlands and sedge meadows include sandhill cranes (*Grus canadensis*), greater yellowlegs (*Tringa melanoleuca*) and solitary sandpipers (*Tringa solitaria*;

Semenchuk, 1992). In addition, much of the variation in avian communities in Canadian peatlands has been found to depend on the vegetation community (Stockwell, 1994; Calmé et al., 2002), peatland size (Calmé & Desrochers, 1999; Calme & Desrochers, 2000) and peatland type (Dawson, 1979; Calmé & Desrochers, 1999; Calme & Desrochers, 2000).

1.5 Comparison of avian surveying techniques

There are several ways to survey avian species in the field such as in-person point count surveys, hand-held recording devices (i.e. zoom recorders, smartphones) and autonomous recording units (ARUs). Traditionally, point count surveys are used but with technological advances there are benefits to using ARUs to supplement point counts for short term study (Leach et al., 2016; Yip et al., 2017), and there are many studies on direct comparisons between point counts and ARU recordings (Table 1.2).

Table 1.2 Comparative list between two avian survey methods, point counts and autonomous recording units (ARU).

Survey Method	Pros	Cons
Point Count	More species detection on average when length of survey time between methods is equal	Requires multiple trained field technicians to accurately identify species
	Secondary detection through visual sightings of species	Requires multiple site visits to adequately sample the avian community
	Surveyors have a larger auditory detection radius for identifying species compared to ARUs	Field technicians' access to sites may be restricted by time of year or weather conditions
	Visual observations aid in reducing uncertainty in relative abundance estimates	
	Better survey method to determine relative abundance	

	since individuals can triangulate species positions in the study site	
ARU	Requires only two site visits	Cost of ARU and equipment can be expensive
	ARUs can be programmed to record for an entire season	It can take many hours for a trained technician to manually analyze recordings and extract data, whereas in-person point counts immediately yield data ready for statistical analysis
	ARUs can be programmed to record at specific times of the day or the entire day	File or data corruption can occur at any point during the time the ARU is left in the field or while processing files
	Does not require a trained technician to install ARU at a site	Because the ARU records regardless of weather and noise conditions, not all recordings are useable
	Has the ability to record species that remain silent when humans are present or species that call infrequently	Not able to determine the number of individuals reliably when more than 3 individuals are present in a recording
	ARUs have weatherproof case that allows surveys to continue no matter the weather	
	ARUs can be programmed to record between a frequency range, such as above 220 Hz and 20,000 Hz, the frequency range of avian species	

For an ornithology study at the community level, field technicians use a surveying technique called point counts (Nichols et al., 2000). Point counts are in-person surveys of specified duration where at least one person identifies the avian species by vocalization or visual identification for the specified survey period (Nichols et al., 2000). The length of each survey depends on the researcher and study objectives and can range from about 5 to 20 minutes (e.g., Zuberogoitia et al., 2011; Tegeler et al., 2012; Sidie-Slettedahl et al., 2015). Point counts are typically only conducted during the dawn chorus (i.e., when there are high amounts of avian vocalization around sunrise, during the breeding season) or conducted at night to observe nocturnal species (e.g., owls; Shonfield et al., 2018). Point count surveys are a useful method to survey avian species in a defined area during the breeding season.

There are two main types of point counts, passive and active surveys. Active surveys are where observers play a species vocalization to try and make individuals of that species respond (Zuberogoitia et al., 2011), whereas in passive surveys the observers only record avian vocalizations and visuals of birds (Nichols et al., 2000). Passive surveys are better suited for long-term study and monitoring avian populations (Campos-Cerqueira & Aide, 2016). However, passive point counts capture mainly conspicuous avian species and are likely to miss rare or secretive birds that will not call while humans are present, creating a biased survey (Darras et al., 2018). Active surveys can be useful when secretive birds are the target of investigation, though they can be disruptive if frequently repeated. For example, intensive monitoring (Sidie-Slettedahl et al., 2015) with multiple visits on different dates during a single breeding season are discouraged from using active surveys and rely on repeated surveys to limit errors of omission.

For avian surveys, autonomous recording units (ARUs) were developed to record vocalizations, especially vocalizations from rare and elusive species (Table 1.2; Shonfield & Bayne, 2017). ARUs provide an alternative to repeated in-person point count surveys that would require multiple site visits by only needing two site visits; one to deploy and one to collect the ARU (Sidie-Slettedahl et al., 2015). These recording devices can be scheduled to record for any time of day or night and for any duration of interest, though recordings are typically 10 - 15 minutes in duration (Sidie-Slettedahl et al., 2015). Recorded files are processed using audio software after the collection period is finished and a field study can generate a large work load for technicians to review after the field season ends (Priyadarshani et al., 2018). However, some automated recognition software has been developed for specific avian species (Priyadarshani et al., 2018). Yet manually scanning each recording for a particular avian species or even to document all species may be faster than automated scanning and identifications due to the amount of incorrect identifications from automatic recognition software (Swiston & Mennill, 2009).

As much as technology has advanced, in-person point counts and ARU recordings remain complementary techniques, each with their own advantages and disadvantaged (Table 1.2; Leach et al., 2016). When looking at species richness rather than relative abundance, ARUs have some advantages. Avian species that do not vocalize frequently and rare species may be missed by in-person point count surveys during the dawn chorus and dusk point counts, as secretive or rare birds may call less when humans are present (Darras et al., 2018) and in-person surveys are usually much more time restricted than ARU recordings (Tegeler et al., 2012). ARUs can record during the entire dawn and dusk chorus, for > 2 h, which is much longer than a typical point count survey duration. With little additional effort, ARUs can also record throughout the day and during the night capture vocalizations outside of the crepuscular chorus times (e.g., King Rail, Yellow Rail, or owls). The main disadvantage of relying on ARUs is that they have a smaller auditory detection radii compared to human observers (Hutto & Stutzman, 2009). During point counts an observer can locate the general area a vocalization is coming from and detect vocalizations accurately in the habitat patch of any shape, unlike ARUs that record vocalizations within about a 100 m radius (Hingston et al., 2018) depending on vegetation density and height (Tegeler et al., 2012). As the distance from the ARU increases species detection probabilities decrease (Yip et al., 2017) and in-person surveys can supplement ARU recordings with visual confirmation of identification of similar calling species or detect species that do not call but are present at the site (Tegeler et al., 2012). ARUs are therefore likely superior to in-person surveys for studies of richness-elevation patterns because they are better at detecting rare or secretive bird occurrences and require fewer visits to the site; however, it is worthwhile assessing the sufficiency of the ARU recordings in terms of the duration of the survey period and the survey effort extended at each peatland.

1.6 Thesis objectives and hypothesis

My overall thesis objectives are to 1) determine the richness-elevation pattern evidenced by birds in the Upper Bow River Basin in relation to McCain's four general patterns and to test if the pattern seen is just an artefact of the influence of habitat area or Natural Subregion on avian species richness, and 2) assess whether ARU richness collection methods substantially under-estimated avian species richness at the mountain peatland sites. I address these two objectives over four chapters. The second and third chapters I intend to publish as original research papers, co-authored with my MSc. supervisor, Dr. Rooney. For chapter 2, my committee member Dr. Heidi Swanson, who made substantial theoretical and analytical contributions to the chapter, is also intended to be a co-author. These two data chapters are introduced by this first chapter, which consisted of a literature review, providing background information and context relevant to my thesis on avian species richness in mountain peatlands, processes and methods that effect avian species richness and avian survey methods. The entire document is then summarized in my fourth chapter, which provides a brief summary of the second and third chapter's findings, as well as natural history notes of conservation interest from my study region.

The second chapter is a data chapter in which I examine the avian species richness-elevation relationship by comparing my estimated avian species richness to McCain's general elevation gradient patterns and account for the effects of area on the richness-elevation relationship. Also, I determine if species richness differs between Natural Subregions (Upper Foothills/ Montane and Subalpine) and if Natural Subregion (or Natural Subregion after accounting for the effect of area) provides a better model fit than McCain's general richness-elevation patterns. I predict that the avian community occupying peatland habitat in the Upper Bow River Basin will follow one of the four richness-elevation patterns described in McCain (2009), though there is little basis for predicting which of the four will exist in my study system. However, I further predict that taking into account habitat area will alter the strength and perhaps the nature of the richness-elevation relationship, as was observed by Rahbek (1997). Similarly, I expect that factors like temperature, productivity, and moisture availability will influence species richness. These factors are somewhat integrated in the compositive variable of Natural Subregion, and hence I predict that species richness will also differ between the Montane and Subalpine Natural Subregions. Again, I expect that peatland area will explain a portion of that difference in richness between Natural Subregions. To test these predictions, I use an AIC framework for three model competitions to determine which of McCain's general elevation patterns occur in my study system and which had more support: richness-area-residuals vs. elevation or richness-area-residuals vs. Natural Subregion to determine possible underlying mechanisms.

In my third chapter I assess whether ARU richness collection methods substantially under-estimated avian species richness at the mountain peatland sites. I predict that species richness estimates at the regional and sub-regional species pool level will plateau within the survey period to indicate that my ARU surveys adequately captured the avian community present in mountain peatlands. Also, I predict that site-level alpha richness will plateau within 240 minutes of survey effort. I make this prediction based off of previous research done in montane meadows that dawn chorus surveys required at least one hour of ARU recordings for a site's cumulative species richness to plateau but may require up to 4.5 hours (Tegeler et al., 2012). I will address both predictions by using species accumulation curves and richness estimators to determine if alpha and gamma richness plateaued. As well as using logistic regression and a contingency table to evaluate the probability of site-level richness plateauing within 240 minutes of survey.

2. Avian species richness patterns

2.1 Introduction

Extensive study of elevation gradients has provided a framework for how species richness, i.e., the total estimated number of species at a particular site, changes along elevation gradients on a global scale (McCain & Grytnes, 2010). Early research indicated that the diversity of all taxa decreased with increasing elevation (e.g., Terborgh, 1977; Rohde, 1992; Stevens, 1992). This simple generalization was later rejected by Rahbek (1995), who found that certain taxa (e.g. birds) had mid-elevation peaks in species richness in certain regions. With more study, avian species richness was shown to follow one of four general patterns with increasing elevation: either 1) species richness decreases almost linearly, 2) species richness increases with elevation to peak at mid-elevations and declines with further increases in elevation (i.e., negative quadratic relationship), 3) species richness plateaus at lower elevations then decreases with increasing elevation, or 4) species richness plateaus at low elevations with a mid-elevation peak and then begins to decline (Figure 1.1; McCain, 2009; McCain & Grytnes, 2010). In her review, McCain (2009) noted that these four general patterns of avian species richness were observed along elevation gradients throughout all terrestrial ecosystems and in each biogeographical region between 24.5 º S and 48.2 º N (McCain, 2009). Yet, the review excluded latitudes above 49 º N. Therefore, habitats from the majority of Canada were omitted (McCain, 2009; McCain & Grytnes, 2010b), including the Canadian Rocky Mountains.

Despite extensive research into richness patterns seen along elevation gradients (Whittaker, 1960; Brown, 1971; Lomolino, 2001; McCain & Grytnes, 2010), there is still little understanding of the underlying mechanisms at play (Colwell et al., 2004; Wu et al., 2013). McCain's four general richness-elevation patterns could be caused by several, possibly interacting, mechanisms. I highlight five different mechanisms that prior research has suggested could be wholly or partially responsible for the observed relationships between richness and elevation, four of which may vary systematically with elevation: the mid-domain effect, the richness-temperature relationship, the richness-productivity relationship, and the richness-area relationship (Table 2.1). The fifth, the richness-heterogeneity relationship, does not necessarily align with an elevation gradient, but may interact with the other four mechanisms I discuss to complicate any richness-elevation relationship.

Table 2.1 McCain's four general elevation patterns represented as a mathematical model with and possible mechanisms responsible for the pattern.

General elevation pattern	Mathematical model	Possible mechanisms
Near linear decline	Linear: $y = mx + b$	Area, or environmental filters like temperature, and productivity
Negative quadratic	Quadratic: $y = - ax^2 + bx + c$	The Mid-Domain Effect (MDE) or productivity
Low elevation plateau	Cubic: $y = ax^3 + bx^2 + cx + d$	Interaction from multiple mechanisms, possibly including habitat heterogeneity
Low elevation plateaus with a mid-elevation peak in richness		

The first possible mechanism to which the richness-elevation relationship has been attributed for richness-elevation studies, whereby species distributions within the elevation domain are randomly placed with respect to other abiotic gradients (e.g., temperature, soil quality) and with respect to the distributions of other species (Colwell et al., 2004). Yet, because a mountain is spatially bounded by the peak and foot of the mountain, even randomly placed species distributions along a mountain slope will result in a negative quadratic relationship (Table 2.1) between richness and elevation (Colwell et al., 2004; i.e., McCain's second pattern; Figure 1.1b). This is because the greatest overlap in species distributions will result at the mid-point of the bounded domain (Figure 2.1). This phenomenon is therefore called the Mid-Domain Effect (MDE) and is described as a geometric constraint on species richness (Colwell & Lees, 2000). McCain (2004) found support for the MDE in small mammals in Costa Rica but climate variables were also correlated with small mammal species richness, suggesting their distributions were not purely random. In their review of 21 MDE studies, Colwell et al. (2004) reported that the strength of the MDE is dependent on the range size of the taxa under consideration, being stronger with larger ranged species. Sanders (2002) suggested the MDE was important in explaining patterns of ant diversity along elevation gradients. Yet, Fuentes and Jaksić (1988) found very little evidence of a negative quadratic richness-elevation pattern for terrestrial vertebrates. Lawton (1999) suggested that the negative quadratic richness-elevation relationship was observed occasionally, contingent on the organism, environment and the scale of study. In isolation, the MDE would be expected to yield McCain's second pattern (a mid-elevation peak in diversity; Figure 2.1), yet Colwell et al. (2004) emphasized that the MDE must be considered as part of a multi-causal framework when considering the mechanisms behind patterns in species richness. Through interacting with other mechanisms, which I describe below, the MDE could potentially generate a low-elevation plateau or peak (McCain's third and fourth patterns).

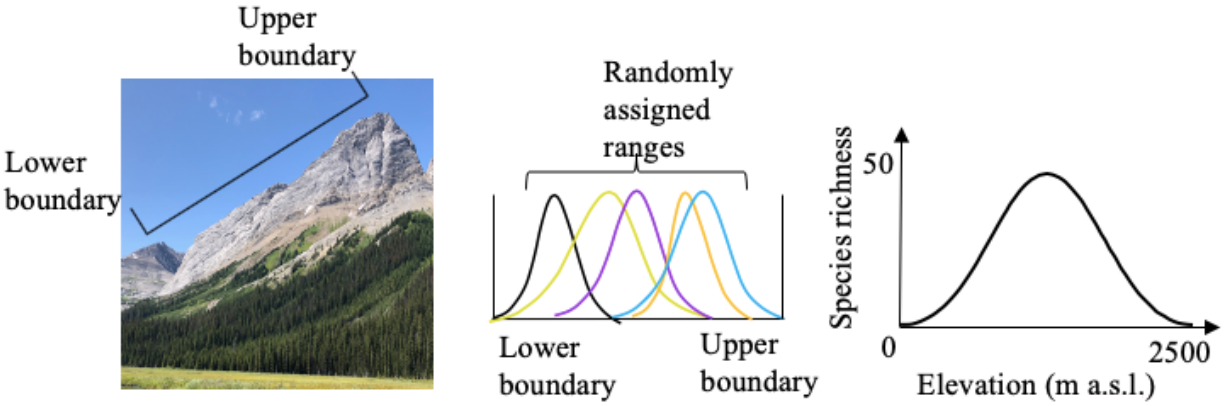

Figure 2.1 Conceptual model of the mid-domain effect and how species ranges are spatially bound along an elevation gradient between the peak and the foot of the mountain even when species ranges are randomly assigned produce a negative quadratic richness-elevation relationship.

An alternative to the MDE would be mechanisms whereby abiotic or biological factors that vary with elevation determine the distribution of species along the elevation gradient through the process of ecological selection or environmental filtering (sensu Vellend, 2010). Many environmental factors, such as temperature, atmospheric pressure, and clear-sky turbidity vary systematically with elevation (Körner, 2007). Such factors can affect the suitability of mountain habitat for bird species. Environmental filters like temperature and productivity can be integrated through ecological land classifications. Mountain habitats, like other ecosystem types, are typically divided into ecological zones on the basis of their climate, soils, and resulting vegetation communities (Kusbach, 2010). In Alberta, Natural Subregions are classified by following a scheme devised by Downing and Pettapiece (2006), which includes three main zones in the Rocky Mountain Natural Region: the Montane, the Subalpine, and the Alpine, and two main zones in the Foothills Natural Region; Lower Foothills, and Upper Foothills, each with its own specific elevation range, climate, vegetation and soil characteristics, which covary with elevation (Table 2.1; Downing & Pettapiece, 2006).

Table 2.2 Natural Subregion classification by Natural Region and each Natural Subregion's elevation range, mean annual temperature, precipitation, and vegetation structure as classified by Downing and Pettapiece (2006).

Natural Region	Natural Subregion	Elevation range (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Vegetation structure
Foothills	Lower Foothills	650 – 1625	1.8	588	Closed canopy mixed stands
	Upper Foothills	950 – 1750	1.3	632	Closed canopy conifer stands
Rocky Mountain	Montane	825 – 1850	2.3	589	Grassland and forest complexes
	Subalpine	1300 – 2300	-0.1	755	Forested
	Alpine	1900 – 3650	-2.4	989	Treeless

Natural Subregions can be used as a surrogate that integrates across a set of ecological filters, including temperature and productivity, through their integration of information about climate, soils, and vegetation assemblages into relatively homogenous spatial units. Though the range of elevation where the Natural Subregions are located overlaps in Alberta's Upper Bow River Basin, typically the Subalpine occurs at higher elevations than the Montane. It is therefore possible that an apparent richness-elevation regression relationship might be more of a richness-Natural Subregion categorical difference reflecting the mechanisms of temperature and productivity as integrated within Natural Subregions.

After the MDE, Temperature is the second possible driver of species richness patterns along elevation gradients (Barry, 2008). Generally, temperature decreases by about 0.6º C with every 100 m increase in elevation due to reduced atmospheric pressure (Barry, 2008). Under the metabolic niche hypothesis, colder temperatures permit the existence of fewer types of energetic lifestyle (Clarke & Gaston, 2006). In support of this hypothesis, Lennon et al. (2001) found that the pattern of bird diversity across Britain was best predicted by summer temperatures. Fewer species of bird can persist at colder temperatures, which occur at higher elevations, and so the temperature-elevation relationship could drive a richness-elevation relationship (Table 2.1).

Third, species richness varies with productivity (Mittelbach et al., 2001). Simply put, higher productivity environments provide fewer constraints and may support a greater number of species (Table 2.1; Tilman et al., 1996; Brown & Lomolino, 1998). Though in some cases, the literature documents a negative quadratic relationship to productivity, whereby above a certain threshold, excessive productivity leads to declines in species richness (e.g., Tilman, 1982; Rosenzweig, 1995; Graham & Duda, 2011). Because productivity is known to be dependent on temperature (Lieth, 1975; Schlesinger, 1991), moisture (Sala et al., 1988), and soil fertility (Osuji & Nwoye, 2007), and these factors can vary with elevation, productivity can also vary with elevation (Chen et al., 2011).

Fourth, it is well known that species richness is dependent on the available habitat area, following the power function $S = c A^z$, wherein species richness (S) is a function of area (A), with the slope (z) in log-log space, and the constant (c) reflecting the unit used to measure area (Connor & McCoy, 1979). This relationship is a key underpinning of MacArthur and Wilson's Theory of Island Biogeography (MacArthur & Wilson, 1967). In essence, habitat area can be conceived of as constraining available niche space, with smaller habitats supporting less niche space and consequently fewer species. A mountain can be described as a cone shape, with diminishing area of habitat available toward the peak (Figure 2.2). Consequently, the lower elevations in a mountain range may have higher species richness than higher elevations, simply because less habitat area is available at the higher end of the elevation gradient (Table 2.1; Rahbek, 1997). In fact, some have argued that the entire richness-elevation relationship is simply a product of elevation and area being confounded (Lawton et al., 1987).

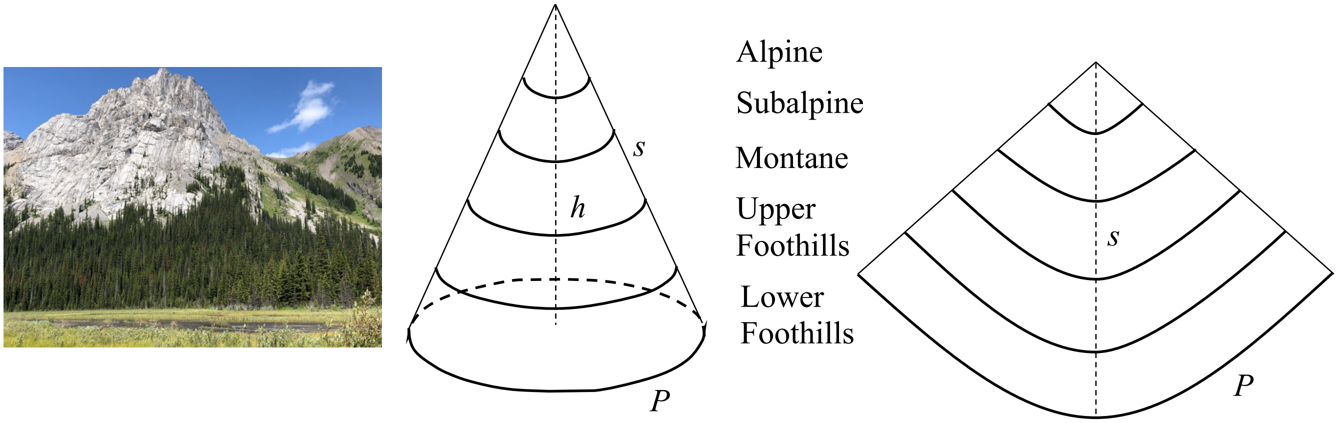

Figure 2.2 Conceptual model of how a mountain can be considered a cone shape and that there is more area available for more species at lower elevations.

Fifth, species richness is positively related to habitat heterogeneity (Freemark & Merriam, 1986; Wiens, 1974), as more diverse habitats provide greater niche space for species to occupy (Tews et al., 2004). Though there is no obvious relationship between habitat heterogeneity and elevation, variation in habitat heterogeneity could complicate the pattern of richness along an elevation gradient, perhaps modifying an otherwise linear or negative quadratic relationship to result in McCain's plateauing patterns (Figure 1.1; Graham & Duda, 2011).

Importantly, it is not clear whether elevation is simply a surrogate for measures of niche space (i.e. habitat area and heterogeneity) or ecological filters (i.e., temperature and productivity) that directly influence species richness, or whether the mid-domain effect is responsible for observed patterns between richness and elevation. A near linear decline in richness, McCain's first pattern, has been reported along several montane elevation gradients where larger sites had higher species richness while smaller sites supported fewer species (Beehler, 1981; Patterson et al., 1998). Similarly, the effect of environmental filters that change linearly with elevation could yield McCain's first pattern (McCain, 2007, 2009). The low plateau pattern, McCain's third pattern, was also found to arise where there was evidence of a strong richness-area relationship or where the influence of environmental filters like temperature and precipitation were accounted for (McCain, 2009). Yet, McCain's second (negative quadratic) and fourth (plateaus at low elevations with a mid-elevation peak in richness) patterns coincided with weak richness-area relationships and were more attributed to the MDE (McCain, 2009).

In this chapter, I will: 1) evaluate which of McCain's (2009) richness-elevation patterns occurred in valley-bottom mountain peatlands along the elevation gradient using Autonomous Recording Units (ARUs), 2) test the relationship between peatland size and avian species richness to evaluate whether the richness-area relationship is a plausible mechanism for explaining any observed richness-elevation relationship, 3) contrast the shape of the richness-elevation relationship with and without accounting for the effect of peatland area to evaluate whether residual richness-elevation variation that remains might be due to the MDE or environmental filtering, and 4) determine if species richness differs between the Montane and Subalpine Natural Subregions with and without accounting for the effects of peatland area to assess whether ecological filters like variation in temperature and productivity could be responsible for any observed richness-elevation relationship. Lastly, I will 5) compare the fit of the best richness-elevation relationship and the richness-Natural Subregion relationship after accounting for the role of habitat area, to compare support for the MDE and the environmental filtering mechanisms.

2.2 Methods

2.2.1 Study design

In 2019, I estimated total avian species richness in mountain peatlands based on acoustic surveys. With these estimates I tested which of McCain's general elevation gradient patterns were present in this system, while taking peatland area and Natural Subregion into account.

I surveyed twenty-four valley-bottom mountain peatlands in a Natural Subregion of interest; Upper Foothills, Montane, or Subalpine, with the site's elevation (m a.s.l.; Figure 2.3) and peatland area (km^2) determined through ArcGIS (ESRI, 2011). From this point forward the Upper Foothills and Montane were grouped and referred to as the Montane Natural Subregion since both Natural Subregions are directly below the Subalpine Natural Subregion depending on their location in respect to the Bow River. The valley-bottom mountain peatlands were 202.0 km^2 on average (± 273.4 SD, range: 5.0 km^2 – 887.9 km^2). The sampled wetlands' elevation ranged from 1300 m.a.s.l. to 2000 m.a.s.l. (Figure 2.3), intersecting the elevation ranges of the Upper Foothills, Montane, and Subalpine Natural Subregions; 950 – 1750 m.a.s.l., 825 m.a.s.l. – 1850 m.a.s.l. and 1300 m.a.s.l. – 2300 m.a.s.l., respectively (Downing & Pettapiece, 2006).

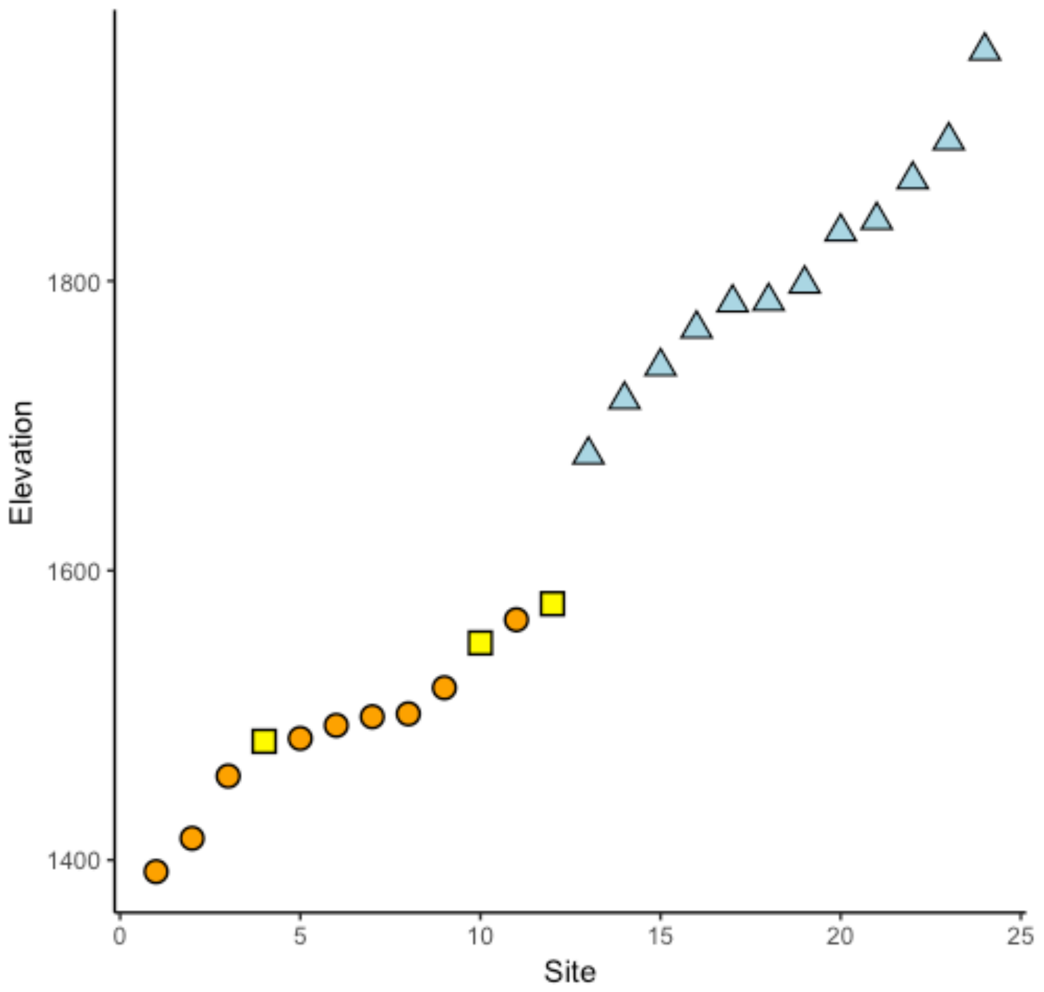

Figure 2.3 Elevation gradient from 2019 sampled mountain peatland sites. Natural Subregion sites are defined by shape and colour for clarity on overlap in elevation ranges between Natural Subregions of interest. The Upper Foothills Natural Subregion sites are shown as yellow squares, Montane Natural Subregion sites are shown as orange circles and the Subalpine Natural Subregion sites are shown as blue triangles.

2.2.2 Study area

I conducted avian surveys from May 22nd to June 12th, 2019 in valley-bottom mountain peatlands located in the Upper Bow River Basin of the Rocky Mountains, in southwestern Alberta, Canada (Figure 2.4). My surveys focused on the Ghost, Elbow and Jumpingpound watersheds.

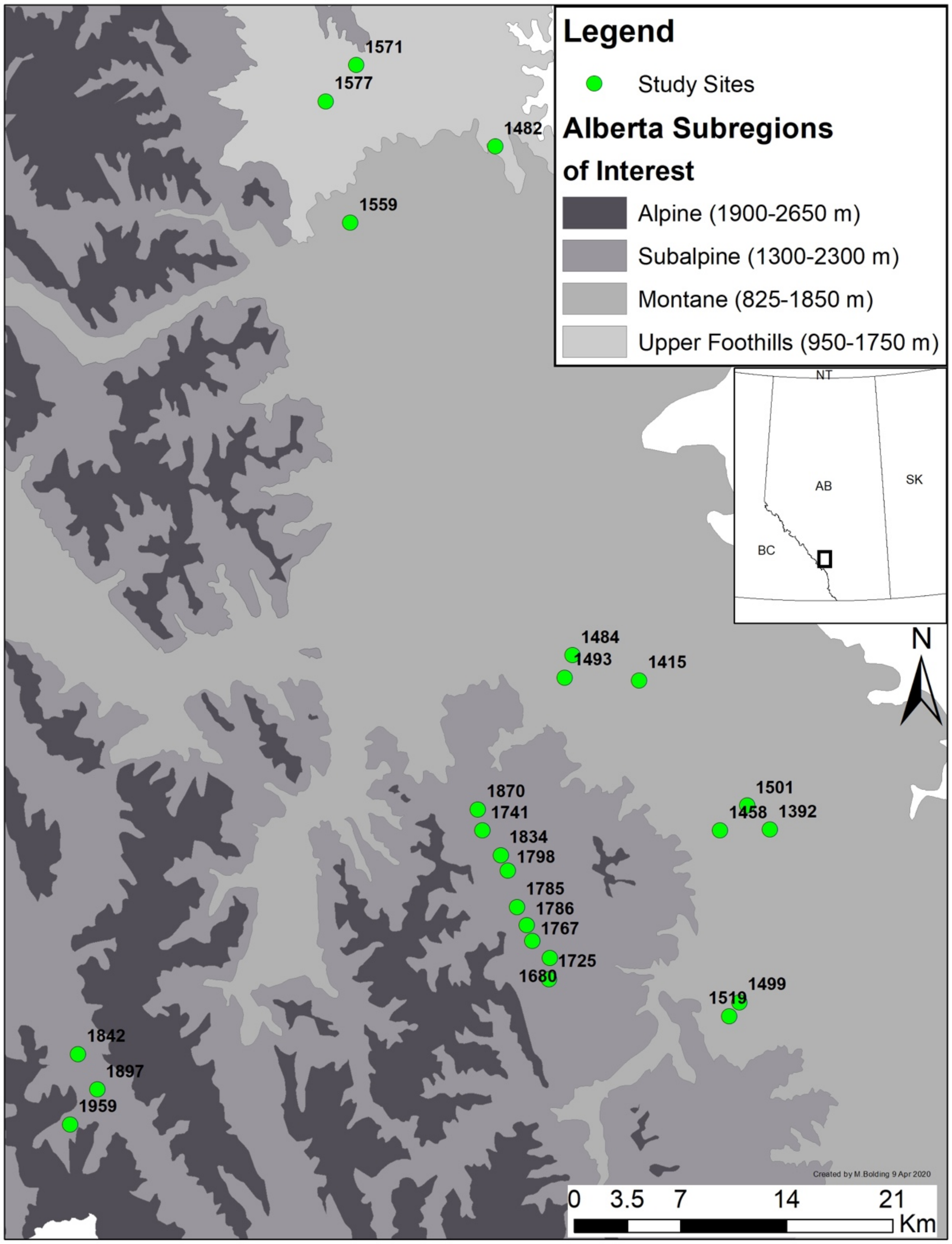

Figure 2.4 Map of study sites (N = 24) sampled in May – June 2019. Sites were in the Montane (Upper Foothills n = 3, and Montane n = 9) and Subalpine (n = 12) Natural Subregions in the Upper Bow River Basin, Alberta, Canada. Shading corresponds to the Alberta Natural Subregions of interest in different shades of grey with green circles indicating site location in the Natural Subregions of interest and corresponding elevation (m a.s.l.).

I chose sites with similar vegetation composition, soils and physical features to ensure all study sites were comparable. All sites had vegetative communities typical of Alberta peatlands, including sparse *Picea* cover, and higher abundances of *Salix*, dwarf birch (*Betula nana*), *Carex* species, as well as brown and *Spagnum* mosses. I sampled soil using a shovel to dig a 40 cm deep hole to ensure soils were high in organic content and low in mineral content, as is characteristic of peatlands. Other physical features used for site selection included ensuring the site was in a depression with ≤ 15° slope, 500 m or more from the nearest neighboring site as to not record the same individual bird in two different peatlands and each peatland was at minimum 100 m wide.

2.2.3 Avian field surveys

I ran avian acoustic surveys during a portion of the avian breeding season from May 22nd to June 12th, 2019 at mountain peatland sites from 06:00 to 07:00. I rotated twelve Autonomous Recording Units (ARU; Song Meter, SM4; Wildlife Acoustics, Maynard, Massachusetts, USA) among 24 mountain peatlands in stratified-random clusters. On each survey date, I deployed ARUs in both Natural Subregions to ensure date and Natural Subregion were never confounded.

I programmed ARUs to record for two consecutive days in two rounds of survey for a total of four recorded days per peatland due to Tegeler et al. (2012) finding survey effort may require up to 4.5 hours to record the avian community at a given site. ARUs recorded avian vocalizations from 06:00 to 07:00 (i.e. during the dawn chorus). Within this hour, all sites of differing latitudes and slope aspect began showing signs of sunrise (Time and Date AS, 2019) which signals the dawn chorus. All hour-long surveys were digitally stored in 10-minute increments. Previous research in Montane meadows found recorded surveys required one hour or more of recorded dawn chorus to approach the site's asymptote of estimated species richness (Tegeler et al., 2012). For analysis of sampling effort adequacy see Chapter 3.

Each ARU was installed within a relatively homogenous patch of peatland measuring at least 50 m from the peatland-upland boundary (Figure 2.5). A 50 m radius was the minimum distance used to reduce the likelihood of recording avian species that only occupy surrounding ecosystems (e.g. coniferous or mixed-wood forests). This minimum distance was determined by the average peatland dimensions and the maximum vocalization-distance recording capacity of the ARUs (typically 100 m radius; Hingston et al., 2018). Each ARU was installed so that the microphones were suspended 1 m above the substrate. Once the ARU was installed at the site, I programmed the ARU to record at 24 kHz, as 16-bit recordings (Bioacoustic Unit, 2015).

Figure 2.5 Photo of study site 220 depicting the layout of the ARU relative to the whole site. At each site, the ARU (indicated by the red dot) was located at the approximate center of the site and a minimum 50 m radius from adjacent ecosystems and roads.

2.2.4 Bioacoustic data processing

I used Audacity® (Audacity®; Audacity Team 2019; version 2.3.3), a sound analysis program, to manually identify avian species in two ways: (1) identifying avian species through their audible vocalizations and (2) identifying avian species visually by inspecting the audio spectrogram. Each 10-minute recorded file was transformed from an audio .WAV file into a spectrogram (Figure 2.6). I changed the spectrogram settings to a logarithmic scale and set it to show frequencies between 1000 – 10000 Hz. The left and right gain were set to 15 dB and range was 80 dB. The widow size and type were changed to 2048 and Gaussian (a = 4.5), respectively. The settings were altered to best hear frequencies and visualize vocalizations that are 1000 Hz and higher, which encompassed the range for most diurnal avian species vocalizations (Hu & Cardoso, 2009). For owl and duck species that vocalize at lower frequencies (≤ 2000 Hz; Hu &

Cardoso, 2009), the window size was changed to 4096 Hz for visual confirmation of their vocalization.

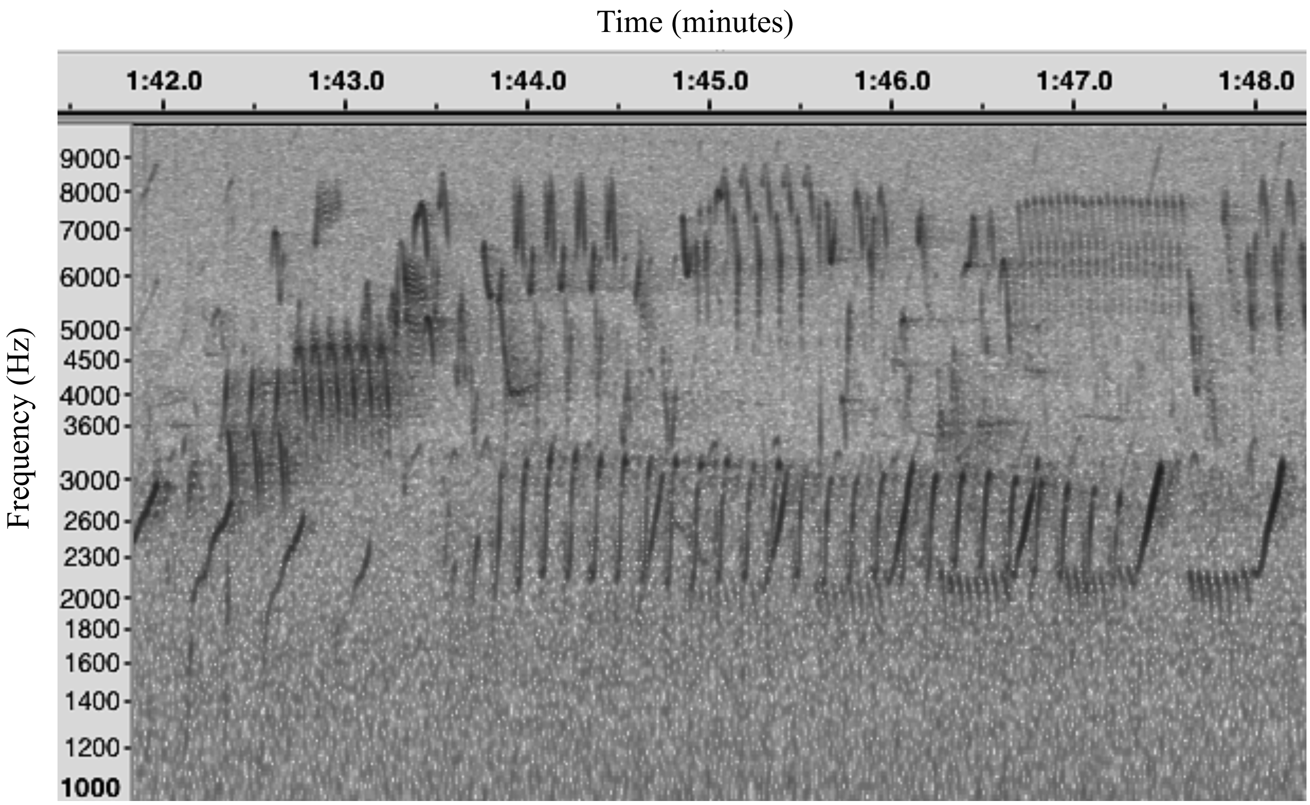

Figure 2.6 An example of several avian songs and calls displayed on a frequency (Hz) spectrum (y-axis) as signals vary over time (x-axis), spectrogram, recorded on an autonomous recording unit from site 201 in Peter Loughheed Provincial Park (1959 m a.s.l.) on June 13, 2018. This clip includes songs from the Lincoln Sparrow (*Melospiza lincolnii*), Dark-eyed Junco (*Junco hyemalis*), and Swainson's Thrush (*Catharus ustulatus*) and calls from a Spotted Sandpiper (*Actitis macularius*).

Manual avian identification for all avian species recorded is time consuming and requires background knowledge of resident species vocalizations but is more accurate and less time consuming than automated species analysis that involves avian recognizer development for each species and testing recognizer accuracy for false positive and false negative errors (Swiston & Mennill, 2009). Hence, each spectrogram was manually analyzed to identify and enumerate all species recorded for an estimate of avian species richness. From the spectrogram, species richness and species identity were collected for further analysis. Indistinguishable calls and songs, such as those which were degraded or too quiet, were omitted from species richness data and unknown species were disregarded from data analysis.

2.2.5 Data analysis

Avian species richness data were analyzed using RStudio (RStudio Team, 2020) statistical software. McCain's general richness-elevation relationship patterns can be described as 1) a near linear decline in richness with increasing elevation, 2) a unimodal peak at mid-elevations, 3) a low plateau before a near linear decline, or 4) low plateau with mid-elevation peak of high richness before declining (McCain & Grytnes, 2010). I quantified these using least squares regression, whereby a linear decline was modelled with a linear relationship, the unimodal peak was modelled with a negative quadratic relationship, the low plateau or low plateau with mid-elevation peak were both modelled with a cubic relationship and I used a dot model as the null model. I grouped the two plateauing patterns since the approach used, least squares regression, could not discriminate between the two different patterns. I compared the AICc values for the model set using an Akaike Information Criterion framework and the lowest AICc value in the table suggested the best supported model for predicting avian species richness in the Upper Bow Basin. I supported my AICc interpretation with additional regression parameters to confirm the best supported model: p-values and R^2.

For my second objective, I analyzed the area-elevation relationship, as this could confound my ability to test for a richness-elevation relationship by virtue of a richness-area relationship. I log-transformed both richness and area and then tested a linear regression that determined how much variance in species richness area explained. I then transformed the resulting residuals by adding the mean predictor value, then took the inverse of each logged residual. I used the transformed residuals from the log richness - log area relationship to statistically control for the influence of area on richness. I used these residuals as the response variable and re-ran my model competition among the linear, quadratic, cubic and null model. Therefore, I tested the richness-elevation models while controlling for the log richness - log area relationship. Then I compared the models' output with the best supported model from the first model competition.

Thirdly, I determined if the richness-Natural Subregion relationship better explained avian species richness in mountain peatlands than a linear, quadratic, or cubic richness-elevation relationship. First, I ran a general linear model on the richness-Natural Subregion relationship, which I then compared to the best fit model from the first model competition (contrasting richness-elevation, without accounting for area) and the null model from the first model competition. Second, I ran a general linear model where the response variable was the unlogged residuals from the log richness - log area relationship and the predictor variable was Natural Subregion. I then compared this model to the best model from my second model competition (contrasting different forms of the polynomial relationship between area-corrected richness and elevation) and the null model from the second model competition. Along with the general linear model, I re-tested the AICc, p-values and R^2 values of the best fit model from the first model competition and the best fit model from the second model competition to determine if Natural Subregion better explained species richness in mountain peatlands compared to the richness-elevation or the area-corrected richness-elevation relationships.

2.3 Results

My avian surveys in 24 valley-bottom mountain peatlands in southwestern Alberta recorded 74 species. Mountain peatland areas were on average 202.0 km^2 (± 273.4 SD, N =24), where small peatlands, 10.00 km^2 or less, averaged 21.33 species (± 2.285 SD, n = 6), medium peatlands, 10.00 to 100.0 km^2, averaged 23.63 species (± 5.243 SD, n = 8), and large peatlands, over 100.0 km^2, averaged 31.6 species (± 5.748 SD, n = 10). Across Natural Subregions, the peatlands situated in the Montane Natural Subregion averaged 31.75 species (± 4.512 SD, n = 12), while those in the Subalpine Natural Subregion averaged 21.00 species (± 3.291 SD, n = 12).

I report how the estimated number of species varied along an elevation gradient (Figure 2.7) and between Natural Subregions of interest (the Montane and Subalpine Natural Subregions; Figure 2.10) in three model competitions. The results of model competition 1 are reported in Table 2.3. See Appendix A for regression output values. Comparing the linear, quadratic and cubic regressions of the richness-elevation relationship (Figure 2.7a-c), the cubic model provided the best fit, although the quadratic model's AICc value was within two of the cubic model's AICc (Table 2.3).

I tested the log area-log elevation relationship (Figure 2.8), which was not statistically significant ($p > 0.05$) and explained 13.04 % of the variance ($R^2 = 0.1304$, $y = -0.0212x + 3.2531$). Then I evaluated the log richness-log area relationship (Figure 2.9), which was statistically significant ($p = 0.001$) and explained 41.9 % of the variance in log-transformed species richness ($R^2 = 0.419$). The resulting relationship was $\log S = 9.167 \times 10^{-2} + (0.0966) \log A$.

The results of my second model competition are reported in Table 2.3. Using the unlogged residuals from my log richness-log area relationship as my response variable, I found that a linear relationship provided the best fit with elevation (Figure 2.7d-f). The linear model had the lowest R^2 value ($R^2 = 0.419$) but the highest adjusted R^2 value ($AdjR^2 = 0.392$). In comparison with the cubic model, which provided the best fit in my first model competition, the AIC and AICc values were higher and R^2 values were lower (Table 2.3). Also, an analysis of covariance (ANCOVA) was run to test if the apparent difference in the richness-area relationship among Natural Subregions was statistically significant and I found that the interaction term was not significant ($F = 0.366$, $p = 0.552$, $df = 1$).

The results of my third model competition are also reported in Table 2.3. Comparing the fit of the richness-Natural Subregion relationship without (Figure 2.10a) and with (Figure 2.10b) controlling for the effect of area on species richness, both models provide a statistically significant fit to the data, but the relationship is substantially weakened once the variance in richness explained by area is accounted for (Table 2.3). In comparison to the first model competition, the Natural Subregion model provided a better model fit than the cubic model. Also, when accounting for the effect of area on species richness, the Natural Subregion model provided a better model fit than the linear model from the second model competition.

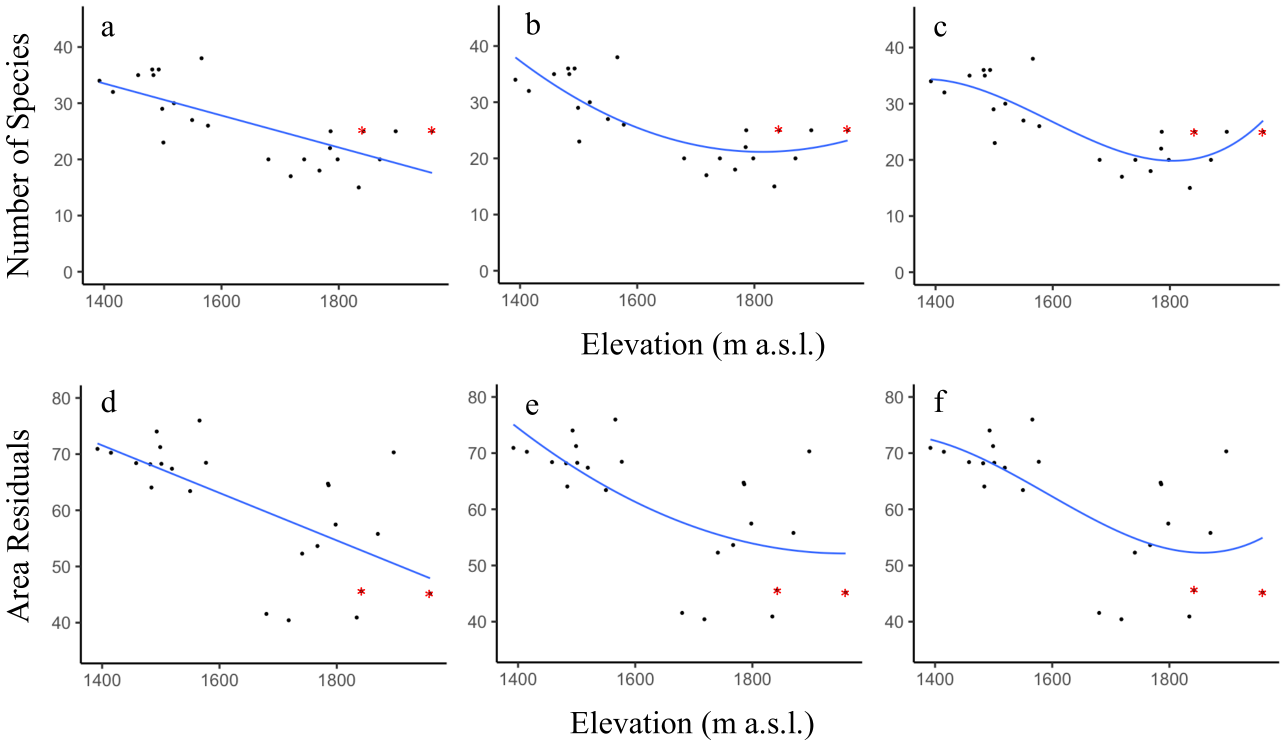

Figure 2.7 Two model competitions that compare McCain's general richness-elevation relationship patterns to avian species richness in valley-bottom mountain peatlands in Southwestern Alberta. Model competition 1 is the richness-elevation relationship using (a) linear, (b) quadratic, and (c) cubic functions to depict the richness-elevation pattern. Model competition 2 is the richness-elevation relationship controlling for the richness-area relationship using (d) linear, (e) quadratic, and (f) cubic functions to depict the richness-elevation pattern. Two large peatlands located at high elevations are indicated by red asterisks in the figure to ascertain if they were outliers.

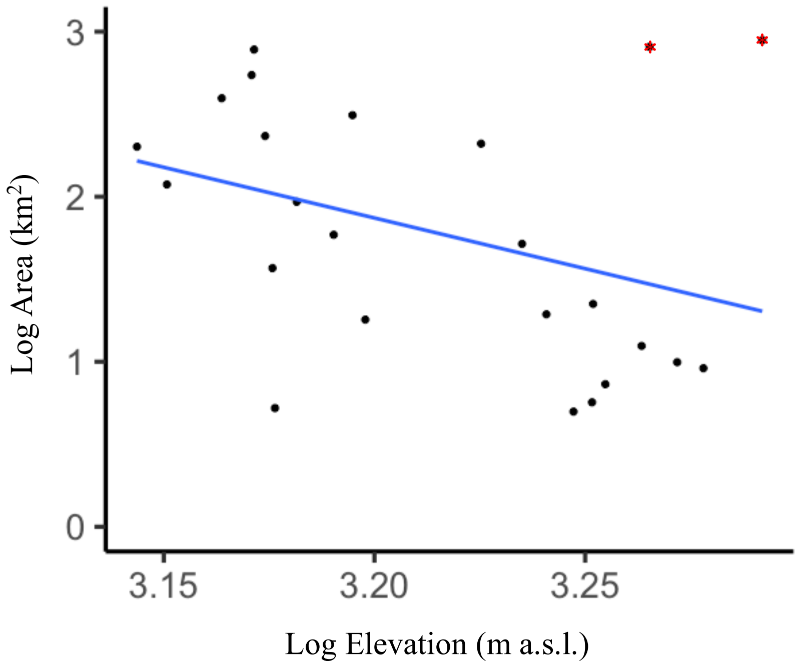

Figure 2.8 The log area- log elevation relationship reported in 24 valley-bottom mountain peatlands in southwestern Alberta. Two large peatlands at high elevation are highlighted as red asterisks here and in Figures 2.7 and 2.9 to facilitate assessment of whether they could be outliers.

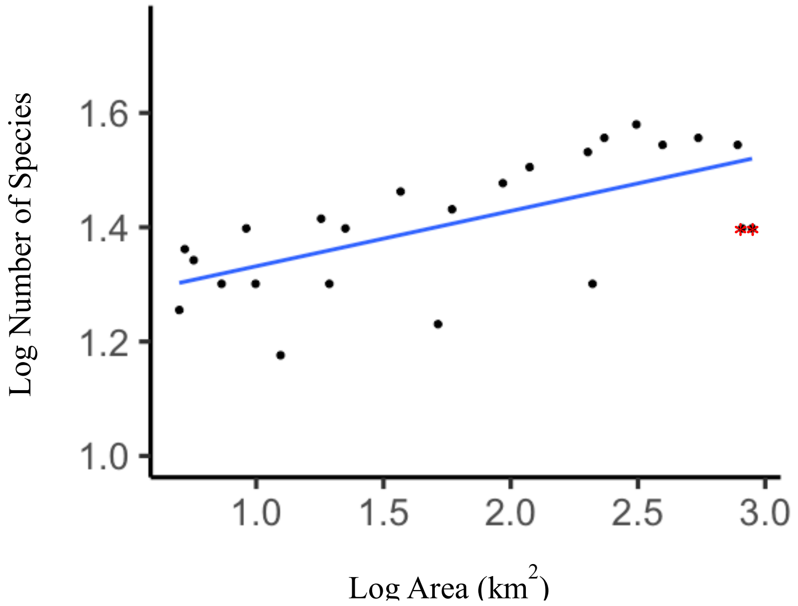

Figure 2.9 The log richness - log area relationship reported in 24 valley-bottom mountain peatlands in Southwestern Alberta. Two large peatlands at high elevation are highlighted as red asterisks here and in Figures 2.7 and 2.8 to facilitate assessment of whether they could be outliers

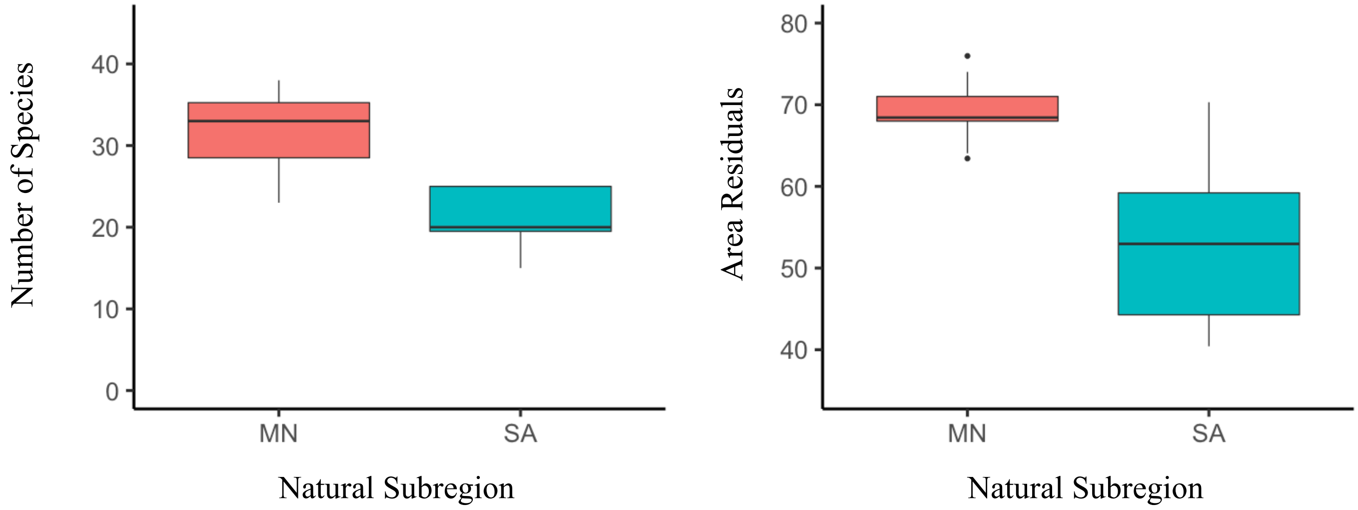

Figure 2.10 Model competition 3 is the richness-Natural Subregion relationship using (a) general linear model, and (b) a general linear model while controlling for the richness-area relationship after back transforming the area residuals to compare to the best models from competition 1 and competition 2, in valley-bottom mountain peatlands in Southwestern Alberta.

Table 2.3 Akaike Information Criterion (AIC) analysis output from each of the three model competitions that compare McCain's general richness-elevation relationship patterns to avian species richness in valley-bottom mountain peatlands in Southwestern Alberta. Model competition 1 is the richness-elevation relationship using linear, quadratic, and cubic functions to depict the richness-elevation pattern along with a null model. Model competition 2 is the richness-elevation relationship controlling for the richness-area relationship using linear, quadratic, and cubic functions to depict the richness-elevation pattern along with a null model. Model competition 3 is the richness-Natural Subregion relationship using general linear model (Natural Subregion), and a general linear model while controlling for the richness-area relationship (controlling for area) to compare to the best models from competition 1 and competition 2 along with a null model.

Competition	Model	k	AICc	ΔAIC	AICc Weight	Cumulative Weight	Log-likelihood	SE
1	Cubic	5	145.84	0	0.48	0.48	-66.25	4.19
	Quadratic	4	146.18	0.34	0.41	0.89	-68.04	4.405
	Linear	3	148.74	2.9	0.11	1	-70.77	4.823
	Null	2	163.76	17.93	0	1	-79.6	6.813
2	Linear	3	177.58	0	0.69	0.69	-85.19	8.796
	Quadratic	4	179.63	2.05	0.25	0.93	-84.76	8.843
	Cubic	5	182.41	4.82	0.06	1	-84.54	8.977
	Null	2	187.99	10.41	0	1	-91.71	6.813
3.1	Natural Subregion without accounting for area	3	141.23	0	0.91	0.91	-67.02	1.191
	Cubic	5	145.84	4.6	0.09	1	-66.25	4.19
	Null	2	163.76	22.53	0	1	-79.6	6.813
3.2	Natural Subregion while accounting for area	3	170.95	0	0.96	0.96	-81.88	3.311
	Linear	3	177.58	6.63	0.04	1	-85.19	8.796
	Null	2	187.99	17.04	0	1	-91.71	6.813

2.4 Discussion

I evaluated avian species richness in mountain peatlands along an elevation gradient to determine which of McCain's (2009) four alternative richness-elevation patterns occurred and determine which of the five mechanisms that were discussed in the introduction were wholly or partially responsible for the observed richness-elevation pattern. McCain's (2009) global meta-analysis on avian species richness patterns with elevation demonstrated near equal frequency of all four patterns among birds, but it excluded analysis of elevation gradients in Canada.

I investigated possible mechanisms that prior research had suggested could be responsible for the richness-elevation pattern by comparing the best fit models from three model competitions. The Mid-Domain Effect (MDE), randomly placed species distributions within a spatially bounded gradient resulting in a negative quadratic relationship between richness and elevation (Colwell & Lees, 2000) was the negative quadratic model and alternative models included environmental filtering of variables that change predictably with elevation (e.g., temperature and precipitation; Barry, 2008), habitat area and habitat heterogeneity which relate to the amount of niche space available to support bird species. The results of my study found a lack of support for the MDE because all quadratic relationships were positive instead of the anticipated negative quadratic relationship. When I compared the richness-elevation relationship after accounting for the effect of area to determine if the residual variation in richness that remains might be attributed to the mid-domain effect, I found no support for the MDE. The environmental filters integrated as ecological land classification into Natural Subregions (Downing & Pettapiece, 2006), did affect avian species richness and better explained the variation in avian species richness compared to elevation alone. Lastly, area was an important factor in determining avian species richness and I did not directly test for the effects of habitat heterogeneity since I standardized my methods to choose sites with similar vegetation structure. Though, diminishing habitat area with increasing elevation was not a significant trend in my study system, a large portion of the variance in avian richness was explained by area. Altogether, I found a lack of support for the MDE, no support for the null models and support for multicausality from both area and Natural Subregion explaining the majority of the variation in avian species richness in the Upper Bow River Basin mountain peatlands of the Canadian Rocky Mountains.

2.4.1 General elevation pattern

In my first comparison, where I did not attempt to compensate for peatland area, a cubic model provided the best fit when I modeled avian species richness as a function of peatland elevation. This could conform to one of McCain's plateauing patterns (McCain, 2009), which are usually attributed to a combination of mechanisms rather than a single factor like the richness-area relationship or the mid-domain effect (MDE). This suggests that several different variables are likely influencing the avian species richness along the Rocky Mountain range in Alberta, potentially interacting to result in a complex richness-elevation relationship.

Working in different states, both Thompson (1978) and Able and Noon (1976) found that avian species displayed plateauing patterns in richness along an elevation gradient. Able and Noon (1976), working in Camel's Hump Mountain in Vermont, attributed this to forest patch size and the structure of the vegetation. Similarly, Thompson (1978) concluded that habitat area and vegetation structure varied with elevation and were critical to avian species richness in Sweetgrass Hills, Montana. Working in Mount Etna, Italy, Massa et al. (1989) also reported that vegetation structure was a key mechanism responsible for the plateauing avian species richness-elevation pattern that they observed. Terborgh (1977) and Kendeigh and Fawver (1981) agreed with these other authors on the primary importance of vegetation structure. Studying avian species in Cordillera Vilcabamba, Peru, Terborgh (1977) concluded that productivity provided a secondary mechanism driving plateauing avian richness-elevation patterns. Kendeigh and Fawver (1981) worked in the Great Smoky Mountains, Tennessee, and found that after vegetation structure, the second most important factor determining avian species richness along their elevation gradient was moisture availability. This emphasizes that complex patterns like the cubic relationship between avian species richness and elevation that I observed in my study can arise from the combination of several mechanisms. Although, the examples above discuss vegetation structure as the effect of habitat heterogeneity on richness, while in my study system, I attempted to standardize vegetation structure among sites to remove the effect of habitat heterogeneity on avian species richness. Also, environmental filters like temperature are commonly reported to vary linearly with elevation (Körner, 2007; McCain & Grytnes, 2010; Sundqvist et al., 2013), interactions between temperature and productivity or temperature and habitat area could also be responsible for the pattern I observed.

I must note that the quadratic model also had substantial support (ΔAICc < 2; Burnham & Anderson, 2002). Contrary to my expectations, however, the quadratic model supported by the data had a *positive* quadratic term. In describing richness-elevation relationships attributed to the MDE, McCain (2009) described a *negative* quadratic relationship (i.e., a unimodal hump-shaped relationship) between richness and elevation. Hence, I reject the quadratic model, because the model that received substantial support in my AIC competition had the opposite relationship to the relationship I was testing for. Consequently, though the MDE or a quadratic relationship between richness and productivity or between productivity and elevation may be mechanisms partially influencing the richness-elevation relationship, I conclude that they are not acting alone.

2.4.2 Effects of habitat area on species richness

Although I did not observe a linear reduction in habitat area with increasing elevation, which has been observed in other studies (e.g., Lawton et al., 1987; Rahbek, 1997), I did find that peatland area was a significant predictor of avian species richness. In fact, log area explained 41.9% of the variance in log richness. This is lower than what has been reported by other studies (e.g., Rahbek, 1997; Kattan & Franco, 2004; McCain, 2007). Rahbek (1997) examined the effects of habitat area on avian species richness in South America and found that area accounted for 67% – 91% of the variation in species richness along an elevation gradient. Similarly, working in forests in Andean ranges in Columbia and La Macarena and Santa Marta, Kattan and Franco (2004) reported that habitat area accounted for 60% – 93% of the variation in species richness along an elevation gradient. The reduction in variation in log richness explained by area in my study system may be due to the total habitat available to the avian species and use, and the fact that mountain peatlands are not a continuous habitat along a mountain. Mountain peatlands develop in depressions and are woven through other habitats (e.g., forest and open grasslands). Therefore, it is possible that the birds recorded on the mountain peatlands also make use of neighboring habitats since bird territories can be quite large and that peatland area may not correspond well to the total area of habitat available to the recorded birds.

The literature's results not only indicate that the effect of area on species richness could account for the majority of variation in avian species richness but accounting for the richness-area relationship could also alter the general elevation pattern reported (McCain, 2007; McCain & Grytnes, 2010). This was certainly the case in my study system, where the avian species richness-elevation relationship followed a cubic model but was altered to a linear pattern once area was accounted for.

Interestingly, it seems as though the richness-area relationship was stronger in the Montane Natural Subregion than in the Subalpine Natural Subregion, since the residuals from the

Montane peatlands grouped more closely together in the second model competition (Figure 2.7d-f). While in the Subalpine Natural Subregion, the richness-area residuals were more spaced apart than in the raw richness-elevation model, thus having the opposite effect, there were more examples of sites that have high richness given their area and examples that sites have low richness given their area. This suggested that the area-elevation relationship differed between the two Natural Subregions, but the richness-area effect was the same, regardless of Natural Subregion. Yet, no significant difference was found in the richness-area relationship among Natural Subregions.

2.4.3 Residual variance in richness, after accounting for area

Although some studies that report a cubic (i.e. plateauing) relationship between richness and elevation, found this pattern after accounting for habitat area (e.g., Kattan & Franco, 2004), other studies did not account for habitat area in evaluating the richness-elevation relationship (e.g., Blake & Loiselle, 2000). In the second model competition, which accounted for the richness-area relationship, I found support for McCain's negative linear model (Figure 2.7d).

The change from a cubic to a negative linear relationship once I accounted for the influence of peatland area on avian species richness suggests that although area was not confounded with elevation in my study, the richness-area relationship nonetheless affected the nature of the richness-elevation relationship, complicating it from a simple negative linear relationship. Thus, I provide evidence of multicausality in the relationship between avian species richness and elevation (Colwell et al., 2004), which perhaps sheds some light on the lack of consistency reported by McCain in her 2009 review. Multicausality can lead to certain studies finding one pattern while other studies find another since drivers may differ from one location to another or drivers may interact differently in different locations.

In terms of what this suggests for mechanisms driving the avian species richness-elevation relationship in the Rocky Mountain peatlands, the linearity of the subsequent richness-elevation relationship suggests that an environmental filter with a linear relationship to elevation could be contributing to the richness-elevation relationship. For example, temperature (Körner, 2007) or productivity (Tilman et al., 1996; Brown & Lomolino, 1998) might be the key mechanisms responsible for the observed richness-elevation relationship.

The linear model likely rules out the MDE as a major mechanism responsible for the richness-elevation relationship. Recall that the MDE best fitting quadratic relationship between area-corrected richness and elevation had a positive, rather than the anticipated negative quadratic term.

2.4.4 Natural Subregion effects on species richness

A significant proportion of the variance in avian species richness was explained by peatland area but elevation and Natural Subregion, a proxy for ecological filters, may still have an effect on avian species richness in these mountain peatlands. Elevation is a continuous variable, which is likely correlated with different factors thought to influence species richness: e.g., temperature (Lennon et al., 2001; Körner, 2007; Barry, 2008) and productivity (Tilman et al., 1996; Brown & Lomolino, 1998; Mittelbach et al., 2001). Natural Subregion, in contrast, is a categorical variable, categorizing habitat into relatively homogenous units on the basis of a common climate, soil type, and vegetation structure (Downing & Pettapiece, 2006). The environmental variables, which discriminate among Natural Subregions under the Alberta Ecological Land Classification System (Downing & Pettapiece, 2006), are also thought to influence avian species richness as environmental filters (Tilman et al., 1996; Brown & Lomolino, 1998; Lennon et al., 2001; Mittelbach et al., 2001; Körner, 2007; Barry, 2008). Though Natural Subregions in the Rocky Mountain Natural Region of Alberta differ in their average elevation, the elevation ranges of the Montane (Upper Foothills: 950 – 1750 m a.s.l. and Montane: 825-1850 m.a.s.l.) and Subalpine (1300-2300 m.a.s.l.) overlap quite extensively. I was therefore interested to know whether Natural Subregion provided a better prediction of avian species richness than elevation, as this would suggest that the mechanism driving the richness-elevation relationship is likely one of the environmental variables that is fairly homogenous within the Natural Subregion rather than one linearly correlated with elevation.

I found that Natural Subregion was a stronger predictor of avian species richness than elevation, both considering raw avian species richness and the richness-area residuals. This corroborates with McCain (2009), who reported that the richness-temperature relationship had a stronger effect than the richness-area relationship on montane birds but both influenced the richness-elevation relationship (McCain, 2009). In my earlier interpretation the richness-elevation relationship after accounting for area was best approximated by a linear model, yet because Natural Subregion better predicted avian species richness than elevation and area, the underlying mechanism was likely an environmental filter that differs in a categorical way between the Natural Subregions but is relatively homogenous within them. More importantly, the environmental filter did not linearly relate to elevation but was categorical in nature, which is unlike the linear findings in McCain's (2009) meta-analysis.

Jointly, my results indicate that both area and environmental filters are key determinants of avian species richness in the Upper Bow River Basin of the Rocky Mountains. My quadratic model that the richness-elevation relationship might be attributed to the geometric constraint of the MDE had very little support in comparison. In general, my results thus align with those of McCain (2009), who also found that climatic variables affected species richness more than other variables but concluded that the richness-area relationship still accounted for some of the variation in avian species richness. My results differ from researchers who found MDE as the key determinant of species richness (e.g., Lawton, 1999; Colwell & Lees, 2000; Sanders, 2002; Colwell et al., 2004; McCain, 2004). These researchers did not all study avian species, and perhaps that explains the discrepancy. It could also be that the studies identifying the MDE as an important driver of the richness-elevation relationship were carried out in different environments than the Canadian peatlands I focused on. Supporting this supposition, Lawton (1999) suggested that when the MDE is observed, it is contingent on the organism, environment and the scale of study.

2.4.5 Next steps

Future research could advance our mechanistic understanding of avian species richness elevation patterns. This research could compare the relative importance of productivity, temperature, soil moisture and vegetative community to avian species richness in mountain peatlands. Productivity could be measured as net ecosystem carbon assimilation, and temperature and soil moisture could be measured with loggers in predicting avian richness in mountain peatlands along an elevation gradient. Lastly, in previous studies the vegetative structure/community was deemed an underlying mechanism that drove species richness along elevation gradients (Able & Noon, 1976; Terborgh, 1977; L. S. Thompson, 1978; Kendeigh & Fawver, 1981; Massa et al., 1989). Therefore, when advancing our mechanistic understanding of avian species richness elevation patterns not only should we examine productivity, temperature and a moisture gradient but we should examine the influence of vegetation structure/vegetative community on the avian community in mountain peatlands.

Another way future research could advance this study is to consider the scale of study. All four richness-elevation patterns identified by McCain could reflect different subsets of a negative quadratic relationship, depending on what extent of the conceivable range of elevation is being considered (Figure 2.11). My mountain peatlands ranged from 1300 to 2000 m a.s.l., which excludes the Alpine Natural Subregion where few to no peatlands were found (Morrison et al., 2015). The elevation range used encompassed about 50% of the maximum possible range in elevation covered by the combined Montane (minimum 825 m.a.s.l.) and Subalpine Natural Subregions (maximum 2300 m.a.s.l.; Downing and Pettapiece, 2006). I therefore hoped that this would prevent me from capturing an elevation range that was too narrow and hence misclassifying the shape of the richness-elevation pattern.

In McCain's 2009 study, she analyzed data from papers that sampled at least 70% of the possible elevation gradient, which would actually exclude my study. However, comparing studies ranging from 55% to 99% of the maximum possible range, McCain's (2009) classified the richness pattern reported and the pattern was not determined by percent of the elevation gradient sampled (i.e., almost-linear pattern studies were not generally a narrower range of elevation and negative quadratic studies were not generally a larger range of elevation; McCain, 2009). Based on the concept of a moving window as depicted in conceptual figure 2.11, I anticipate that the sampled elevation range should alter the elevation pattern reported, but future research should examine whether studies restricted to a small proportion of the elevation gradient would likely misclassify the richness-elevation pattern present in their systems.

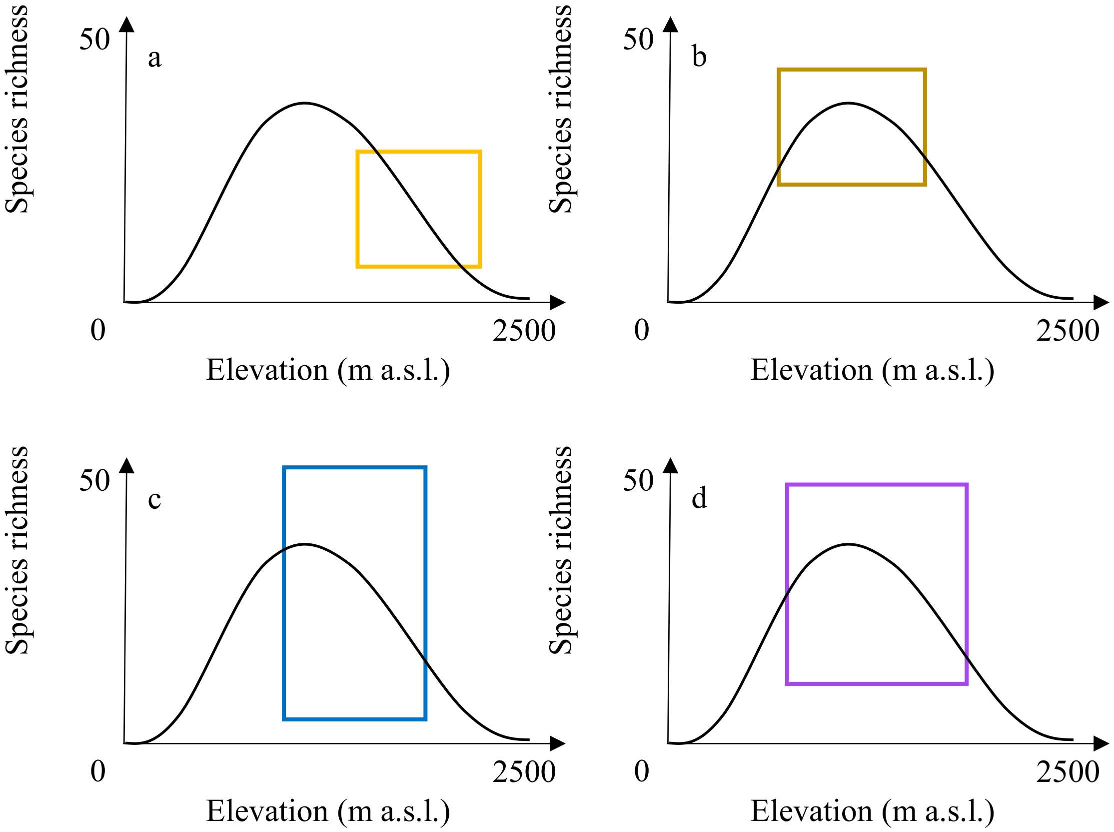

Figure 2.11 Narrowed elevation ranges could reflect different subsets of the full quadratic relationship depending on the range being considered where (a) is the almost linear model, (b) is the negative quadratic model, (c) is the low plateau, cubic model and (d) is the mid plateau, cubic model.

Future research could assess a disturbance gradient since my study was not able to standardize the level of anthropogenic disturbance and this potentially influenced the avian species richness at each peatland. Three of the twelve sites in the Subalpine Natural Subregion are located in Peter Lougheed Provincial Park, and these have the highest avian species richness. The other nine peatlands are located along the Powderface Trail that experienced logging in the early 2000s which may have reduced available nesting and foraging opportunities and increased interspecific and intraspecific competition for limited resources. This pairs with the findings that deforestation is detrimental to the avian community (Pavlacky et al., 2015), and reduces avian functional diversity (Ibarra & Martin, 2015). Therefore, the location and amount of disturbance at each site may have affected avian species richness more than the ecological mechanisms being tested for in this study. Consequently, I recommend that future research examines the influence of anthropogenic disturbance, namely logging activity, as a key driver of avian species richness-elevation patterns or test anthropogenic disturbance as a confounding factor of the richness-elevation relationship.

2.5 Conclusion

Avian species richness in valley-bottom mountain peatlands in the Upper Bow River Basin displayed a plateauing pattern along an elevation gradient from 1300 to 2000 m.a.s.l. However, richness was significantly positively correlated with peatland area, and although area was not related to elevation, once I accounted for the richness-area relationship, the function best fitting the richness-elevation relationship changed from the cubic model to the negative linear model. Also, interestingly, avian species richness in my peatlands was better predicted by Natural Subregion than by elevation. Clearly peatland area, which can be considered a measure of niche space, is an important driver of avian species richness at a given peatland. Moreover, the linearity of the richness-elevation relationship after accounting for area and the superiority of the Natural Subregion model in predicting avian species richness combine to suggest that environmental filters like temperature and productivity are probably also key determinants of avian species richness in these peatlands. Critically, I found no support for the mid-domain effect (MDE) as a mechanism responsible for the richness-elevation relationship nor did I find support for the null models. Thus, I conclude that peatland area and environmental filters characteristic of Natural Subregions likely combine to determine avian species richness in mountain peatlands along an elevation gradient. This multicausality likely explains why research in different geographies observe differing patterns of richness-elevation: drivers may differ in different ranges or interact in different ways in different locations.

Certainly, future research in this area should move beyond descriptions of the pattern of the richness-elevation relationship to focus on the mechanisms responsible for those patterns. Importantly, future studies should look into multicausality where a combination of mechanisms are driving species richness. My results emphasize the importance of the richness-area relationship and should contrast alternative models with the MDE. New studies should aim to separate different environmental filtering mechanisms to test their relative influence, such as temperature and productivity, as these appeared key to predicting richness in my study system.

Extensive research effort has been focused on describing the change in species richness along elevation gradients (e.g., Lawton et al., 1987; Rahbek, 1995; Patterson et al., 1998; McCain, 2009; McCain & Grytnes, 2010). Despite this investment of research effort, we have reached little consensus in what pattern is seen for birds along an elevation gradient (McCain & Grytnes, 2010). In particular, highly mobile avian species, which in McCain's 2009 review concluded fit about equally across four distinct patterns. To advance the science, we need to move beyond describing the richness-elevation patterns, and into understanding the mechanisms giving rise to these patterns. My thesis makes an important step in that direction, suggesting that area and some environmental filters associated with the division among Natural Subregions in the Rocky Mountain peatlands share responsibility for the observed cubic relationship pattern between avian species richness and elevation. My results reject the quadratic model that the geometric constraint of the MDE (Colwell & Lees, 2000) plays an important role in determining avian species richness. The complexity of the cubic pattern observed is likely tied to this multicausality (Colwell & Lees, 2000), as removing the influence of area on richness left a simple linear richness-elevation relationship, even though area and elevation were not significantly correlated in my dataset. I therefore suggest that the lack of consistency among published studies in terms of the function best fitting the richness-elevation relationship can be attributed to multicausality, with different drivers dominating or combining in different ways in different locations.

3. Species richness estimation accuracy

3.1 Introduction

Biodiversity is being lost globally at an alarming rate (Hoffmann et al., 2010; Rands et al., 2010; Sandbrook et al., 2019), and conserving biodiversity requires that we are able to accurately quantify it. Species richness is a frequently used measurement of biodiversity (Bovendorp et al., 2017) and is defined as the number of different species estimated from a survey in a defined area at a particular time (Boulinier et al., 1998; Gwinn et al., 2016). A major branch of ecological research is focused on quantifying and understanding patterns of species richness in the environment, for example, the relationship between species richness and area (Chapter 2; Preston, 1962), species richness and productivity (Waide et al., 1999; Mittelbach et al., 2001), species richness and elevation (Chapter 2; McCain & Grytnes, 2010), or species richness and latitude (Rahbek & Graves, 2001). A prerequisite for conservation of biodiversity and testing the relationship between richness and other features of the environment is that species richness be measured accurately.

Researchers are constrained in terms of time and resources for biodiversity surveys (Sims et al., 2008). As an ecologist, we try to find the most effective and efficient methods to survey species richness in a particular area (Bovendorp et al., 2017). This is due to the fact that repeated and long-duration surveys of a single site may not always be an option due to prohibitive cost and constraints around the availability of trained personnel (Mackenzie & Royle, 2005) as ecological research typically includes many sites. Thus, it is pertinent to determine which methods provide accurate estimates of avian species richness with the least amount of effort. This challenge is faced by researchers working with any taxa and two issues that must be addressed when planning surveys are 1) determining when to survey within the breeding season and 2) optimizing the duration of the survey at each site, i.e. the survey effort.

3.1.1 When to survey within the breeding season

In Canada, we typically carry out avian surveys during the breeding season when male songbirds are vocalizing to attract a mate, defending territories, and their plumage colours are most distinctive (Shonfield et al., 2018). Consequently, surveying during the breeding season is standard practice in avian research (e.g., Conway, 2009, 2011; Alberta Biodiversity Monitoring Institute, 2015), especially when using autonomous recording units (ARUs; Alberta Biodiversity

Monitoring Institute, 2015). Yet, avian species do not all breed during the exact same period of time (Winternitz, 1976).

Avian species temporally partition the breeding season, in part because each species responds to unique life history and environmental triggers that help synchronize breeding within the species and the temporal match between brood rearing and food availability (A. Dawson, 1985; Wyndham, 1986). Where food is insufficient, it can restrict thyroid activity that determines the gonadal development rate, as seen in European Starlings, *Sturnus vulgaris* (A. Dawson, 1985). Warming temperatures and the indication of a season change such as lengthening daylight can trigger gonadal development and the start of an avian species breeding season, such as in the Great Tit (*Parus major*) in the Netherlands (Marvelde et al., 2012). Also, both species in the tropics and at high latitudes have evidence to support for the existence of endogenous annual rhythms that trigger reproduction and the onset of the breeding season (Baker, 1938). An example of this mechanism was found in the red-billed weaver (*Quelea quelea*; Lofts, 1964). Because birds have different triggering mechanisms, different species may come into peak breeding activity at different points of time within the more generally defined bird breeding season (Winternitz, 1976).

Typically, the breeding season commences with early-season breeders like the Black-capped Chickadee (*Poecile atricapillus*; Foote et al., 2020). These early-breeding species begin breeding activities in April or May with snowmelt and the arrival of the first migrant species (Foote et al., 2020). The amount of species engaged in breeding activity then increases to a peak before dwindling down to the late season breeders (e.g. Alder Flycatcher; *Empidonax alnorum*; Lowther, 2020). Consequently, the optimal time for surveys of avian species richness depends on what species are members of the community and a comprehensive survey will require data collection on multiple dates to catch both early-season and late-season breeders.

If surveys are concentrated during the peak breeding period, they might capture the greatest number of breeding bird species on a single visit, but risk missing the early or late breeders (Winternitz, 1976). Working in remote locations, such as the mountains (Chapter 2), can introduce additional constrains on site access. For example, in the mountain system I studied in Chapter 2, avalanche risks and closed roads prevent access to sites early in the breeding season. These restrictions can determine when surveys begin but it is up to the researcher to decide how many surveys to complete, when to end the survey period, and how long each survey should last.

3.1.2 Optimizing survey effort

The main obstacle when using ARUs is the subsequent effort to analyze the recordings (Swiston & Mennill, 2009), though the survey effort comes from transcribing the recordings of passive surveys by ARUs. When ARU survey effort is too low, the study will suffer from errors of omission due to failure to detect bird species that were present (Mackenzie & Royle, 2005), but as survey effort increases, it will yield diminishing returns (Thompson & Thompson, 2010). Avian surveys are typically constrained by a finite amount of money, the availability of trained personnel and the time required to access each site or transcribe the recordings (Mackenzie & Royle, 2005; Sims et al., 2008). Investing more effort in better characterizing an individual recorded site may mean less frequent recorded surveys in a long-term monitoring program or fewer opportunities to record during the breeding period. It also means that less time remains to be allocated to sampling more recorded sites (Reynolds et al., 2011) and hence reduced statistical power. Optimizing ARU survey effort to adequately survey each site without investing more survey effort than necessary frees up resources that can instead be invested in increasing the study's sample size and thus maximize the study's power to detect the ecological effects, processes, or changes in pattern that the researcher is interested in (Sims et al., 2008).

The return on survey effort invested is sometimes depicted as a species accumulation curve, where the cumulative number of species at the site or region is plotted against survey effort (See Appendix B, Figure 5.1; Ugland et al., 2003). Typically, this relationship between the cumulative number of species detected and survey effort is a logarithmic curve (Thompson & Thompson, 2010). Depending on the research objectives, the duration of ARU surveys transcribed may run anywhere between 1 minute to several hours, though 10 to 15 minutes is common (e.g., Farina et al., 2011; Tegeler et al., 2012; Sidie-Slettedahl et al., 2015; Frommolt, 2017). This may be inadequate, however, as research investigating survey effort adequacy has reported that an hour of passive acoustic monitoring on montane meadows was required before cumulative avian species richness reached a plateau (Tegeler et al., 2012). Survey effort should be allocated judiciously in estimating avian species richness, such that only enough of the recordings are transcribed to reach a plateau in cumulative avian species richness (Mackenzie & Royle, 2005; Sims et al. 2008).

The problem is that not all sites require the same amount of survey effort to get an accurate measure of their avian species richness, so different levels of survey effort are required at different sites (Boulinier et al., 1998). Sites with greater richness tend to require more survey effort to adequately characterize them than less rich sites (Watson et al., 2000; Nally & Horrocks, 2002). As well, larger habitat patches may require more survey effort than small habitat patches (Watson et al., 2000; Nally & Horrocks, 2002). Therefore, to optimize ARU survey methods, the amount of survey effort required may depend on habitat area, species richness, and other influential factors such as elevation or Natural Subregion that may covary with richness (Chapter 2). However, using different levels of survey effort at different sites would introduce a bias into standardized methods, where some sites would be more intensively surveyed than others. In order to fairly compare the avian species richness at different sites, the survey effort among sites must be standardized.

One option that researchers struggling with errors of omission and optimizing survey effort can pursue is the application of statistical richness estimators (Gwinn et al., 2016). Richness estimators fall under two categories: nonparametric estimators and parametric estimators. Nonparametric estimators use the frequency of unique or rare species to estimate the ‘true’ species richness from the observed species richness and are therefore sensitive to sample units with a high frequency of unique species (Burnham & Overton, 1978; Chao, 1987; Lee & Chao, 1994). By contrast, parametric estimators use occurrence and detection probabilities to calculate species richness (Dorazio et al., 2006). Both nonparametric and parametric estimators are used to determine survey accuracy and compare the calculated ‘true’ richness and estimated richness from a survey. Here, it is defined that an adequate estimate of species richness is the estimated species richness detected by the ARU is at least 80% of the ‘true’ richness as calculated by the richness estimator and the species accumulation curve plateauing withing the survey period.

Each nonparametric estimator was built to handle particular data types. For example, the Chao 1 is used for abundance datasets and Chao 2 is used for incidence datasets (Chao, 1987), and so choice of estimator is important. Moreover, each estimator varies in terms of its optimal conditions of application. For example, Chao 2 and 2nd order Jackknife estimates are preferred estimators of richness for small samples (Thompson & Thompson, 2010); however, Chao 2 is quite conservative and also assumes homogeneity of variance among samples (Chao, 1987). The ICE (incidence-based coverage estimator) is useful for incidence datasets and small samples (Thompson & Thompson, 2010; Taylor & Banos, 2014). Jackknife estimators reduce estimator bias while Chao 2 estimators have a stopping rule; richness has plateaued at 'true' richness when all species are surveyed twice in a sample (Gotelli & Colwell, 2011).

Generally, when using nonparametric estimators of 'true' richness to assess the accuracy of observed species richness measurements, it is recommended that multiple estimators be applied and compared to obtain a robust estimate of 'true' richness (Thompson & Thompson, 2010). The combination of multiple estimators and estimates from ARU recordings can improve the efficiency of estimating 'true' species richness (La & Nudds, 2016) and if ARU observed estimates align with nonparametric estimators of "true" richness, this corroboration gives increased confidence that observed estimates are representative of the 'true' species richness.

3.1.3 Objectives

My objective in this chapter is to assess whether ARU richness collection methods substantially under-estimated avian species richness at the mountain peatland sites that I discussed in Chapter 2. I will test whether 1) the timing of my surveys within the breeding season and 2) the degree of survey effort I devoted to each site were adequate to yield accurate estimates of species richness. The observed richness was deemed accurate if the species accumulation curves plateaued by the end of the survey period, and the observed richness was at least 80% of the 'true' richness calculated by richness estimators.

3.2 Methods

3.2.1 Study design

I used acoustic surveys to estimate avian species richness in 24 valley-bottom mountain peatlands in the Upper Bow River basin of Alberta. They cover an elevation gradient from 1300 to 2000 m a.s.l. The sites were evenly split between lower elevation Montane (Upper Foothills and Montane Natural Subregion) and higher elevation Subalpine Natural Subregions. Sites were surveyed for avian species richness using ARUs. The peatlands were spaced at least 500 m apart to control for spatial dependence.

I deployed ARUs in stratified random clusters where a set of sites within 50 km of each other in the Montane and another set of sites within 50 km of each other in the Subalpine were randomly selected for surveys on each date. The set of sites for each cluster varied between one and five sites. This design ensured that the surveys were not biased in terms of when the Montane and Subalpine Natural Subregion sites were surveyed and permitted logistical efficiencies from sampling multiple sites in a single dawn chorus. Sites recorded during the dawn chorus on four different dates between May 22nd and June 12th, 2019, which I anticipated was within the breeding season.

3.2.2 Study area

Details about the study area are described in chapter 2. In brief, I conducted surveys in mountain peatlands located in Kananaskis country, southwestern Alberta, Canada (Figure 2.4). The 24 sites were distributed between three Natural Subregions; Upper Foothills (n = 3), Montane (n = 9) and Subalpine (n = 12).

For my analysis, I combined the Upper Foothills and Montane Natural Subregions, based on similarities in elevation and peatland soil characteristics. Also, depending on location in the Bow River basin, both of these can adjoin the Subalpine Natural Subregion directly (Figure 2.4; Downing & Pettapiece, 2006). Generally, the Upper Foothills covers 3.3% of the province, with an area totaling 21,537 km^2 (Downing & Pettapiece, 2006). Elevation ranges from 950 – 1750 m a.s.l. (mean = 1300 m a.s.l.; Downing & Pettapiece, 2006). This Natural Subregion is considered a transition zone between warmer and drier conditions in the Lower Foothills Natural Subregion and the wetter and cooler climate in the Subalpine Natural Subregion (Downing & Pettapiece, 2006). Black spruce (*Picea Mariana*), tamarack (*Larix laricina*), shrubs and herbs dominate wetlands in the Upper Foothills Natural Subregion. Wetlands in this Natural Subregion have terric and typic mesisols with peaty and orthic gleysols (Downing & Pettapiece, 2006). The Montane Natural Subregion covers 8768 km^2; about 1.3% of the province (Downing & Pettapiece, 2006). Elevation in this Natural Subregion ranges from 825 – 1850 m a.s.l. (mean = 1400 m a.s.l.; Downing & Pettapiece, 2006). Different aspects, slope position and wind exposure produce variable microclimates and vegetative communities throughout the Montane Natural Subregion (Downing & Pettapiece, 2006). This Natural Subregion has mild summers and warm winters (Downing & Pettapiece, 2006). Dominant vegetation in wet areas includes Douglas fir

(*Pseudotsuga menziesii*), aspen (*Populus* species), lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*; Downing & Pettapiece, 2006). Montane peatlands contain gleysols and organic soils (Downing & Pettapiece, 2006).

The Subalpine Natural Subregion covers 25,218 km^2; about 3.8% of the province (Downing & Pettapiece, 2006). The elevation ranges from 1300 – 2300 m a.s.l. (mean = 1750 m a.s.l; Downing & Pettapiece, 2006). This Natural Subregion occurs directly above the Montane Natural Subregion south of the Bow River and above the Upper Foothills north of the Bow River (Figure 2.4). The summers are short, cold and wet while the winters are long, cold and have heavy snowfall (Downing & Pettapiece, 2006). Wetlands occur in valley-bottoms that contain sedge (*Carex* species), dwarf birch (*Betula nana*), Engelmann spruce (*Picea engelmannii*) and horsetail (*Equisetum* species; Downing & Pettapiece, 2006). Wetland soils in this Natural Subregion are chiefly gleysols, although organic soils do occur (Downing & Pettapiece, 2006).

3.2.3 Avian field surveys

Detailed methods of avian surveys are described in chapter 2. In brief, on each of the four survey dates at each peatland, I deployed an ARU programmed to commence recording in 10 minute increments for a period of one hour between 06:00 and 07:00. I set the ARUs to record at 24 kHz, as 16-bit recordings (Alberta Biodiversity Monitoring Institute, 2015). I placed the ARU so that it was at least 50 m from the boundary with upland forest and 1 m above the ground.

3.2.4 Bioacoustic data processing

Detailed methods of bioacoustic data processing are described in chapter 2. In brief, I manually analyzed bioacoustic field recordings with a sound analysis program, Audacity ® (Audacity; Audacity Team 2019; version 2.3.3). I analyzed each file for all avian species present and manual analysis included both visual analysis of spectrograms and auditory aid in identifying avian species. I collected the presence and absence of avian species from each recording. I omitted unknown species and degraded songs and calls. For example, I did not include a vocalization in my analysis if the song or call did not register on the spectrogram, if a partial song or call could be identified as a number of different species so no accurate identification was possible, or if weather or man-made noise obscured visual and auditory identification of a song or call.

3.2.5 Data analysis

I completed statistical analysis and data visualizations in RStudio (RStudio Team, 2020). To evaluate whether my chosen survey period within the breeding season impacted the observed avian species richness estimates, I plotted the cumulative richness from all sites across the survey period. This is essentially a species accumulation curve that reflects the regional species pool. If the curve reached a plateau by the end of my survey period, it would indicate that I caught all breeding bird species in the region, and hence did not miss late breeding species (e.g. Alder Flycatcher; *Empidonax alnorum;* Lowther, 2020). I made figures first combining the two Natural Subregions and then for each Natural Subregion separately. I made these figures using the ggplot2 package (Wickham, 2016). In addition to the cumulative richness figures, I calculated richness estimators, Chao 2, ICE, 1st and 2nd order Jackknife, and 95% confidence interval using the SpadeR package (Chao et al., 2015). This estimated the total richness in the regional species pool (i.e., gamma diversity; sensu Whittaker, 1972) and sub-regional species pool and I used the confidence intervals to compare to my observed values. If the lower bound confidence interval encompassed the observed avian species richness estimated from ARU recordings, then a complete measure of the gamma richness was collected and if 80% of the calculated richness was observed then the survey adequately sampled the avian species richness.

To evaluate the adequacy of my survey effort, I analyzed site-level data in RStudio using the ggplot2 package (Wickham, 2016) and vegan package (Oksanen et al., 2019) to plot the species-accumulation curves and SpadeR package (Chao et al., 2015) to calculate richness estimators and their confidence intervals. For each site, I constructed a species-accumulation curve to determine if the hour-long surveys over a four-day period (240 minutes) during the breeding season captured a sufficient proportion of the avian species richness at that site. Each figure was produced using the number of recorded files and randomly selecting a files' species composition. The random selection was permutated 999 times (permutation = 999, seed = 412) so an average number of species present for each time increment was produced under all possible permutations. Survey effort was deemed sufficient if the site's species-accumulation curve approached an asymptote or plateaued. As well, I calculated site-level richness estimator: Chao 2 and 95% confidence interval to assess the distance between my observed site-level species richness (i.e. alpha diversity; sensu Whittaker, 1972) and the estimated true richness level.

Survey effort that produced a richness estimate of 80% or higher of the ‘true’ richness is considered an adequate estimate of richness as suggested by Thomson and Thompson (2010), where ‘true’ richness is represented by the richness estimator output and if the lower bound confidence interval encompassed the observed richness then a complete measure of alpha richness was collected.

Then I ran three logistic regressions: one to test whether peatland size effected the probability of a site’s observed species richness reaching a plateau within 240 min of recording or not, a second to test for the effect of total estimated number of species, and a third to test for the effect of elevation. To measure the goodness of fit, I used a likelihood ratio test to assess whether the logistic regressions provided significantly better fit to the data than a null model comprising only an intercept. Lastly, I conducted a contingency table analysis to test whether the probability of a site’s observed avian species richness plateauing within 240 min of observation was contingent on which Natural Subregion the site was located in. I used a Pearson’s test of association, yielding a Chi-squared test statistic and an associated p-value for the null hypothesis of independence.

3.3 Results

3.3.1 Richness estimates and day of year

Over the course of the survey period, 74 avian species were recorded, and the alpha diversity recorded at each site ranged from 15 to 38 species. These 74 species included ten species who are recorded as Sensitive species in Alberta (Alberta Environment and Parks, 2015). Three species found are considered Threatened or At Risk at the national or provincial level (Alberta Environment and Parks, 2015; Government of Canada, 2019). One of these is considered Threatened federally and At Risk in Alberta: Canada Warbler (*Cardellina canadensis*; Alberta Environment and Parks, 2015; Government of Canada, 2019); another is considered of Special Concern federally and May Be At Risk in Alberta: Olive-sided Flycatcher (*Contopus cooperi*; Alberta Environment and Parks, 2015; Government of Canada, 2019); and the Western Wood-Pewee (*Contopus sordidulus*) May Be At Risk in Alberta (Alberta Environment and Parks, 2015). The remaining species are believed to have Secure populations both nationally and provincially (Alberta Environment and Parks, 2015; Government of Canada, 2019). See Appendix C for a full list of species and their conservation status.

I report the cumulative number of avian species observed during the course of my survey period for (a) all sites combined, (b) the Montane Natural Subregion, and (c) the Subalpine Natural Subregion (Figure 3.1). Cumulative species richness for all sites increased from day 142 to 162, from 38 to 74 species (Figure 3.1a). Montane Natural Subregion cumulative richness increased from day 142 to 163, from 33 to 69 species (Figure 3.1b). Subalpine Natural Subregion cumulative richness increased over the survey period from day 142 to 162, from 18 to 50 species (Figure 3.1c). Each figure showed a logistic trend and where the curve started to flatten as cumulative richness approached an asymptote.

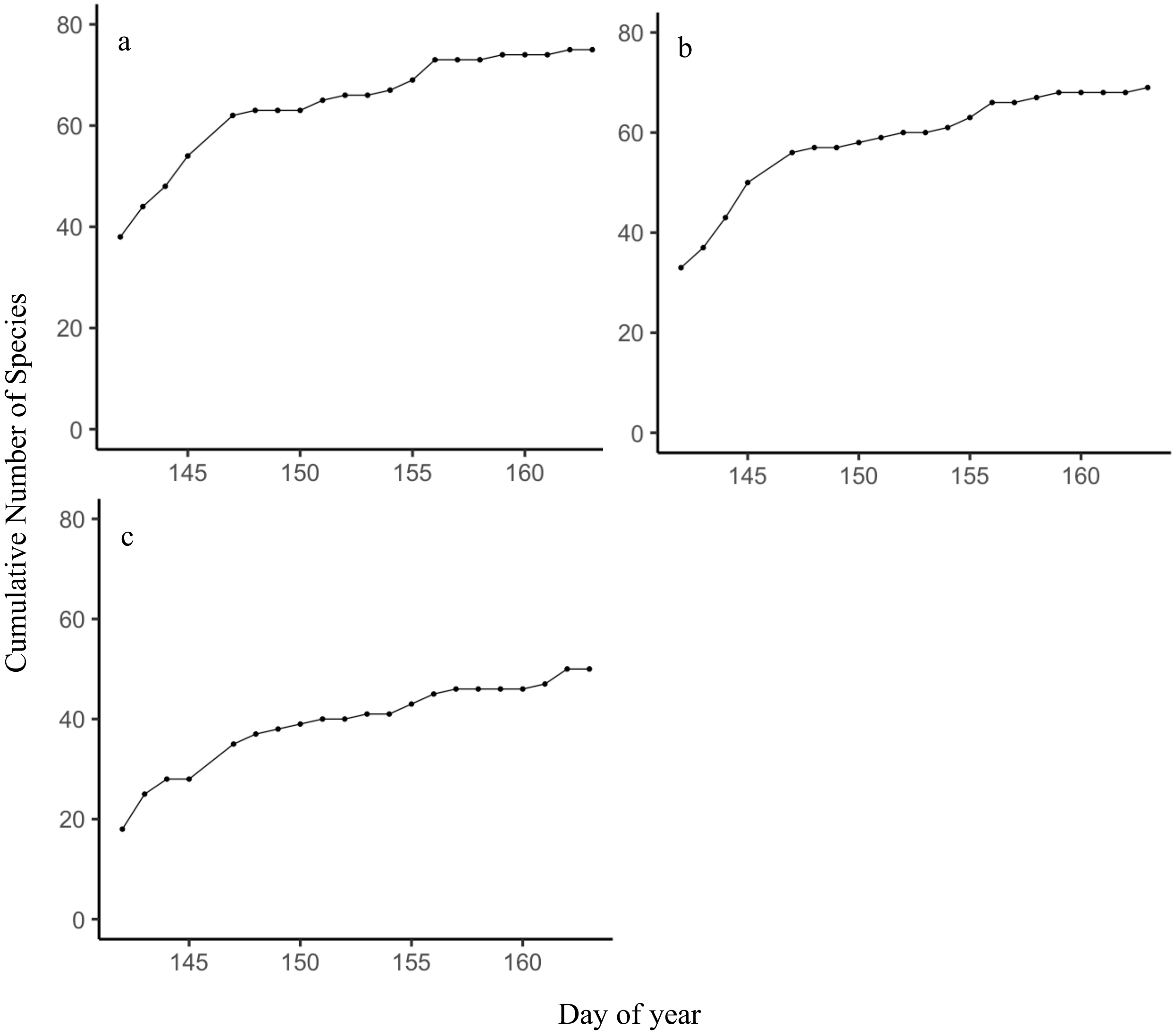

Figure 3.1 Cumulative number of avian species identified in valley-bottom mountain peatlands in southwestern Alberta during the survey period from May 22nd (DOY 142) to June 12th (DOY

163). Depicted are (a) all sites (n = 24), (b) sites lying in the Montane Natural Subregion (n = 12), and (c) sites lying in the Subalpine Natural Subregion (n = 12).

In addition to graphing cumulative richness over the course of the survey period, I calculated richness estimators to compare to observed gamma richness. I heard a total of 74 different avian species combining all sites, while the richness estimators, Chao 2, ICE, 1st and 2nd order Jackknife, estimated 79.7 to 86.0 species (Table 3.1). The 95% confidence interval for each estimator did not encompass the observed cumulative avian species richness for all mountain peatlands but in relation to all estimators the observed richness was more than 80% of each of the calculated richness. Chao 2 was the estimator with the lowest expected number of species, 79.7, and the lower bound 95% confidence interval was 1.5 above my observed gamma richness for all sites combined.

I observed a total of 69 avian species when combining all Montane Natural Subregion peatlands, whereas the richness estimators ranged from 82.5 to 91.7 species (Table 3.1). The 95% confidence intervals for each estimator did not encompass the observed richness, 69 avian species but in relation to the ICE and Jack 1 estimator the observed richness was more than 80% of the calculated richness. The ICE estimator had the lowest expected number of species, 82.5 and the lower bound 95% confidence interval was 5 above the observed species richness.

I observed a total of 50 avian species when combining all Subalpine Natural Subregion peatlands, whereas the richness estimators ranged from 55.3 to 60.8 species (Table 3.1). The 95% confidence intervals for each estimator did not encompass the observed richness, 50 avian species but in relation to all estimators the observed richness was more than 80% of each of the calculated richness. The Chao 2 estimator had the lowest expected number of avian species, 55.3 and the lower bound 95% confidence interval was 1.3 above the observed species richness.

Table 3.1 Richness estimators, Chao 2, incidence-based coverage estimator (ICE), 1st (Jack 1) and 2nd order Jackknife (Jack 2), for avian species richness estimates calculated for all mountain peatlands, Montane and Subalpine Natural Subregion and 95% confidence intervals (CI), 95% CI lower and upper bound. Estimated richness from ARU surveys in all mountain peatlands during the survey period was 74 avian species, in Montane Natural Subregion was 69 avian species, and Subalpine Natural Subregion was 50 avian species.

All Sites	Estimate	95% Lower	95% Upper
Chao 2	79.7	75.5	95.7
ICE	82.7	77.0	99.5
Jack 1	85.4	79.2	98.9
Jack 2	86.0	77.7	112.8
Montane			
Chao 2	86.9	74.2	130.5
ICE	82.5	74.0	105.1
Jack 1	83.3	76.1	97.8
Jack 2	91.7	79.8	116.7
Subalpine			
Chao 2	55.3	51.3	72.1
ICE	60.7	53.7	81.3
Jack 1	59.5	54.1	72.2
Jack 2	60.8	53.3	85.6

3.3.2 Species accumulation curves and richness estimators

The ARU sampling method that I used to survey avian species richness in valley-bottom mountain peatlands recorded 74 species in total and site-level alpha richness ranged from 15 to 38 species. See Appendix C for a full list of species at each site. Sites 128, 226 and 204 were the only sites that did not record for the full 240 minutes. Access to site 128 was restricted during the survey period and only three days were available for survey. At sites 226 and 204, malfunctioning of the ARUs resulted in the ARU not recording for 20 minutes.

I report the estimated number of avian species at each time increment over the survey period for each individual site using species accumulation curves (Figure 3.2 – 3.4). Richness estimates generally increased initially and began to plateau anywhere from 50 to 240 min into the recording (Figure 3.2 – 3.3). Although 11 of the 24 sites (45.8%) had not reached a plateau, even after 240 min (Figure 3.2h, 3.3f, 3.4). There were zero sites that plateaued by 60 minutes of survey and the lowest survey effort that produced two sites to plateau was 90 minutes (Figure 3.2a – b).

Splitting sites by Natural Subregion, in the Subalpine Natural Subregion, richness plateaued in 58.3% of sites in less than 200 minutes and another 8.3% sites between 200 and 240 minutes. Finally, 33.3% of Subalpine Natural Subregion sites did not plateau in 240 minutes (Figure 3.2 – 3.4). Whereas, in the Montane Natural Subregion, richness plateaued in 41.7% of sites after 200 minutes, and 58.3% of sites did not plateau within 240 minutes (Figure 3.2 – 3.4).

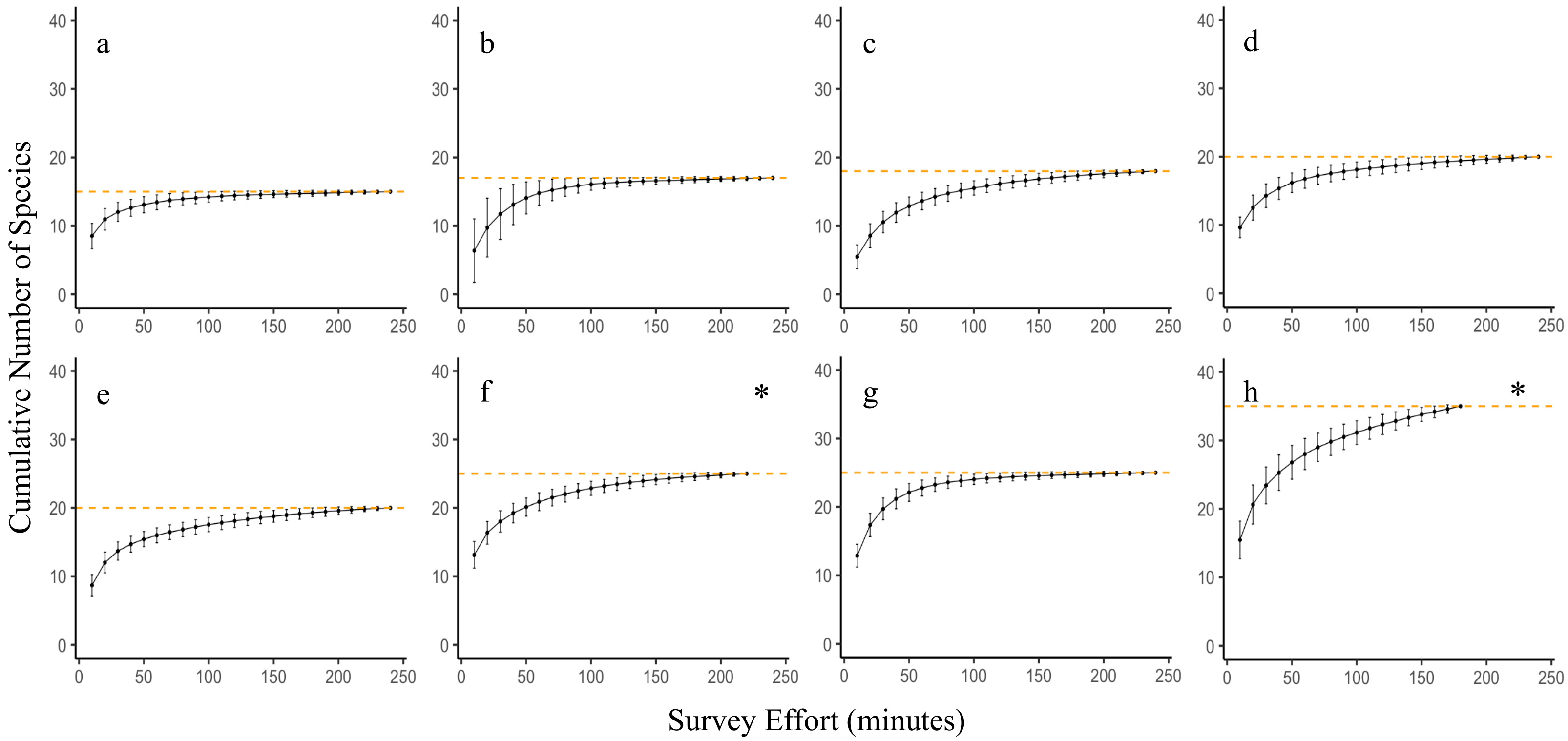

Figure 3.2 Species accumulation curves for vocalizing avian species recorded in valley-bottom mountain peatlands in southwestern Alberta, grouped as sites that plateaued before or did not record past 200 minutes. Each curve shows the cumulative number of avian species detected at each site as a function of survey effort in minutes. Subalpine Natural Subregion sites (a) 220, (b) 230, (c) 224, (d) 225, (e) 203, (f) 226, and (g) 227 approached an asymptote in less than 200 minutes and Montane Natural Subregion site (h) 128 richness had still not plateaued by the end of the survey period, which was cut short at 180 minutes. Sites are ordered from lowest richness to highest, then from lowest elevation to highest. Asterisks indicate sites that recorded for less than 240 minutes due to equipment failure or site access restrictions.

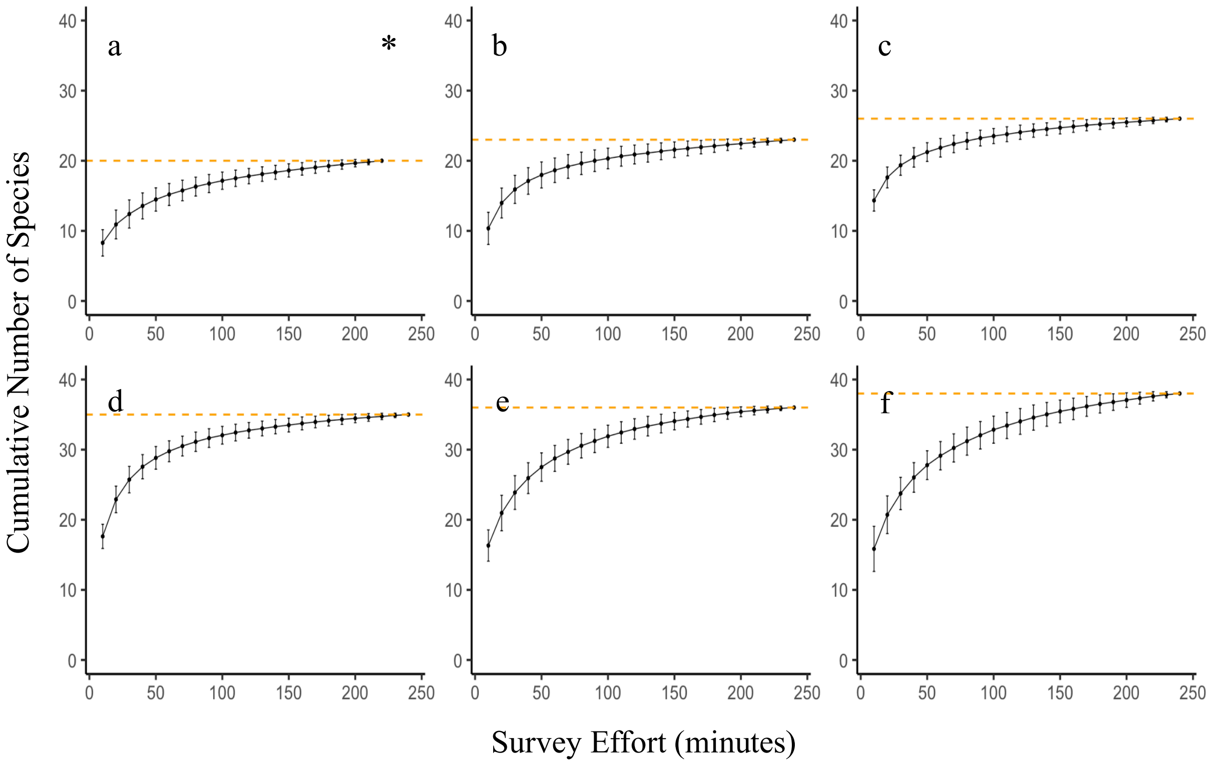

Figure 3.3 Species accumulation curves for vocalizing avian species recorded in valley-bottom mountain peatlands in southwestern Alberta, grouped as sites that plateaued before or did not record for the full 240 minutes. Each curve shows the cumulative number of avian species detected at each site as a function of survey effort in minutes. Subalpine Natural Subregion site (a) 204, and Montane Natural Subregion sites (b) 126, (c) 120, (d) 101, (e) 121, and (f) 131 approached asymptote between 200 and 240 minutes. Sites are ordered from lowest richness to highest, then from lowest elevation to highest. Asterisks indicate sites that recorded for less than 240 minutes.

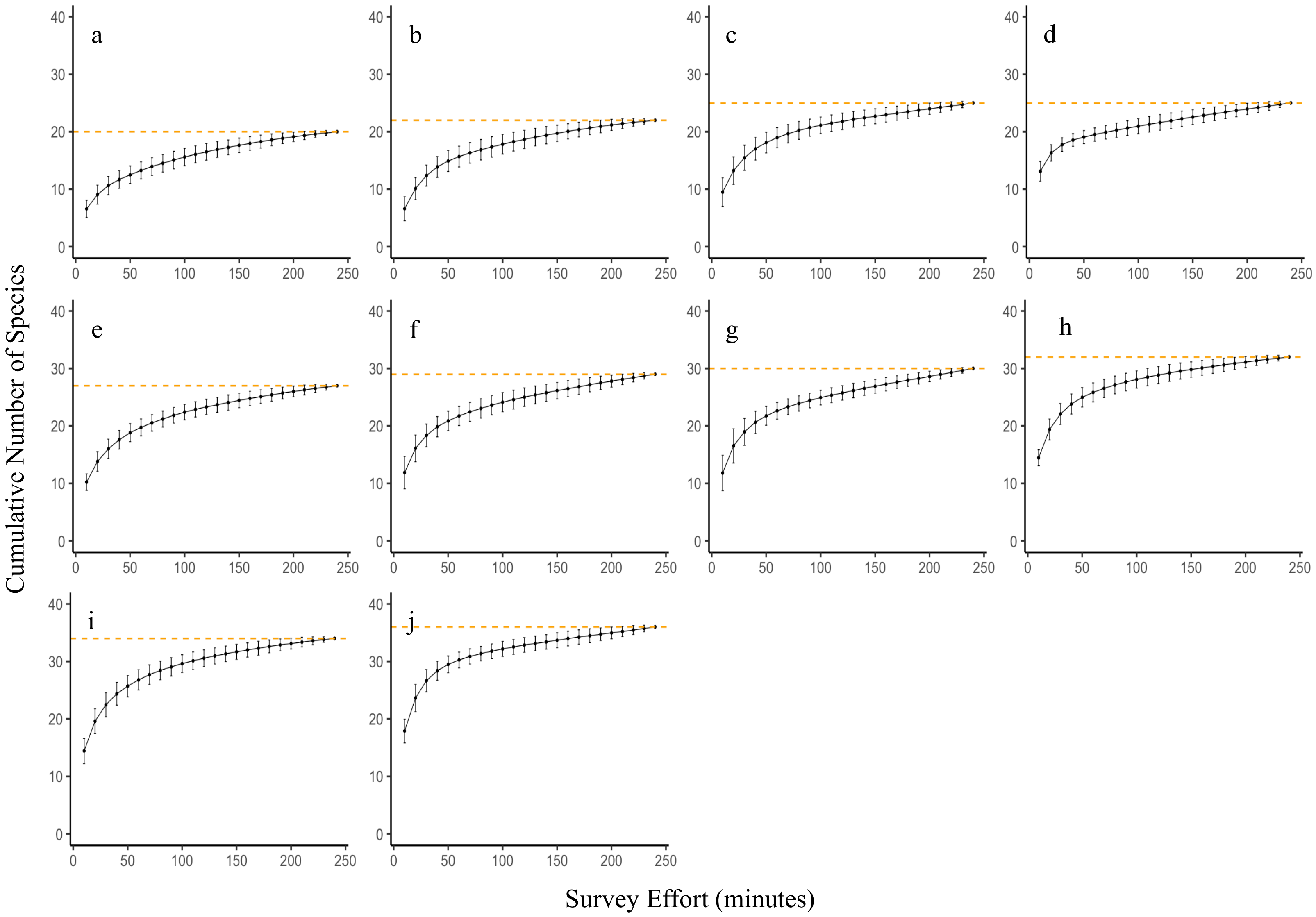

Figure 3.4 Species accumulation curves for vocalizing avian species recorded in valley-bottom mountain peatlands in southwestern Alberta, grouped as sites that did not plateau within 240 minutes. Each curve shows the cumulative number of avian species detected

at each site as a function of survey effort in minutes. Subalpine Natural Subregion site (a) 221, (b) 222, (c) 223, and (d) 201, and Montane Natural Subregion sites (e) 130, (f) 122, (g) 125, (h) 106, (i) 102, and (j) 106 richness had not plateaued within the 240 minute survey period. Sites were ordered from lowest richness to highest, then from lowest elevation to highest.

Furthermore, I calculated site-level "true" alpha richness using the Chao 2 estimator and 95% confidence intervals to compare to my observed alpha richness. I heard between 23 and 38 different avian species at sites in the Montane Natural Subregion and 15 to 25 species at sites within the Subalpine Natural Subregion (Table 3.2). Of the 12 sites in the Montane Natural Subregion, the level of observed richness at 8 (66.7%) sites were within 1 species of the lower bound confidence interval around the Chao 2 estimated true richness, but none were actually encompassed by the 95% confidence intervals (Table 3.2). Although, 75% of Montane Natural Subregion sites observed 80% of the calculated 'true' site-level richness. In comparison, at the Subalpine Natural Subregion sites, the alpha richness observed was typically lower, but at 25% of my 12 sites, the observed richness fell within the 95% confidence interval around the Chao 2 estimated true richness and another 58.3 % of sites were within 1 species of the lower confidence interval (Table 3.2). Although, 83.33% of Subalpine Natural Subregion sites observed 80% of the calculated 'true' site-level richness.

Table 3.2 Observed avian richness (S) and calculated Chao 2 "true richness" along with its upper and lower 95% confidence interval (CI) limit for each valley-bottom mountain peatland site in each Natural Subregion of interest; the Montane and Subalpine Natural Subregion. Asterisks indicates that S lies within 1 species of the 95% CI for the Chao 2 at that site.

Site	Natural Subregion	n	S	Chao 2	Lower CI	Upper CI	CI within 1 species
101	Montane	24	35	37.16	35.25	53.34	*
102	Montane	24	32	37.99	32.93	70.57	*
106	Montane	24	36	50.38	39.10	102.8	
120	Montane	24	26	30.31	26.47	65.31	*
121	Montane	24	36	36.86	36.09	44.10	*
122	Montane	24	29	52.48	32.44	189.4	
125	Montane	24	30	56.83	37.08	131.8	
126	Montane	24	23	25.16	23.25	41.34	*
127	Montane	24	34	39.99	34.93	72.57	*
128	Montane	18	35	42.71	36.48	75.23	
130	Montane	24	27	31.79	27.83	54.82	*

131	Montane	24	38	41.00	38.48	56.61	*
201	Subalpine	24	25	43.00	27.53	153.0	
203	Subalpine	24	20	20.64	20.05	27.56	*
204	Subalpine	22	20	27.64	20.94	81.98	*
220	Subalpine	24	15	15.00	15.00	16.43	*
221	Subalpine	24	20	24.17	20.67	45.77	*
222	Subalpine	24	22	26.17	22.67	47.77	*
223	Subalpine	24	25	39.38	28.11	91.40	
224	Subalpine	24	18	18.96	18.09	28.69	*
225	Subalpine	24	20	22.00	20.18	42.13	*
226	Subalpine	22	25	25.96	25.07	35.65	*
227	Subalpine	24	25	25.00	25.00	26.54	*
230	Subalpine	24	17	17.00	17.00	18.53	*

The likelihood that observed site-level alpha richness plateaued within 240 minutes of avian survey was not a function of peatland size (logistic regression; $\chi^2 = 0.8081$, df = 23, p-value = 0.854 where $\text{logit(Plateau)} = \ln(\text{odds}_{\text{plateau}}) = -0.0936 + 3.661\text{x}10^{-4}x$), the number of species present at a site (logistic regression; $\chi^2 = 0.1212$, df = 23, p-value = 0.127 where $\text{logit(Plateau)} = \ln(\text{odds}_{\text{plateau}}) = 2.806 + 9.954\text{x}10^{-2}x$), peatland elevation (logistic regression; $\chi^2 = 0.2192$, df = 23, p-value = 0.249 where $\text{logit(Plateau)} = \ln(\text{odds}_{\text{plateau}}) = -4.878 + 3.064\text{x}10^{-3}x$), or the Natural Subregion the site is located in (Chi-Squared test; p-value = 0.219, df = 2). The effect of peatland size on the probability of the curve plateauing was $\text{odds}_{\text{plateau}} = 1.000$ (95% CI 0.997, 1.004), where the model explained 0.33% (Nagelkerke R^2) of the variance in site-level alpha richness plateauing within 240 minutes. The effect of the number of species present at a site on the probability of the curve plateauing was $\text{odds}_{\text{plateau}} = 0.905$ (95% CI 0.782, 1.026), where the model explained 1.27% (Nagelkerke R^2) of the variance in site-level alpha richness plateauing within 240 minutes. The effect of peatland elevation on the probability of the curve plateauing was $\text{odds}_{\text{plateau}} = 1.003$ (95% CI 0.998, 1.009), where the model explained 8.15% (Nagelkerke R^2) of the variance in site-level alpha richness plateauing within 240 minutes.

3.4 Discussion

Two important considerations when designing any breeding survey with ARUs is what range of dates to survey on and how much survey effort to invest in each survey date. Survey for too brief a range of dates, and you risk missing early or late breeding species. Survey for too short a duration, and you may not give secretive or rare species sufficient time to vocalize during your ARU recordings. These topics are interconnected, as you may economize by surveying fewer dates and thus have resources to survey for longer on each date. However, common practice is to survey for only 10-15 min on any individual date, and then to survey for 2-4 dates within the breeding period (e.g., Farina et al., 2011; Tegeler et al., 2012; Sidie-Slettedahl et al., 2015; Frommolt, 2017). I sought to evaluate whether these standard avian survey practices were adequate to comprehensively survey avian species richness, which would be key in any research study focused on biodiversity, rare species, or species with secretive behaviour.

Examining my dawn chorus survey period during the breeding season, I found that regional avian species richness (i.e., gamma diversity, sensu Whittaker, 1972), site-level richness (i.e. alpha diversity, sensu Whittaker, 1972), and sub-regional richness (grouped by Natural Subregion, sensu Downing & Pettapiece, 2006) all plateaued within my chosen survey period from May 22nd to June 12th. I calculated richness estimators and their 95% confidence intervals to compare against my observed alpha, gamma, and sub-regional richness. Although the 95% confidence intervals of the richness estimator value only encompassed the observed avian species richness at 3 sites, and the observed richness that the estimators did not encompass was only 0.5 to 5 species higher than the observed richness at the alpha, gamma and Natural Subregion levels.

From this I conclude that my survey period encompassed an adequate portion of the breeding season to capture most species, even though deployment of my ARUs was limited by site access due to snow and road closures during the onset of the avian breeding season. This is corroborated by the fact that I did detect several early season and late season breeders in my surveys. For example, I detected Pine Siskin (*Spinus pinus*) and Clark's Nutcracker (*Nucifraga columbiana*) despite their being recognized as early breeding species (Birds Canada, 2020). The Pine Siskin (*Spinus pinus*) was recorded at all but one site while the Clark's Nutcracker (*Nucifraga columbiana*) was recorded at one Subalpine Natural Subregion site. Similarly, I observed several late breeding species: Flycatcher species (*Empidonax* spp.) and Nelson

Sparrows (*Ammodramus nelsoni*) were recorded at 15 and 2 of my 24 sites, respectively. Both of these are thought to breed toward the end of the season, usually in late June (Birds Canada, 2020). Detecting both early and late breeding species substantiates my interpretation of my species accumulation curves and richness estimators that I adequately captured the breeding period. If the research objectives involved looking directly at a late breeders, a longer survey period could be warranted.

ARU-based bird research in the Rocky Mountain peatlands should continue to deploy as soon as the weather permits to ensure that early breeding species are captured, though it appears that initiating surveys from May 22nd and terminating on June 12th were adequate to capture both early and late breeding birds in my study. It may be possible to deploy ARUs overwinter that are programmed to commence recording in early spring, before mountain peatlands are safe to access by researchers, however, researchers would need to investigate the risk of battery issues arising and ARUs would likely suffer damage unless precautions are put in place.

The second concern is whether individual surveys were of sufficient duration to capture rare or secretive birds that vocalize infrequently. Summing the 60-minute dawn chorus surveys across the four survey dates at each site separately, I found that sites where we comprehensively estimated avian species richness required more than 100 minutes of survey time (54.2% of sites). The remaining sites did not exhibit a plateau within 240 minutes of surveying. As in the introduction, I defined a comprehensive estimate of species richness as the proportion of richness detected by the ARU was at least 80% of the richness determined by the lowest richness estimator estimate (Thompson & Thompson, 2010). Also, at 75% of my sites, the observed richness values fell within one species of the lower 95% confidence interval and 79.17% of sites observed at least 80% of the calculated richness. From this, I conclude that a minimum of 150 minutes of survey is necessary to adequately capture avian species richness in mountain peatlands. This is an order of magnitude longer than most standard methods (e.g., Farina et al., 2011; Tegeler et al., 2012; Sidie-Slettedahl et al., 2015; Frommolt, 2017). The longer survey method raises concerns that typical ARU survey methods under-detect rare and secretive species and, in many ecosystems, ARUs are not adequately capturing avian species richness. For example, if this study only surveyed avian species richness for 10 minutes, richness detected at a site would reduce by 47 to 73% compared to the total richness that I observed in 240 minutes of observation.

Reporting this reduction in richness would be detrimental to both the stewardship groups of the Upper Bow River Basin that have objectives to maintain biodiversity and stated gaps in bird diversity data. Currently mountain peatlands are not included in the provincial wetland inventory and lack protection. Mountain peatlands are important bird habitat that contain about 25% of Alberta's bird species as detected during this study thus warranting greater protection for this underappreciated bird habitat. Therefore, inaccurate or reduced richness reported from standardized surveys should be updated to surveys that use adequate survey effort that surveys at least 80% or more of the 'true' richness at these mountain peatlands.

Splitting the sites by Natural Subregion, it appears that avian species richness plateaued earlier within the survey period in the Subalpine Natural Subregion compared to the Montane Natural Subregion. Although, the probability that richness would plateau within my 240-minute survey window did not differ significantly between the Montane and Subalpine Natural Subregions. The Subalpine was significantly less species rich than the Montane Natural Subregion (Chapter 2); however, it seems unlikely that this difference is richness explains the apparent earlier plateau in the species accumulation curves from Subalpine Natural Subregion because the number of species present at a site did not significantly influence the probability of site-level richness plateauing within the 240-minute survey window. Nor did area or elevation of the peatland have an effect on the probability of site-level richness plateauing within the 240-minute survey window.

For 75% of my mountain peatlands, 240-minute ARU surveys were adequate to capture a comprehensive estimate of species richness. Additional survey effort may have been warranted at the remaining 25% of sites, highlighting the trade-off nature of methodological decisions like setting the level of survey effort to a standard level. Importantly, both the cumulative and site-level estimates of avian species richness required substantially more survey effort than most literature suggests (e.g., Farina et al., 2011; Tegeler et al., 2012; Sidie-Slettedahl et al., 2015; Frommolt, 2017). Consequently, I recommend that future bird richness research using ARUs undertake a power analysis or use species accumulation curves to optimize survey effort. I further recommend that ARUs be set to record a minimum of one hour during the dawn chorus over the course of four days spread across the breeding season. Future research should also look into the trade-offs between surveying for less time during the dawn chorus on more days versus surveying for more time during the dawn chorus on fewer days.

Based on this study, I conclude that ARUs can be used to adequately estimate avian species richness during the breeding season. In fact, ARUs have a major advantage over in-person surveys of avian richness in that they can be programed to record for a prolonged duration (e.g. >240 minutes) and then the decision of how much of that recording to transcribe (i.e. how much survey effort to expend) can be adjusted to ensure richness estimation accuracy without overshooting the plateau in a site's species accumulation curve. In contrast, in-person survey requires that the amount of survey effort to allocate to each site be determined in advance and optimization relies on pilot studies and expert judgement. Although current recommendations for survey period are adequate to capture the full breeding season, recommendations for survey effort are inadequate. To comprehensively estimate the richness of breeding birds in mountain peatlands in the Rocky Mountains, a minimum of one-hour recording during the dawn chorus over the course of four days must replace the standard 10 – 15 minute surveys.

4. Conclusions and recommendations for stewardship groups

4.1 Thesis summary

In chapter 2, I evaluated the nature of the avian species richness-elevation relationship and found evidence of multicausality, suggesting that peatland area combined with one or more environmental filters that were consistent within Natural Subregion were responsible for the cubic pattern I observed. Yet, for my interpretation to be sound, it must be grounded in accurate estimates of avian species richness at the peatland- and Natural Subregion-levels. To evaluate whether my survey methods were adequate to accurately capture avian species richness, in Chapter 3, my results confirmed that the standardized ARU survey methods produced adequate estimates of avian species richness. Although, survey effort required to produce accurate estimates of avian species richness were significantly longer than the literature suggested. Based on the outcome of Chapter 3, I have confidence in my conclusions regarding the richness-elevation relationship in mountain peatlands in the Upper Bow Basin, Alberta.

4.2 Recommendations for stewardship groups

Around the globe, biodiversity is being lost (Sandbrook et al., 2019) and conservation efforts require the understanding of ecological patterns and mechanisms that determine species richness (Chapter 2), as well as accurately quantifying species richness estimates (Chapter 3). Habitat loss is one main concern for species richness decline, thus anthropogenic disturbance (e.g., logging and human activities) is one of the main drivers of habitat loss and reduced biodiversity (Ambarli & Bilgin, 2014; Ibarra & Martin, 2015; Pavlacky et al., 2015). Stewardship groups in the Upper Bow Basin prioritize the maintenance of the water quality and preservation of the environmental and economic importance of the watershed (Elbow River Watershed Patnership, 2009; The Bow River Project Research Consortium, 2010; Jumpingpound Creek Watershed Partnership, 2014; MacDonald, 2018). Concerns within each Sub-Basin include the conservation and in-depth survey of wildlife and biodiversity (Elbow River Watershed Patnership, 2009; The Bow River Project Research Consortium, 2010; Jumpingpound Creek Watershed Partnership, 2014; MacDonald, 2018). While each Sub-Basin has put in place management plans to maintain or improve current water quality, these plans can have the additive effect of sustaining overall habitat quality and wildlife populations (Elbow River

Watershed Patnership, 2009; The Bow River Project Research Consortium, 2010; Jumpingpound Creek Watershed Partnership, 2014; MacDonald, 2018).

An objective that recent reports from the Ghost, Elbow and Jumpingpound watersheds want to meet is to sustain wildlife populations and biodiversity (Elbow River Watershed Patnership, 2009; The Bow River Project Research Consortium, 2010; Jumpingpound Creek Watershed Partnership, 2014; MacDonald, 2018). Yet, the Ghost and Bow River Basin have stated a gap in bird diversity data within their respective watershed and Basin (The Bow River Project Research Consortium, 2010; MacDonald, 2018).

One major anthropogenic pressure of concern in the Upper Bow River Basin is logging. For example, mountain peatlands are experiencing continued logging activity around Horse Lake and The Aura Sand Hills: both considered environmentally sensitive areas. Horse Lake (site 121) has an estimate of 36 bird species that occupy this peatland. Of these species four are Sensitive to habitat change (Alder Flycatcher; *Empidonax alnorum*, Common Yellowthroat; *Geothlypis trichas*, Least Flycatcher; *Empidonax minimus*, and Pileated Woodpecker; *Dryocopus pileatus*), the Western Wood-Pewee (*Contopus sordidulus*) May Be At Risk in Alberta, and the Canadian Warbler (*Cardellina canadensis*) is At Risk in Alberta (Alberta Environment and Parks, 2015) and is considered a Threatened species in Canada (Government of Canada, 2019). See Appendix C for the list of species conservation statuses in Alberta and Canada and see Appendix D for details on bird species at each site.

Of the Sensitive to At Risk species, the Canadian Warbler (*Cardellina canadensis*) and Least Flycatcher (*Empidonax minimus*) are sensitive to changes or loss of their winter habitat, while species such as the Alder Flycatcher (*Empidonax alnorum*) have declining populations in Canada but the cause of the decline is not well understood (Cornell Lab of Ornithology, 2019). The Common Yellowthroat (*Geothlypis trichas*) is sensitive to habitat loss and the degradation from disturbances such as logging (Cornell Lab of Ornithology, 2019). This species is especially sensitive to wetland degradation and poor water quality. Both sensitivities can be maintained through the conservation of wetland habitats which are objectives in the Jumpingpound watershed (Jumpingpound Creek Watershed Partnership, 2014) and maintaining water quality is an objective for all three watersheds and the Bow River Basin (Elbow River Watershed Patnership, 2009; The Bow River Project Research Consortium, 2010; Jumpingpound Creek Watershed Partnership, 2014; MacDonald, 2018). The most sensitive species to logging around

Horse Lake include the Pileated Woodpecker (*Dryocopus pileatus*) and Western Wood-Pewee (*Contopus sordidulus*). The species that rely on mature to Old growth forest such as the Pileated Woodpecker (*Dryocopus pileatus*) and understory nesters and foragers such as the Common Yellowthroat (*Geothlypis trichas*) would be lost from habitats undergoing major changes (Cornell Lab of Ornithology, 2019) such as logging. With continued logging in areas such as Horse Lake, avian species and species abundances may be lost or reduced from a reduction of potential nesting habitats and foraging locations (Norton & Hannon, 1997; Sekercioglu, 2002; LaManna & Martin, 2016). Although, when anthropogenic disturbance was examined at the entire watershed scale, the Ghost Watershed was determined to be under low pressure from habitat loss due to anthropogenic disturbance (MacDonald, 2018).

Also, historic and current logging disturbance is present along the Powderface Trail in the Elbow and Jumpingpound watersheds. The Subalpine Natural Subregion peatlands may contain fewer species than the Montane Natural Subregion, as found in Chapter 2's third model competition, but there are species unique to higher elevations (e.g., Horned Lark; *Eremophila alpestris*; Ambarli & Bilgin, 2014) and Sensitive or At Risk species. The Powderface Trail contained five species Sensitive to habitat change (Alder Flycatcher; *Empidonax alnorum*, Clark's Nutcracker; *Nucifraga columbiana*, Northern Pygmy Owl; *Glaucidium californicum*, Pileated Woodpecker; *Dryocopus pileatus*, and Sora; *Porzana carolina*) and the Olive-sided Flycatcher (*Contopus cooperi*) May Be At Risk in Alberta (Alberta Environment and Parks, 2015) and is of Special Concern as of 2018 in Canada (Government of Canada, 2019). These species rely on specific nesting and foraging habitats and are described to be sensitive to habitat changes such as logging activity (Alberta Environment and Parks, 2015; Cornell Lab of Ornithology, 2019).

The Clark's Nutcracker (*Nucifraga columbiana*) and Pileated Woodpecker (*Dryocopus pileatus*) rely on specific nesting habitats in their breeding grounds in Canada (Cornell Lab of Ornithology, 2019). The Clark's Nutcracker (*Nucifraga columbiana*) requires pine trees to nest in and logging practices that remove or fell pine trees would negatively impact the Clark's Nutcracker population (*Nucifraga columbiana*; Alberta Environment and Parks, 2015) along the Powderface Trail. As mentioned above, the Pileated Woodpecker (*Dryocopus pileatus*) requires mature to Old-growth forests to excavate their nests (Alberta Environment and Parks, 2015) and the past and current logging activity along the Powderface Trail may reduce the area considered as mature to Old-growth forests and consequently impact the Pileated Woodpecker (*Dryocopus pileatus*) population in the area. The Northern Pygmy Owl (*Glaucidium californicum*) and Olive-sided Flycatcher (*Contopus cooperi*) are both considered sensitive to changes to their breeding grounds (Alberta Environment and Parks, 2015; Cornell Lab of Ornithology, 2019). In Alberta, the Olive-sided Flycatcher (*Contopus cooperi*) is also impacted from the decline in aerial insects since they are aerial foragers (Alberta Environment and Parks, 2015). Moreover, Soras (*Porzana carolina*) are negatively impacted by wetland loss (Alberta Environment and Parks, 2015), which is one of the Jumpingpound watershed's objectives; to preserve wetlands within the watershed (Jumpingpound Creek Watershed Partnership, 2014). Meeting this objective would assist generalist and specialist species that are found on wetlands in the Jumpingpound watershed.

Despite the notable risks to species of conservation priority from logging, the state of the watershed report for the Ghost Watershed actually concluded that erosion and OHV (Off-Highway Vehicles; i.e., ATVs) are the major threats of concern (MacDonald, 2018). The Ghost Watershed Alliance Society has recently undertaken restoration efforts at my study site in Johnson's Creek (site 120) where recreational ATV use had severely degraded the peatland (MacDonald, 2018). The ATV use through the peatland removed native plant species and potential ground, and shrub nesting locations for avian species.

Johnson's Creek had one of the lowest number of species in the Montane Natural Subregion with only 26 species present (Montane Natural Subregion richness average = 31.75, SD = 4.51) and two avian species of note. The Common Yellowthroat (*Geothlypis trichas*) that is Sensitive to habitat change and the Western Wood-Pewee (*Contopus sordidulus*) that May Be At Risk in Alberta (Alberta Environment and Parks, 2015). Yet, after the restoration of vegetation species, avian species that were removed or abundances reduced by the disturbance may increase during the subsequent breeding seasons in riparian areas (Gardali et al., 2006; Dybala et al., 2018). This suggest**s** the restoration efforts on the peatland may have brought the Common Yellowthroat (*Geothlypis trichas*) and Western Wood-Pewee (*Contopus sordidulus*) back but the continued ATV use around the area may produce avoidance behaviours (i.e., respond to vehicles as if they were predators; Frid & Dill, 2002; Blackwell & Seamans, 2009; DeVault et al., 2018) from other avian species such as the Brown-headed Cowbirds (*Molothrus ater*; DeVault et al., 2018).

The management strategy documents for each watershed set the goals of 1) maintaining or improving water quality, 2) mitigating drought, and 3) conserving biodiversity (Elbow River Watershed Patnership, 2009; The Bow River Project Research Consortium, 2010; Jumpingpound Creek Watershed Partnership, 2014; MacDonald, 2018). Wetlands have the capability to improve and maintain water quality, assist with drought and flood mitigation and host a variety of species, especially mountain peatlands (Laine et al., 1995; Squeo et al., 2006; Warner & Asada, 2006). By prioritizing the maintenance of current wetlands, namely peatlands that are sensitive to change (Erwin, 2009), each watershed can meet multiple objects of maintaining water quality, drought and flood mitigation and conserve wildlife populations. Presently, only the Jumpingpound Integrated Watershed Management Plan includes the goal of retaining the current percentage of wetlands in their Integrated Watershed Management Plan (Jumpingpound Creek Watershed Partnership, 2014). I strongly recommend that other watersheds within the Bow River Basin incorporate a similar goal, in recognition of the critical role wetlands can play in helping them achieve their existing goals.

5. References

Able, K. P., & Noon, B. R. (1976). Avian community structure along elevational gradients in the northeastern United States. *Oecologia*, *26*(3), 275–294. https://doi.org/10.1007/BF00345296

Alberta Biodiversity Monitoring Institute. (2015). *Terrestrial field data collection protocols (10001), Version 20190410*. Alberta Biodiversity Monitoring Institute, Alberta, Canada. Internal Report.

Alberta Environment and Parks. (2015). *Wild Species Status Search*. https://extranet.gov.ab.ca/env/wild-species-status/default.aspx

Alberta Goverment. (2017). *Alberta merged wetland inventory*. https://geodiscover.alberta.ca/geoportal/catalog/search/resource/details.page?uuid=%7BA73F5AE1-4677-4731-B3F6-700743A96C97%7D

Ambarli, D., & Bilgin, C. C. (2014). Effects of landscape, land use and vegetation on bird community composition and diversity in Inner Anatolian steppes. *Agriculture, Ecosystems & Environment*, *182*, 37–46. https://doi.org/10.1016/j.agee.2013.11.006

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Austin, G., & Cooper, D. J. (2016). Persistence of high elevation fens in the Southern Rocky Mountains, on Grand Mesa, Colorado, U.S.A. *Wetlands Ecology and Management*, *24*(3), 317–334. https://doi.org/10.1007/s11273-015-9458-7

Baker, J. R. (1938). *The evolution of breeding season. In: Evolution. (Essays presented to E. S. Goodrich),*. 161–177.

Barry, R. G. (2008). *Mountain weather and climate*. Cambridge University Press.

Beehler, B. (1981). Ecological structuring of forest bird communities in New Guinea. *Monographiae Biologicae*, *42*, 837–861.

Bernhardt, G. E., Blackwell, B. F., DeVault, T. L., & Kutschbach-Brohl, L. (2010). Fatal injuries to birds from collisions with aircraft reveal anti-predator behaviours: Bird collisions with aircraft. *Ibis*, *152*(4), 830–834. https://doi.org/10.1111/j.1474-919X.2010.01043.x

Bioacoustic Unit. (2015). *Acoustic recording analysis protocol*. Alberta Biodiversity Monitoring Institute, Alberta, Canada. Internal Report.

Birds Canada. (2020). *Nesting Calendar Query*. https://www.birdscanada.org/apps/rnest/index.jsp

Blackwell, B. F., & Seamans, T. W. (2009). Enhancing the Perceived Threat of Vehicle Approach to Deer. *Journal of Wildlife Management*, *73*(1), 128–135. https://doi.org/10.2193/2008-014

Blake, J. G., & Loiselle, B. A. (2000). Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *The Auk*, *117*(3), 663–686.

Blann, K. L., Anderson, J. L., Sands, G. R., & Vondracek, B. (2009). Effects of Agricultural Drainage on Aquatic Ecosystems: A Review. *Critical Reviews in Environmental Science and Technology*, *39*(11), 909–1001. https://doi.org/10.1080/10643380801977966

Boulinier, T., Nichols, J. D., Sauer, J. R., Hines, J. E., & Pollock, K. H. (1998). Estimating species richness: The importance of heterogeneity in species detectability. *Ecology*, *79*(3), 1018–1028. https://doi.org/10.1890/0012-9658(1998)079[1018:ESRTIO]2.0.CO;2

Bovendorp, R. S., MCCleery, R. A., & Galetti, M. (2017). Optimising sampling methods for small mammal communities in Neotropical rainforests. *Mammal Review*, *47*(2), 148–158. https://doi.org/10.1111/mam.12088

Breining, G. (1992). Rising from the bog. *Nature Conservancy*, *42*, 25–29.

Brown, J. H. (1971). Mammals on Mountaintops: Nonequilibrium Insular Biogeography. *The American Naturalist*, *105*(945), 467–478. https://doi.org/10.1086/282738

Brown, J. H., & Lomolino, M. V. (1998). *Biogeography* (2nd ed.). Sinauer Associates, Inc., Sunderland, Massachusetts.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference A Practical Information-Theoretic Approach* (2nd ed). Springer Science & Business Media.

Burnham, K. P., & Overton, W. S. (1978). Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika*, *65*(3), 625–633.

Calmé, S., & Desrochers, A. (1999). Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia*, *118*(3), 361–370. https://doi.org/10.1007/s004420050737

Calme, S., & Desrochers, A. (2000). Biogeographic aspects of the distribution of bird species breeding in Quebec's peatlands. *Journal of Biogeography*, *27*(3), 725–732. https://doi.org/10.1046/j.1365-2699.2000.00434.x

Calmé, S., Desrochers, A., & Savard, J.-P. L. (2002). Regional significance of peatlands for avifaunal diversity in southern Québec. *Biological Conservation*, *107*(3), 273–281. https://doi.org/10.1016/S0006-3207(02)00063-0

Campos-Cerqueira, M., & Aide, T. M. (2016). Improving distribution data of threatened species by combining acoustic monitoring and occupancy modelling. *Methods in Ecology and Evolution*, *7*, 1340–1348. https://doi.org/10.1111/2041-210X.12599

Chao, A, Ma, K. H., & Hsieh, T. C. (2015). *Species-Richness Prediction and Diversity Estimation with R. R package version 0.1.0. URL http://chao.stat.nthu.edu.tw/blog/software-download/.*

Chao, Anne. (1987). Estimating the Population Size for Capture-Recapture Data with Unequal Catchability. *Biometrics*, *43*(4), 783–791. https://doi.org/10.2307/2531532

Chen, L., Wu, S., & Pan, T. (2011). Variability of climate–growth relationships along an elevation gradient in the Changbai Mountain, northeastern China. *Trees*, *25*(6), 1133–1139. https://doi.org/10.1007/s00468-011-0588-0

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

Clymo, R. S., & Hayward, P. M. (1982). The Ecology of Sphagnum. In: Smith A.J.E. (eds) Bryophyte Ecology. *Springer, Dordrecht*, 229–289.

Colwell, R. K., Mao, C. X., & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, *85*(10), 2717–2727. https://doi.org/10.1890/03-0557

Colwell, Robert. K., & Lees, D. C. (2000). The mid-domain effect: Geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, *15*(2), 70–76. https://doi.org/10.1016/S0169-5347(99)01767-X

Connor, E. F., & McCoy, E. D. (1979). The Statistics and Biology of the Species-Area Relationship. *The American Naturalist*, *113*(6), 791–833. https://doi.org/10.1086/283438

Conway, C. J. (2009). *Standardized North American marsh bird monitoring protocols. U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, Arizona, USA.*

Conway, C. J. (2011). Standardized North American marsh bird monitoring protocol. *Waterbirds*, *34*, 319–346.

Cornell Lab of Ornithology. (2019). *All About Birds*. Cornell Lab of Ornithology, Ithaca, New York. https://www.allaboutbirds.org

Darras, K., Batáry, P., Furnas, B., Celis-Murillo, A., Van Wilgenburg, S. L., Mulyani, Y. A., & Tscharntke, 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

Dawson, A. (1985). The effect of restricting the daily period of food availability on testicular growth of Starlings Sturnus vulgaris. *Ibis*, *128*(4), 572–575. https://doi.org/10.1111/j.1474-919X.1986.tb02709.x

Dawson, D. K. (1979). *Bird communities associated with succession and management of lowland conifer forests. In DeGraaf, R.M. and K.E. Evans, compilers. Management of Northcentral and Northeastern Forests for Nongame Birds: Proceedings of the workshop; 1979 January 23-25; Minneapolis, MN, U.S.A. Gen. Tech. Rep. NC-51. St. Paul, MN, US Department of Agriculture, Forest Service, North Central Forest Experiment Station: 120-131.*

DeVault, T. L., Seamans, T. W., Blackwell, B. F., Lima, S. L., & Fernández-Juricic, E. (2018). Individual variation in avian avoidance behaviours in response to repeated, simulated vehicle approach. *Canadian Journal of Zoology*, *96*(5), 441–446. https://doi.org/10.1139/cjz-2017-0142

Dorazio, R. M., Royle, J. A., Söderström, B., & Glimskär, A. (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, *87*(4), 842–854. https://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2

Downing, D. J., & Pettapiece, W. W. (2006). *Natural Regions and Subregions of Alberta. Government of Albeta. Pub. No. T/852.*

Dybala, K. E., Engilis, A., Trochet, J. A., Engilis, I. E., & Truan, M. L. (2018). Evaluating Riparian Restoration Success: Long-Term Responses of the Breeding Bird Community in

California's Lower Putah Creek Watershed. *Ecological Restoration*, *36*(1), 76–85. https://doi.org/10.3368/er.36.1.76

Elbow River Watershed Patnership. (2009). *Elbow River Basin Water Management Plan*. Victoria Pleavin.

Erwin, K. L. (2009). Wetlands and global climate change: The role of wetland restoration in a changing world. *Wetlands Ecology and Management*, *17*(1), 71–84. https://doi.org/10.1007/s11273-008-9119-1

ESRI. (2011). *ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.*

Farina, A., Lattanzi, E., Malavasi, R., Pieretti, N., & Piccioli, L. (2011). Avian soundscapes and cognitive landscapes: Theory, application and ecological perspectives. *Landscape Ecology*, *26*(9), 1257–1267. https://doi.org/10.1007/s10980-011-9617-z

Foote, J. R., Mennill, D. J., Ratcliffe, S. M., & Smith, S. M. (2020). *Black-capped Chickadee (Poecile atricapillus), version 1.0. In Birds of the World (A. F. Poole, Editor)*. Cornell Lab of Ornithology, Ithaca, NY, USA.

Freemark, K. E., & Merriam, H. G. (1986). Importance of Area and Habitat Heterogeneity to Bird Assemblages in Temperate Forest Fragments. *Biological Conservation*, *36*, 115–141.

Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11.

Frommolt, K.-H. (2017). Information obtained from long-term acoustic recordings: Applying bioacoustic techniques for monitoring wetland birds during breeding season. *Journal of Ornithology*, *158*(3), 659–668. https://doi.org/10.1007/s10336-016-1426-3

Fuentes, E. R., & Jaksić, F. M. (1988). The Hump-Backed Species Diversity Curve: Why Has It Not Been Found among Land Animals? *Oikos*, *53*(1), 139. https://doi.org/10.2307/3565674

Gardali, T., Holmes, A. L., Small, S. L., Nur, N., Geupel, G. R., & Golet, G. H. (2006). Abundance Patterns of Landbirds in Restored and Remnant Riparian Forests on the Sacramento River, California, U.S.A. *Restoration Ecology*, *14*(3), 391–403. https://doi.org/10.1111/j.1526-100X.2006.00147.x

Gorham, E., & Janssens, J. A. (1990). Concepts of fen and bog re-examined in relation to bryophyte cover and the acidity of surface waters. *Acta SocietatisBotanicorum Poloniae*, *61*, 7–20.

Gotelli, N. J., & Colwell, R. K. (2011). *Estimating species richness. Pages 39–54 in A. E. Magurran and B. J. McGill, editors. Biological diversity: Frontiers in measurement and assessment. Oxford University Press, New York, New York, USA.* 16.

Government of Canada. (2019). *Species at risk public registry*. https://species-registry.canada.ca/index-en.html#/species?sortBy=commonNameSort&sortDirection=asc&pageSize=10

Graham, J. H., & Duda, J. J. (2011). The Humpbacked Species Richness-Curve: A Contingent Rule for Community Ecology. *International Journal of Ecology*, *2011*, 1–15. https://doi.org/10.1155/2011/868426

Gwinn, D. C., Allen, M. S., Bonvechio, K. I., Hoyer, M. V., & Beesley, L. S. (2016). Evaluating estimators of species richness: The importance of considering statistical error rates. *Methods in Ecology and Evolution*, *7*(3), 294–302. https://doi.org/10.1111/2041-210X.12462

Hingston, A., Wardlaw, T., Baker, S., & Jordan, G. (2018). Data obtained from acoustic recording units and from field observer point counts of Tasmanian forest birds are similar but not the same. *Australian Field Ornithology*, *35*, 30–39. https://doi.org/10.20938/afo35030039

Hoffmann, M. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, *330*, 1503–1509.

Hu, Y., & Cardoso, G. C. (2009). Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioral Ecology*, *20*(6), 1268–1273. https://doi.org/10.1093/beheco/arp131

Hutto, R. L., & Stutzman, R. J. (2009). Humans versus autonomous recording units: A comparison of point-count results. *Journal of Field Ornithology*, *80*(4), 387–398. https://doi.org/10.1111/j.1557-9263.2009.00245.x

Ibarra, J. T., & Martin, K. (2015). Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. *Biological Conservation*, *192*, 418–427. https://doi.org/10.1016/j.biocon.2015.11.008

Jumpingpound Creek Watershed Partnership. (2014). *Jumpingpound Creek: Integrated watershed management plan—Final*. Palliser Environmental Services Ltd.

Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity: Experimental evolution in variable environments. *Journal of Evolutionary Biology*, *15*(2), 173–190. https://doi.org/10.1046/j.1420-9101.2002.00377.x

Kattan, G. H., & Franco, P. (2004). Bird diversity along elevational gradients in the Andes of Colombia: Area and mass effects: Relationships between bird diversity,elevation and area. *Global Ecology and Biogeography*, *13*(5), 451–458. https://doi.org/10.1111/j.1466-822X.2004.00117.x

Kendeigh, S. C., & Fawver, B. J. (1981). Breeding Bird Populations in the Great Smoky Mountains, Tennessee and North Carolina. *The Wilson Bulletin*, *93*(2), 218–242.

Kessler, M., Herzog, S. K., Fjeldsa, J., & Bach, K. (2001). Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity Distributions*, *7*(1–2), 61–77. https://doi.org/10.1046/j.1472-4642.2001.00097.x

Kimmel, K., & Mander, Ü. (2010). Ecosystem services of peatlands: Implications for restoration. *Progress in Physical Geography*, *34*(4), 491–514. https://doi.org/10.1177/0309133310365595

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kusbach, A. (2010). *Terrestrial Ecosystem Classification in the Rocky Mountains , Northern Utah*. Utah State University.

La, V. T., & Nudds, T. D. (2016). Estimation of avian species richness: Biases in morning surveys and efficient sampling from acoustic recordings. *Ecosphere*, *7*(4). https://doi.org/10.1002/ecs2.1294

Laine, J., Vasander, H., & Sallantaus, T. (1995). Ecological effects of peatland drainage for forestry. *Environmental Reviews*, *3*(3–4), 286–303. https://doi.org/10.1139/a95-015

LaManna, J. A., & Martin, T. E. (2016). Logging impacts on avian species richness and composition differ across latitudes and foraging and breeding habitat preferences: Logging impacts differ across latitudes. *Biological Reviews*, *92*(3), 1657–1674. https://doi.org/10.1111/brv.12300

Lawton, J. H., MacGarvin, M., & Heads, P. A. (1987). Effects of Altitude on the Abundance and Species Richness of Insect Herbivores on Bracken. *The Journal of Animal Ecology*, *56*(1), 147. https://doi.org/10.2307/4805

Lawton, John H. (1999). Are There General Laws in Ecology? *Oikos*, *84*(2), 177. https://doi.org/10.2307/3546712

Leach, E. C., Burwell, C. J., Ashton, L. A., Jones, D. N., & Kitching, R. L. (2016). Comparison of point counts and automated acoustic monitoring: Detecting birds in a rainforest biodiversity survey. *Emu - Austral Ornithology*, *116*(3), 305–309. https://doi.org/10.1071/MU15097

Lee, S.-M., & Chao, A. (1994). Estimating Population Size Via Sample Coverage for Closed Capture-Recapture Models. *Biometrics*, *50*(1), 88–97. https://doi.org/10.2307/2533199

Lennon, J. J., Koleff, P., GreenwooD, J. J. D., & Gaston, K. J. (2001). The geographical structure of British bird distributions: Diversity, spatial turnover and scale. *Journal of Animal Ecology*, *70*(6), 966–979. https://doi.org/10.1046/j.0021-8790.2001.00563.x

Lieth, H. (1975). *Modeling the primary productivity of the world. Primary productivity of the biosphere (ed. By H. Lieth andR.H. Whittaker)*. Springer-Verlag, New Yor.

Locky, D. A. (2003). Peatlands and creatures great and small: Part I – Vertebrates. *The Wagner Natural Area Newsletter*, *17*(2), 3–6.

Lofts, B. (1964). Evidence of an Autonomous Reproductive Rhythm in an Equatorial Bird (Quelea quelea). *Nature*, *201*, 523–524.

Lomolino, Mark. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, *10*(1), 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

Lowther, P. E. (2020). *Alder Flycatcher (Empidonax alnorum), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors)*. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.aldfly.01

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press.

MacDonald, R. (2018). *Ghost River state of the watershed report*. Ghost Watershed Alliance Society.

https://www.ghostwatershed.ca/GWAS/ewExternalFiles/GHOSTSOW_FINAL_April2018s.pdf

Mackenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, *42*(6), 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

Marvelde, L. T., Schaper, S. V., & Visser, M. E. (2012). A Single Long Day Triggers Follicle Growth in Captive Female Great Tits (Parus major) in Winter but Does Not Affect Laying Dates in the Wild in Spring. *PLoS ONE*, *7*(4), e35617. https://doi.org/10.1371/journal.pone.0035617

Massa, B., Lo Valvo, M., & Catalisano, A. (1989). Bird communities on Mount Etna (Sicily, Italy). *Bolletino Di Zoologia*, *56*(4), 349–356. https://doi.org/10.1080/11250008909355661

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica: Species richness of small mammals along an elevational gradient. *Journal of Biogeography*, *31*(1), 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

McCain, C. M. (2005). Elevational gradients in diversity of small mammals. *Ecology*, *86*, 366–372. https://doi.org/10.1890/03-3147

McCain, C. M. (2007). Area and mammalian elevational diversity. *Ecology*, *88*(1), 76–86. https://doi.org/10.1890/0012-9658(2007)88[76:AAMED]2.0.CO;2

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, *18*(3), 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

McCain, C. M. (2010). Global analysis of reptile elevational diversity. *Global Ecology and Biogeography*. https://doi.org/10.1111/j.1466-8238.2010.00528.x

McCain, C. M., & Grytnes, J.-A. (2010). Elevational Gradients in Species Richness. *Encyclopedia of Life Sciences*. https://doi.org/10.1002/9780470015902.a0022548

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I., & Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, *82*(9), 2381–2396. https://doi.org/10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2

Montaño-Centellas, F. A., McCain, C., & Loiselle, B. A. (2020). Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients. *Global Ecology and Biogeography*, *29*(2), 232–245. https://doi.org/10.1111/geb.13021

Moore, T. R., Bubier, J. L., Heyes, A., & Flett, R. J. (1995). Methyl and Total Mercury in Boreal Wetland Plants, Experimental Lakes Area, Northwestern Ontario. *Journal of Environmental Quality*, *24*(5), 845–850. https://doi.org/10.2134/jeq1995.00472425002400050007x

Morrison, A., Westbrook, C. J., & Bedard-Haughn, A. (2015). Distribution of Canadian Rocky Mountain Wetlands Impacted by Beaver. *Wetlands*, *35*(1), 95–104. https://doi.org/10.1007/s13157-014-0595-1

Nally, R. M., & Horrocks, G. (2002). Proportionate spatial sampling and equal-time sampling of mobile animals: A dilemma for inferring areal dependence. *Austral Ecology*, *27*, 405–415.

Nichols, J. D., Hines, J. E., Sauer, J. R., Fallon, F. W., Fallon, J. E., & Heglund, P. J. (2000). A Double-Observer Approach for Estimating Detection Probability and Abundance from Point Counts. *The Auk*, *117*(2), 393–408.

Norton, M. R., & Hannon, S. J. (1997). Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Journal of Forest Restoration*, *27*, 10.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community Ecology Package. R package version 2.5-6. Https://CRAN.Rproject.or/package=vegan*.

Osuji, L. C., & Nwoye, I. (2007). An appraisal of the impact of petroleum hydrocarbons on soil fertility: The Owaza experience. *African Journal of Agricultural Research*, *2*(7), 318–324.

Patterson, B. D., Stotz, D. F., Solari, S., Fitzpatrick, J. W., & Pacheco, V. (1998). Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeatern Peru. *Journal of Biogeography*, *25*, 593–607.

Pavlacky, D. C., Possingham, H. P., & Goldizen, A. W. (2015). Integrating life history traits and forest structure to evaluate the vulnerability of rainforest birds along gradients of deforestation and fragmentation in eastern Australia. *Biological Conservation*, *188*, 89–99. https://doi.org/10.1016/j.biocon.2014.10.020

Preston, F. W. (1962). The Canonical Distribution of Commonness and Rarity: Part I. *Ecology*, *43*(2), 185. https://doi.org/10.2307/1931976

Priyadarshani, N., Marsland, S., & Castro, I. (2018). Automated birdsong recognition in complex acoustic environments: A review. *Journal of Avian Biology*, *49*(5), 1–27. https://doi.org/10.1111/jav.01447

Rahbek, C. (1995). The elevational gradient of species richness: A uniform pattern? *Ecography*, *18*(2), 200–205. https://doi.org/10.1111/j.1600-0587.1995.tb00341.x

Rahbek, C. (1997). The Relationship Among Area, Elevation, And Regional Species Richness In Neotropical Birds. *The American Naturalist*, *149*(5), 875–902. https://doi.org/10.1086/286028

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns: Scale and species-richness patterns. *Ecology Letters*, *8*(2), 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, *98*(8), 4534–4539. https://doi.org/10.1073/pnas.071034898

Randin, C. F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., & Guisan, A. (2009). Climate change and plant distribution: Local models predict high-elevation persistence. *Global Change Biology*, *15*(6), 1557–1569. https://doi.org/10.1111/j.1365-2486.2008.01766.x

Rands, M. R. W., Adams, W. M., Bennun, L., Butchart, S. H. M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J. P. W., Sutherland, W. J., & Vira, B. (2010). Biodiversity Conservation: Challenges Beyond 2010. *Science*, *329*(5997), 1298–1303. https://doi.org/10.1126/science.1189138

Reynolds, J. H., Thompson, W. L., & Russell, B. (2011). Planning for success: Identifying effective and efficient survey designs for monitoring. *Biological Conservation*, *144*(5), 1278–1284. https://doi.org/10.1016/j.biocon.2010.12.002

Rohde, K. (1992). Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. *Oikos*, *65*(3), 514. https://doi.org/10.2307/3545569

Rosenzweig, M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, New York.

RStudio Team. (2020). *RStudio: Integrated Development for R. RStudio, PBC, Boston, MA*. http://www.rstudio.com/

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary Production of the Central Grassland Region of the United States. *Ecology*, *69*(1), 40–45. https://doi.org/10.2307/1943158

Sandbrook, C., Fisher, J. A., Holmes, G., Luque-Lora, R., & Keane, A. (2019). The global conservation movement is diverse but not divided. *Nature Sustainability*, *2*(4), 316–323. https://doi.org/10.1038/s41893-019-0267-5

Sanders, N. J. (2002). Elevational gradients in ant species richness: Area, geometry, and Rapoport's rule. *Ecography*, *25*(1), 25–32. https://doi.org/10.1034/j.1600-0587.2002.250104.x

Schlesinger, W. H. (1991). *Biogeochemistry: An analysis of globalchange*. Academic Press, San Diego, CA, USA.

Sekercioglu, C. H. (2002). Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biological Conservation*, 12.

Semenchuk, G. (1992). *Atlas of the Breeding Birds in Alberta*. Federation of Alberta Naturalists, Edmonton, AB, Canada.

Shonfield, J., & Bayne, E. M. (2017). Autonomous recording units in avian ecological research: Current use and future applications. *Avian Conservation and Ecology*, *12*(1), art14. https://doi.org/10.5751/ACE-00974-120114

Shonfield, J., Heemskerk, S., & Bayne, E. M. (2018). Utility of Automated Species Recognition For Acoustic Monitoring of Owls. *Journal of Raptor Research*, *52*(1), 42. https://doi.org/10.3356/JRR-17-52.1

Sidie-Slettedahl, A. M., Jensen, K. C., Johnson, R. R., Arnold, T. W., Austin, J. E., & Stafford, J. D. (2015). Evaluation of autonomous recording units for detecting 3 species of secretive marsh birds. *Wildlife Society Bulletin*. https://doi.org/10.1002/wsb.569

Sims, M., Bjorkland, R., Mason, P., & Crowder, L. B. (2008). Statistical power and sea turtle nesting beach surveys: How long and when? *Biological Conservation*, *141*(12), 2921–2931. https://doi.org/10.1016/j.biocon.2008.07.021

Squeo, F. A., Warner, B. G., Aravena, R., & Espinoza, D. (2006). Bofedales: High altitude peatlands of the central Andes. *Revista Chilena de Historia Natural*, *79*, 245–255. https://doi.org/10.4067/S0716-078X2006000200010

Stevens, G. C. (1992). The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude. *The American Naturalist*, *140*(6), 893–911. https://doi.org/10.1086/285447

Stockwell, S. S. (1994). *Habitat selection and community organization of birds in eight peatlands in Maine. Ph.D. thesis, University of Maine, Orono, ME, U.S.A.*

Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 261–280. https://doi.org/10.1146/annurev-ecolsys-110512-135750

Swiston, K. A., & Mennill, D. J. (2009). Comparison of manual and automated methods for identifying target sounds in audio recordings of Pileated, Pale-billed, and putative Ivory-billed woodpeckers. *Journal of Field Ornithology*, *80*(1), 42–50. https://doi.org/10.1111/j.1557-9263.2009.00204.x

Takakai, F., Morishita, T., Hashidoko, Y., Darung, U., Kuramochi, K., Dohong, S., Limin, S. H., & Hatano, R. (2006). Effects of agricultural land-use change and forest fire on N_2O emission from tropical peatlands, Central Kalimantan, Indonesia. *Soil Science and Plant Nutrition*, *52*(5), 662–674. https://doi.org/10.1111/j.1747-0765.2006.00084.x

Taylor, M. D. M. R. B., & Banos, J. C. B. (2014). Estimating species richness and density of a bird community in a coastal lagoon on the Mexican Pacific. *Huitzil*, *15*(2), 64–81.

Tegeler, A. K., Morrison, M. L., & Szewczak, J. M. (2012). Using extended-duration audio recordings to survey avian species. *Wildlife Society Bulletin*, *36*(1), 21–29. https://doi.org/10.1002/wsb.112

Terborgh, J. (1977). Bird Species Diversity on an Andean Elevational Gradient. *Ecology*, *58*(5), 1007–1019. https://doi.org/10.2307/1936921

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: Animal species diversity driven by habitat heterogeneity. *Journal of Biogeography*, *31*(1), 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

The Bow River Project Research Consortium. (2010). *Bow River Project Final Report*. Alberta Water Research Institute.

Thompson, L. S. (1978). Species Abundance and Habitat Relations of an Insular Montane Avifauna. *The Condor*, *80*(1), 1. https://doi.org/10.2307/1367785

Thompson, S. A., & Thompson, G. G. (2010). *Terrestrial vertebrate fauna assessments for ecological impact assessments*. Terrestrial Ecosystems, Mt Claremont, Western Australia.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey.

Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, *379*(6567), 718–720.

Time and Date AS. (2019). *Canmore, Alberta, Canada—Sunrise, Sunset, and Daylength*. https://www.timeanddate.com/sun/@5914894

Turetsky, M., Wieder, K., Halsey, L., & Vitt, D. (2002). Current disturbance and the diminishing peatland carbon sink. *Geophysical Research Letters*, *29*(11), 1526. https://doi.org/10.1029/2001GL014000

Ugland, K. I., Gray, J. S., & Ellingsen, K. E. (2003). The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, *72*(5), 888–897. https://doi.org/10.1046/j.1365-2656.2003.00748.x

U.S. Fish and Wildlife Service. (2018). *Birds, bird watching and the U.S. economy*. U.S. Fish and Wildlife Service. https://www.fws.gov/birds/bird-enthusiasts/bird-watching/valuing-birds.php#:~:text=More%20than%2045%20million%20people,a%20total%20of%20nearly%20%2480

Vellend, M. (2010). Conceptual Synthesis in Community Ecology. *The Quarterly Review of Biology*, *85*(2), 183–206. https://doi.org/10.1086/652373

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., & Parmenter, R. (1999). The Relationship Between Productivity and Species Richness. *Annual Review of Ecology and Systematics*, *30*(1), 257–300. https://doi.org/10.1146/annurev.ecolsys.30.1.257

Warner, B. G., & Asada, T. (2006). Biological diversity of peatlands in Canada. *Aquatic Sciences*, *68*(3), 240–253. https://doi.org/10.1007/s00027-006-0853-2

Watson, D. M., Mac Nally, R., & Bennett, A. F. (2000). The avifauna of severely fragmented, Buloke Allocasuarina luehmannii woodland in western Victoria, Australia. *Pacific Conservation Biology*, *6*, 46–60.

White, J. D., & Running, S. W. (1994). Testing scale dependent assumptions in regional ecosystem simulations. *Journal of Vegetation Science*, *5*(5), 687–702. https://doi.org/10.2307/3235883

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *TAXON*, *21*(2–3), 213–251. https://doi.org/10.2307/1218190

Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4*. https://ggplot2.tidyverse.org.

Wiens, J. A. (1974). Habitat Heterogeneity and Avian Community Structure in North American Grasslands. *American Midland Naturalist*, *91*(1), 195. https://doi.org/10.2307/2424522

Wildlife Acoustics. (2018). *Song Meter, SM4*. Wildlife Acoustics, Maynard, Massachusetts, USA. https://www.wildlifeacoustics.com/products/song-meter-sm4

Wilsey, B. J., & Potvin, C. (2000). Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology*, *81*(4), 887–892. https://doi.org/10.1890/0012-9658(2000)081[0887:BAEFIO]2.0.CO;2

Winner, W. E., Bewley, J. D., Krouse, H. R., & Brown, H. M. (1978). Stable sulfur isotope analysis of SO2 pollution impact on vegetation. *Oecologia*, *36*(3), 351–361. https://doi.org/10.1007/BF00348061

Winternitz, B. L. (1976). Temporal Change and Habitat Preference of Some Montane Breeding Birds. *The Condor*, *78*(3), 383–393. https://doi.org/10.2307/1367700

Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, *40*(12), 2310–2323. https://doi.org/10.1111/jbi.12177

Wyndham, E. (1986). Length of Birds' Breeding Seasons. *The American Naturalist*, *128*(2), 155–164. https://doi.org/10.1086/284551

Yip, D. A., Leston, L., Bayne, E. M., Sólymos, P., & Grover, A. (2017). Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. *Avian Conservation and Ecology*, *12*(1), art11. https://doi.org/10.5751/ACE-00997-120111

Zoltai, S. C., & Vitt, D. H. (1995). Canadian wetlands: Environmental gradients and classification. *Vegetatio*, *118*(1–2), 131–137. https://doi.org/10.1007/BF00045195

Zuberogoitia, I., Zabala, J., & Martínez, J. E. (2011). Bias in little owl population estimates using playback techniques during surveys. *Animal Biodiversity and Conservation*, 7.

Appendix A. AIC, AICc values and regression output table

Table 5.1 Akaike Information Criterion (AIC) framework and regression analysis output from each of the three model competitions that compare McCain's general richness-elevation relationship patterns to avian species richness in valley-bottom mountain peatlands in Southwestern Alberta. Model competition 1 is the richness-elevation relationship using linear, quadratic, and cubic functions to depict the richness-elevation pattern. Model competition 2 is the richness-elevation relationship controlling for the richness-area relationship using linear, quadratic, and cubic functions to depict the richness-elevation pattern. Model competition 3 is the richness-Natural Subregion relationship using general linear model (Natural Subregion), and a general linear model while controlling for the richness-area relationship (controlling for area) to compare to the best models from competition 1 and competition 2. For each model competition AIC and AICc, R^2 and adjusted R^2, p-value and coefficient values were calculated and compared to determine the best model.

Model Competition 1	**AIC**	**AICc**	**R^2**	**Adjusted R^2**	**p-value**	**Coefficient values**
Linear	147.5	148.7	0.521	0.499	<0.001	$y = -0.0285x + 73.38$
Quadratic	144.1	146.2	0.618	0.582	<0.001	$y = 9.488x10^{-5}x^2 – 0.344x + 333.0$
Cubic	142.5	145.8	0.671	0.622	<0.001	$y = 3.818x10^{-7}x^3 – 1.825x10^{-3}x^2 + 2.856x – 1.435$
Model Competition 2	**AIC**	**AICc**	**R^2**	**Adjusted R^2**	**p-value**	**Coefficient values**
Linear	176.4	177.6	0.419	0.392	0.001	$y = -0.042x + 130.8$
Quadratic	177.5	179.6	0.439	0.386	0.002	$y = 7.177x10^{-5}x^2 – 0.281x + 327.2$
Cubic	179.1	182.4	0.450	0.367	0.007	$y = 2.822x10^{-7}x^3 – 1.347x10^{-3}x^2 + 2.084x – 979.3$

Model Competition 3	**AIC**	**AICc**	**Multiple R^2**	**Adjusted R^2**	**p-value**	**Coefficient values**
Natural Subregion	140.0	141.2	0.649	0.633	<0.001	y = -10.75x + 31.75
Natural Subregion after Controlling for area	169.8	171.0	0.559	0.539	<0.001	y = -16.53x + 69.22

Appendix B. Idealized species accumulation curve

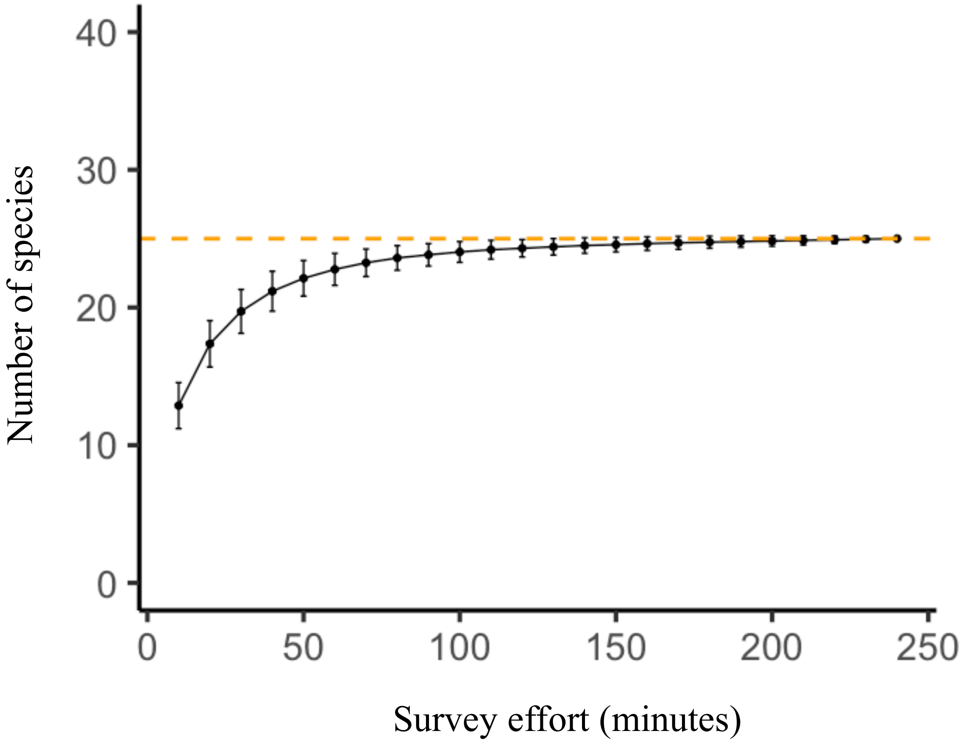

Figure 5.1 Example of an idealized species accumulation curve depicting the theoretical number of bird species in a mountain peatland in Alberta as a cumulative total over a 240 minute survey period. The dashed line indicates the plateau for this logarithmic curve, which is reached by the end of the survey.

Appendix C. Avian species conservation status

Table 5.2 Four letter alpha code for the 74 avian species and each species' conservation status in Canada (Government of Canada, 2019) and Alberta (Alberta Environment and Parks, 2015).

Species	Canada	Alberta 2015 status	Comments/ threats
ALFL	Not at risk	Sensitive	
AMCR	Not at risk	Secure	
AMRO	Not at risk	Secure	
BAOW	Not at risk	Sensitive	- Sensitive to forest fragmentation (Alberta Environment and Parks, 2015)
BARS	Threatened 2017	Sensitive	- Decline not well understood (Government of Canada, 2019) - Population declining (Alberta Environment and Parks, 2015)
BCCH	Not at risk	Secure	
BHCO	Not at risk	Secure	
BHGR	Not at risk	Secure	
BLJA	Not at risk	Secure	
BOCH	Not at risk	Secure	
CANG	Not at risk	Secure	
CAQU	Not at risk	Incidental	
CAVI	Not at risk	Undetermined	
CAWA	Threatened 2010	At risk	- Loss of wintering ground (Government of Canada, 2019) - Possible vulnerability to habitat loss (Alberta Environment and Parks, 2015)
CCSP	Not at risk	Secure	
CHSP	Not at risk	Secure	

CLNU	Not at risk	Sensitive	- Dependent on pine species and susceptible to West Nile Virus (Alberta Environment and Parks, 2015)
COLO	Not at risk 1997	Secure	- Threats from changing lake conditions (Government of Canada, 2019)
COME	Not at risk	Secure	
CORA	Not at risk	Secure	
COYE	Not at risk	Sensitive	- Sensitive to habitat threats (Alberta Environment and Parks, 2015)
DEJU	Not at risk	Secure	
GCKI	Not at risk	Secure	
GCSP	Not at risk	Secure	
GRAJ	Not at risk	Secure	
HETH	Not at risk	Secure	
LEFL	Not at risk	Sensitive	- Possible threat from changing wintering grounds (Alberta Environment and Parks, 2015)
LESP	Not at risk	Secure	
LEYE	Not at risk	Secure	
LISP	Not at risk	Secure	
MALL	Not at risk	Secure	
MOCH	Not at risk	Secure	
MODO	Not at risk	Secure	
NESP	Not at risk	Secure	
NOFL	Not at risk	Secure	
NOMO	Not at risk	Secure	

NOPO	Not at risk	Sensitive	- Sensitive to change in breeding habitat (Alberta Environment and Parks, 2015)
NOWA	Not at risk	Secure	
OCWA	Not at risk	Secure	
OSFL	Special concern 2018	May be at risk	- Possible threat from changing breeding grounds and decline of aerial insect prey items (Government of Canada, 2019)
OVEN	Not at risk	Secure	
PISI	Not at risk	Secure	
PIWO	Not at risk	Sensitive	- Only nests in mature to old-growth trees (Alberta Environment and Parks, 2015)
RBNU	Not at risk	Secure	
RCKI	Not at risk	Secure	
RNSA	Not at risk	Undetermined	
ROPT	Not at risk	Accidental	
RUGR	Not at risk	Secure	
RWBL	Not at risk	Secure	
SACR	Not at risk	Sensitive	- Sensitive to wetland loss and human disturbance (Alberta Environment and Parks, 2015)
SAPH	Not at risk	Secure	
SAVS	Not at risk	Secure	
SORA	Not at risk	Sensitive	- Sensitive to wetland loss (Alberta Environment and Parks, 2015)
SPSA	Not at risk	Secure	
SPTO	Not at risk	Secure	
STJA	Not at risk	Secure	

SWTH	Not at risk	Secure	
TEWA	Not at risk	Secure	
TRES	Not at risk	Secure	
VATH	Not at risk	Secure	
VEER	Not at risk	Secure	
VGSW	Not at risk	Secure	
WAVI	Not at risk	Secure	
WCSP	Not at risk	Secure	
WEME	Not at risk	Secure	
WIFL	Not at risk	Secure	
WISN	Not at risk	Secure	
WIWA	Not at risk	Secure	
WIWR	Not at risk	Secure	
WTSP	Not at risk	Secure	
WWPE	Not at risk	May be at risk	
YBSA	Not at risk	Secure	
YEWA	Not at risk	Secure	
YRWA	Not at risk	Secure	

Appendix D. Avian species presence and absence recorded

Table 5.3 Four letter alpha code for the 74 avian species present (1) or absent (0) in the 12 Montane Natural Subregion mountain peatlands.

	101	102	106	120	121	122	125	126	127	128	130	131
ALFL	1	1	1	0	1	0	1	0	1	0	0	1
AMCR	0	0	0	1	0	0	0	0	0	0	0	0
AMRO	1	1	1	1	1	1	1	1	1	1	1	1
BAOW	1	0	0	0	0	0	0	0	0	0	0	0
BARS	0	1	0	0	0	0	1	0	0	0	0	1
BCCH	1	1	1	1	1	1	1	1	1	1	1	0
BHCO	1	1	1	1	1	1	1	1	1	1	1	1

BHGR	0	0	0	0	0	1	0	0	0	0	0	0
BLJA	1	0	1	0	0	0	0	0	1	0	0	0
BOCH	0	0	0	0	0	0	0	0	0	0	0	0
CANG	1	1	1	1	1	1	1	1	1	1	1	1
CAQU	0	0	0	0	0	0	1	0	0	0	0	0
CAVI	0	0	0	0	0	0	0	1	0	0	1	0
CAWA	0	1	1	0	1	1	1	0	1	0	1	1
CCSP	1	0	1	1	1	1	1	0	0	1	1	1
CHSP	1	1	1	1	1	1	1	1	1	1	1	1
CLNU	0	0	0	0	0	0	0	0	0	0	0	0
COLO	1	0	0	0	0	0	0	0	0	0	0	1
COME	0	0	0	0	0	0	0	0	1	1	0	0
CORA	1	1	1	0	1	1	1	1	1	1	1	1
COYE	1	1	1	1	1	0	1	0	1	1	1	1
DEJU	1	1	1	1	1	1	1	1	1	1	1	1
GCKI	0	1	1	1	1	1	0	1	0	0	0	0
GCSP	0	0	0	0	0	0	0	0	1	0	0	0
GRAJ	1	1	1	1	1	1	1	1	1	1	1	1
HETH	0	0	1	0	1	0	0	0	0	0	0	1
LEFL	0	0	0	0	1	0	0	0	0	0	0	1
LESP	1	1	0	0	0	1	0	0	0	0	0	0
LEYE	0	1	0	1	1	0	1	1	1	0	0	1
LISP	1	1	1	1	1	1	1	1	1	1	1	1
MALL	1	1	1	1	0	0	0	1	1	1	0	0
MOCH	0	0	0	0	1	1	0	0	0	0	0	0
MODO	0	0	0	0	0	0	0	0	0	0	0	1
NESP	0	0	0	0	0	0	0	0	0	0	0	0
NOFL	0	0	0	0	0	0	0	0	0	1	0	0
NOMO	0	0	0	0	0	0	0	0	0	1	0	0
NOPO	0	0	1	0	0	0	0	0	0	0	0	0

NOWA	1	0	1	0	0	0	0	0	1	0	0	1
OCWA	0	0	0	1	1	0	0	0	1	1	1	0
OSFL	0	1	0	0	0	0	1	1	0	1	1	1
OVEN	0	0	0	0	1	0	0	0	0	0	0	0
PISI	1	1	1	1	1	1	1	1	1	1	1	1
PIWO	1	1	1	0	1	1	1	1	1	1	0	1
RBNU	1	1	1	0	1	1	1	1	1	1	0	1
RCKI	1	1	1	1	1	1	1	1	1	1	1	1
RNSA	0	0	0	0	1	1	0	0	0	0	0	0
ROPT	0	0	0	0	0	0	0	0	0	1	0	0
RUGR	0	0	0	0	1	0	0	0	0	0	0	0
RWBL	1	1	1	0	0	0	0	0	1	1	1	1
SACR	0	0	0	0	0	0	0	0	1	0	0	1
SAPH	0	1	0	0	0	0	0	0	0	0	0	0
SAVS	1	0	0	1	0	0	0	0	0	0	0	1
SORA	1	0	1	0	0	0	0	0	0	1	0	1
SPSA	1	0	1	1	1	1	1	0	1	1	1	1
SPTO	0	0	0	0	0	1	0	0	0	0	0	0
STJA	0	0	1	0	0	0	0	0	1	0	0	0
SWTH	0	0	1	1	1	1	1	1	1	1	1	1
TEWA	1	1	1	0	1	0	0	0	1	0	0	0
TRES	0	0	0	0	0	0	0	0	0	0	0	1
VATH	1	1	1	1	1	1	1	1	1	1	1	0
VEER	0	0	0	0	0	0	0	0	0	0	0	0
VGSW	0	0	0	0	0	0	1	0	0	0	0	0
WAVI	0	0	0	0	0	0	0	0	0	0	0	0
WCSP	1	1	1	1	1	1	1	0	0	1	1	1
WEME	0	0	0	0	0	0	0	0	0	0	0	1
WIFL	1	0	1	0	0	0	0	0	0	1	0	1
WISN	1	1	1	1	1	1	1	0	1	1	1	1

WIWA	1	1	1	0	0	1	1	0	1	1	1	1
WIWR	0	0	0	0	0	0	0	1	0	0	1	0
WTSP	1	1	1	0	1	0	0	1	1	1	1	1
WWPE	0	1	0	1	1	1	0	0	0	1	0	0
YBSA	0	0	0	0	1	0	0	0	0	1	0	0
YEWA	1	0	0	1	0	0	1	0	0	0	0	0
YRWA	1	1	1	1	1	1	1	1	1	1	1	1

Table 5.4 Four letter alpha code for the 74 avian species present (1) or absent (0) in the 12 Subalpine Natural Subregion mountain peatlands.

	201	203	204	220	221	222	223	224	225	226	227	230
ALFL	0	0	0	0	1	0	0	0	0	0	0	0
AMCR	0	0	0	0	0	1	0	0	0	0	0	1
AMRO	1	1	1	1	1	1	1	1	1	1	1	1
BAOW	0	0	0	0	0	0	0	0	0	0	0	0
BARS	0	0	0	0	0	0	0	0	0	0	0	0
BCCH	1	0	1	1	0	1	1	0	0	1	1	1
BHCO	0	1	1	1	1	1	1	1	1	0	0	1
BHGR	0	0	0	0	0	0	0	0	0	0	0	0
BLJA	0	0	0	0	0	0	0	0	0	0	0	0
BOCH	0	0	0	0	0	1	0	0	0	0	0	0
CANG	1	0	0	0	0	0	0	1	0	1	1	0
CAQU	0	0	0	0	0	0	0	0	0	0	0	0
CAVI	1	0	0	0	0	0	0	0	0	0	0	0
CAWA	0	0	0	0	0	0	0	0	0	0	0	0
CCSP	1	1	0	0	0	0	0	0	1	0	0	0
CHSP	1	1	1	1	1	1	1	1	1	1	1	1
CLNU	0	0	0	0	0	0	1	0	0	0	0	0
COLO	0	1	1	0	0	0	0	0	0	0	0	0
COME	0	0	0	0	0	0	0	0	0	0	0	0

CORA	0	0	1	0	0	1	1	1	1	1	1	0
COYE	0	0	0	0	0	0	0	0	0	1	0	0
DEJU	1	1	0	1	1	1	1	1	0	1	1	1
GCKI	1	1	0	0	0	1	1	0	0	1	1	0
GCSP	0	0	0	0	0	0	0	0	0	0	0	0
GRAJ	1	1	1	1	1	1	1	1	1	1	1	1
HETH	1	0	1	0	0	0	1	0	0	1	1	0
LEFL	0	0	0	0	0	0	0	0	0	0	0	0
LESP	0	0	0	0	0	0	0	0	0	0	0	0
LEYE	0	1	0	0	0	0	0	0	0	0	0	0
LISP	1	1	1	1	1	1	1	1	1	1	1	1
MALL	0	0	0	0	0	0	0	0	0	0	1	0
MOCH	0	0	0	0	1	0	0	0	0	1	0	0
MODO	0	0	0	0	0	0	0	0	0	0	0	0
NESP	0	0	0	0	0	1	0	0	1	0	0	0
NOFL	0	0	0	0	0	0	0	0	0	1	1	0
NOMO	0	0	0	0	0	0	0	0	0	0	0	0
NOPO	0	0	1	0	0	0	0	0	0	0	0	0
NOWA	1	1	0	0	1	0	0	0	1	0	1	0
OCWA	0	0	0	0	1	0	1	0	0	0	0	0
OSFL	0	0	1	0	0	0	1	0	0	0	0	1
OVEN	0	0	0	0	0	0	0	0	0	0	0	0
PISI	1	1	1	1	1	1	1	1	1	1	1	1
PIWO	0	0	1	0	1	1	0	0	0	1	1	0
RBNU	1	0	1	0	0	1	0	0	1	1	1	0
RCKI	1	1	1	1	1	1	1	1	1	1	1	1
RNSA	0	0	0	0	0	0	0	0	0	0	0	0
ROPT	0	0	0	0	0	0	0	0	0	0	0	0
RUGR	0	0	0	0	0	0	1	0	0	0	0	0
RWBL	0	0	0	0	0	0	1	0	1	0	0	0

SACR	0	0	0	0	0	0	0	0	0	0	0	0
SAPH	0	0	0	0	0	0	0	0	0	0	0	0
SAVS	1	0	0	0	0	0	0	1	0	1	0	0
SORA	0	0	0	0	0	0	1	0	0	0	0	0
SPSA	1	1	0	1	0	1	0	0	1	1	1	1
SPTO	0	0	0	0	0	0	0	0	0	0	0	0
STJA	0	0	0	0	0	0	0	0	0	0	0	0
SWTH	1	1	1	1	1	1	1	1	1	1	1	1
TEWA	0	0	0	0	0	0	0	0	0	0	0	0
TRES	0	0	0	0	0	0	0	0	0	0	0	0
VATH	1	1	1	1	1	1	1	1	1	1	1	1
VEER	1	0	0	0	0	0	0	0	0	0	0	0
VGSW	0	1	0	0	0	0	0	0	0	0	0	0
WAVI	0	0	0	0	0	0	0	1	0	0	0	0
WCSP	1	1	0	1	1	1	1	1	1	1	1	1
WEME	0	0	0	0	0	0	0	0	0	0	0	0
WIFL	0	0	0	0	0	0	0	0	1	0	0	0
WISN	1	0	1	1	1	1	1	1	0	1	1	0
WIWA	1	1	1	0	1	0	1	1	1	1	1	1
WIWR	0	0	0	0	1	0	0	0	0	0	0	0
WTSP	0	0	0	0	0	0	0	0	0	0	1	0
WWPE	0	0	0	0	0	0	0	0	0	0	0	0
YBSA	0	0	0	0	0	0	0	0	0	0	0	0
YEWA	1	0	0	0	0	0	1	0	0	0	0	0
YRWA	1	1	1	1	1	1	1	1	1	1	1	1