Vegetation diversity in mountain peatland systems

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.

I understand that my thesis may be made electronically available to the public.

Statement of Contributions

While I am the sole author of this thesis, I acknowledge the contribution of Dr. Rebecca Rooney in assisting with editing and providing feedback for my thesis manuscript. Dr. Rebecca Rooney will be invited to be a co-author when publishing the manuscripts of my data chapters.

Abstract

Mountain valley bottom peatlands are poorly studied systems, particularly in Alberta, Canada, where the provincial inventory has neither mapped nor characterized them. Nonetheless, these ecosystems provide valuable ecosystem services, including supporting biodiversity. Though elevation gradients are well studied in ecology, little is known about the drivers that determine the patterns of plant distribution in peatlands along an elevation gradient, nor do we fully understand the factors that influence plant survey efficacy and detection probabilities in peatland ecosystems. To fill these knowledge gaps, I conducted vegetation surveys at twenty mountain valley bottom peatlands sites ranging from 1415 – 1959 meters above sea level in the upper Bow River basin area of the Albertan Rocky Mountains. I recorded plant species identities and abundance data at each site using quadrat-transect surveys, and 15-minute timed walk surveys conducted by two simultaneous, independent observers. I present my results in two chapters.

In Chapter 2, I describe and characterize the peatland vegetation communities along an elevation gradient to determine if the distribution of plant species is contingent on elevation, and to characterize how the distributions of plant species change along an elevation gradient. Contrary to my expectations, elevation was not the most important factor in predicting variation among my vegetation communities, based on my Mantel test, dbRDA and NMS ordination results. Rather, I found that pH and conductivity were more strongly associated with my NMS axes to explain more variation among my vegetation communities. Plant species responded individualistically to elevation in my LOESS elevation niche plots, suggesting a stronger effect of abiotic filters relative to biotic filters in structuring plant community composition in my mountain peatlands (i.e. the Gleasonian view of communities). Yet, I present some evidence that co-occurring species formed predictable, distinct assemblages in my mountain peatlands (i.e. the Clementsian view of communities), derived from my indicator species analysis.

In Chapter 3, I determine potential sources of detection errors in peatland vegetation surveys and recommend an optimal strategy to minimize detection errors. Site species richness of vascular plants estimated using timed-walk surveys showed some pseudoturnover (i.e. differences in species lists between observers caused by imperfect detections such as errors of omission or errors of commission), but only using short survey times (< 10 minutes). Pseudoturnover averaged about 24% among my twenty sites, which was comparable to reported values in the literature, but these errors were ultimately corrected by using two independent observers. I also compare the timed-walk surveys to quadrat-transect surveys. I find little survey-method bias in missed detections, using a two-way repeated measures ANOVA to compare missed detections grouped by the growth forms (i.e. forb, graminoid, shrub and tree), and an indicator species analysis to compare the species detections by each survey approach. However, the two methods did identify distinct species and each has unique advantages and disadvantages in its implementation. Thus, I suggest future surveys of peatland vegetation employ combined survey approaches to ensure a robust and accurate measure of species richness and biodiversity.

My research contributes to a better understanding of these mountain valley bottom peatlands by providing valuable vegetation data to ecologists and hydrologists studying peatlands in this region. Also, it provides methodological recommendations to future surveyors when studying peatlands to minimize their imperfect detections. My species lists and

biodiversity data support stakeholders in determining the health of these peatlands and their abilities to provide ecosystem services and may also have conservation implications by identifying vulnerable species to extirpation.

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Table of Contents

List of Figures

List of Tables

List of Abbreviations

ACE	Abundance-based coverage estimator
AICc	Akaike information criterion corrected for small sample sizes
ANOVA	Analysis of variance
Chao1	Incidence-based Chao index
Chao2	Abundance-based Chao index
dbRDA	Distance-based redundancy analysis (ordination)
GLM	General linear model
ICE	Incidence-based coverage estimator
Jack1	First-order Jackknife
LOESS	Locally estimated scatterplot smoothing
m a.s.l.	Meters above sea level
NMS	Nonmetric multidimensional scaling (ordination)
SLA	Specific leaf area

1 Introduction: Thesis context and literature

1.1 Introduction

1.1.1 Peatland formation and classification

Peatlands are wetlands characterized by peat formation, resulting from high and relatively stable water tables that keep decomposition rates consistently below primary production to form peat, the incompletely decayed organic material of plants (Clymo et al. 1998, Limpens et al. 2008, Keddy 2010). North American peatlands are commonly formed by three processes: primary peat formation, when peat accumulates directly on newly exposed wet mineral soil, for instance following glacial retreat (Lacourse et al. 2019); paludification, the accumulation of peat directly on inundated flat to gently sloping mineral soils (Craft 2016), occurring due to an increase in local water table to allow for peat-forming plants like *Sphagnum* mosses to invade an existing plant community (Lacourse et al. 2019); and terrestrialization, where a water body is gradually filled by sediment and peat, converting a basin into a peatland (Craft 2016, Lacourse et al. 2019). These processes and the formation of peatlands can span a timescale of thousands of years (Harbert and Cooper 2017).

Peatlands are generally classified as either bogs or fens (Keddy 2010). Bogs are ombrotrophic (i.e. dependent on rainfall) and are thus acidic (pH < 4.5), nutrient poor (Alberta Environment and Sustainable Resource Development (ESRD) 2015) and have low conductivity due to low concentrations of dissolved minerals (Bridgham et al. 1996, Wheeler and Proctor 2000, Keddy 2010). Bogs are commonly dominated by Sphagnaceae (i.e. *Sphagnum* family of mosses), sedges, and ericaceous shrubs or evergreen trees that can tolerate the acidic conditions (Keddy 2010). Fens are minerotrophic, with some proportion of groundwater input to their water budgets (Keddy 2010, Chimner et al. 2010). Depending on their groundwater source, fens vary

along the acidity-alkalinity gradient and are classified as either a poor fen, moderate-rich fen, or extreme-rich fen (Alberta Environment and Sustainable Resource Development (ESRD) 2015). They are generally circumneutral to slightly basic in pH and are more conductive due to a higher concentration of cations supplied by mineral soils (Cooper and Andrus 1994, Bridgham et al. 1996, Keddy 2010). Poor fens have a pH of less than 5.5 and conductivity less than 0.1 mS/cm; moderate-rich fens have a pH between 5.5 and 7.0 and conductivity between 0.1 to 0.25 mS/cm; and extreme-rich fens have a pH greater than 7.0 and conductivity between 0.25 to 20 mS/cm (Alberta Environment and Sustainable Resource Development (ESRD) 2015). Fens are commonly dominated by moss species of the Amblystegiaceae family (i.e. brown mosses), sedges, and wetland-obligate grasses (Zoltai and Vitt 1990, Keddy 2010).

1.1.2 Mountain peatlands

Although minimum peat depths of 30 centimeters are commonly used for assessing global inventories of peatlands, there are no real minimum peat depths for a site to be an actual peatland (Joosten and Clarke 2002, Craft 2016). Such may be the case for many mountain peatlands where peat depths may not be as thick due to layering of rocks deposited into peatlands by rockslide or avalanche events (Woodhurst and de Scally 2018). Mountain peatlands differ from boreal peatlands in that mountains may provide high annual precipitation, cool temperatures, and high humidity (Cooper et al. 2012). Additionally, slopes can be extreme, and aspect may also have a big effect on day length, growing seasons, and seasonal temperature fluctuations (Cooper et al. 2012). These conditions of mountain peatlands may enhance regional biodiversity by providing habitat for species that usually have more Northern ranges at more Southern latitudes, such as species usually found thousands of kilometers North in the boreal (Schimelpfenig et al. 2014). Compared to boreal peatlands, mountain peatlands and typically

small, confined by their valleys, steep slopes and small catchment sizes (Cooper et al. 2012).

Most mountain peatlands, being commonly fens, occur on slopes supported by groundwater

discharge within depressions made by glaciers that have since retreated (Squeo et al. 2006,

Chimner et al. 2010). Thus, water table stability is important and can influence mountain

peatland function and vegetation composition (Schimelpfenig et al. 2014). At higher elevations,

the presence of permafrost can also influence peatland dynamics and function, but in lower

elevations, where my work was focused, permafrost is discontinuous or absent, and not pertinent

(Gruber et al. 2015). Nonetheless, these mountain peatlands share the micro-topographical

characteristics of typical peatlands, such as hummocks and hollows (Harbert and Cooper 2017).

Mountain peatlands are often remote, with access to sites being seasonal (i.e. after snow has

melted, mountain roads re-open, and avalanche advisories are lifted).

1.2 Peatland ecosystem services

Peatlands provide many important ecosystem services including global carbon sinks

(Clymo et al. 1998, Roulet 2000, Limpens et al. 2008, Minayeva and Sirin 2012), mitigation of

major flood and drought events (Richardson and Siccama 2000, Bacon et al. 2017), and habitat

to support abundant biodiversity of plants and animals (Keddy et al. 2009).

1.2.1 Carbon storage

Even though peatlands cover only 3% of the Earth's land surface (Limpens et al. 2008),

they contain more carbon than the entire forest biomass in the world (Joosten 2015). This

represents an estimated 21% of the organic carbon stock globally (Scharlemann et al. 2014), with

literature estimates of carbon storage by global peatlands being approximately 644 gigatons

(Leifeld and Menichetti 2018). Thus, peatlands can have a major influence on climate change.

While established peatlands are carbon stores providing cooling via negative radiative forcing,

new or disturbed peatlands may be potential emitters of methane causing warming via positive

radiative forcing (Frolking et al. 2006). By preserving peatlands and protecting them from

anthropogenic disturbances and destruction, carbon is kept within accumulating peat and the

burden of atmospheric carbon is reduced (Frolking et al. 2006).

1.2.2 Flood-drought mitigation

The formation of peat is central to a peatland's ability to store large amounts of water

(Richardson and Siccama 2000), with water content of peat ranging from 75 – 98% by volume

(Hobbs 1986). Although climate change is expected to increase the risk of flooding and drought

(Wetherald and Manabe 2002), healthy peatlands have the potential to mitigate the severity of

these events (Hey and Philippi 1995, Bacon et al. 2017). In fact, peatlands are natural, low-cost

alternatives to built infrastructure such as levees and bypasses to manage flooding events (Hey

and Philippi 1995, Liquete et al. 2016). In periods of drought, the surface albedo of peatlands

may change to reduce water loss by evaporation (Waddington et al. 2015), and provide constant

baseflows of groundwater which is important for maintaining downstream water flow and

availability (Branfireun and Roulet 1998).

1.2.3 Biodiversity

Peatlands can support high biodiversity of flora and fauna and may become significant

hotspots of biodiversity (Keddy 2010), especially as the collapse of biodiversity continues due to

climate change (Thomas et al. 2004). Species, especially plants, have adapted to the unique

environmental conditions of peatlands, promoting high morphological and phenotypic diversity

(Minayeva et al. 2017). Mountain peatlands are also important refugia for rare plant and animal

species that are usually limited to the colder climates of boreal and arctic regions (Cooper 1996,

Chimner et al. 2010). In addition, these peatlands are habitats for mammals such as elk and

moose (Chimner et al. 2010), amphibians (Minayeva and Sirin 2012) and reptiles (Minayeva et al. 2017), and are critical breeding habitats (Warner and Asada 2006), staging areas and feeding grounds for many avian species (Minayeva and Sirin 2012).

In Alberta, stakeholders including watershed groups, governments, and researchers are particularly interested in the biodiversity of peatlands because biodiversity is often an indicator of both ecosystem health and the peatland's ability to perform its ecosystem services (Li et al. 2014). Moreover, the presence of rare or at-risk species is often justification to protecting these valuable ecosystems from competing land use interests and anthropogenic threats such as logging of surrounding trees, and recreational all-terrain-vehicle use.

1.3 Research topics of interest

Peatlands occupy approximately 12% (1.136 million km^2) of the total land surface of Canada (Tarnocai 2009). The total, Canadian coverage of unfrozen mountain peatlands is approximately 8290.7 km^2 (Warner and Asada 2006). However, mapping is limited and this number likely underestimates the extent of mountain peatlands like those found in the Rocky Mountains of Alberta. These mountain peatlands are understudied compared to boreal peatlands (Harbert and Cooper 2017), and are missing from the Alberta Merged Wetland Inventory, meaning they have not been mapped or characterized by the government (Alberta Environment and Parks 2018). Thus, there is a strong need to locate and study these peatlands in order to fill existing knowledge gaps.

In particular, mountain valley bottom peatlands in the upper Bow River basin region of the Rocky Mountains of Alberta are particularly important as they provide potential flood-drought mitigation ecosystem services to the downstream city center of Calgary. In addition, these peatlands face anthropogenic threats such as logging which threaten the integrity of these

5

peatlands and its ability to provide habitat for biodiversity when they are rolled over to harvest surrounding trees. Therefore, stakeholders in the region are particularly interested in determining the species richness and identities of vegetation within these peatlands to better conserve and protect them from competing land-use. Consequently, the diversity of vascular plants occupying these peatlands is of major interest to my research and the focus of my thesis.

1.3.1 Modelling species distributions & the Clements-Gleason dichotomy

Receding glaciers as a result of climate change is expected to increase the total land coverage of wetlands, including peatlands (Dangles et al. 2017). These emerging peatlands are expected to support high diversity. With the current biodiversity crisis, understanding the drivers that control succession, the distribution of species and the conditions that determine co-occurring species within these peatlands is both practical and imperative.

Community ecologists have, for decades, been interested in the drivers of community assembly that produce the patterns of plant community composition we observe along environmental gradients. In the early 20th century, Frederic Clements proposed the idea of stable climax communities, where species are tightly associated to form predictable assemblages following succession (Clements 1916, 1936). Clements (1936) proposed that climate has a deterministic relationship to the dominant species present, but then the dominant species determine the conditions under which all the remaining species exist, resulting in stable species associations. In the absence of disturbance, these stable associations among species may persist through millions of years (Clements 1936). Modelling a Clementsian view of communities, species composition would change abruptly along an environmental gradient such as elevation, as different climax communities replace one another across the gradient in environmental conditions (Vellend 2016).

In contrast, Henry Gleason asserted that species respond uniquely and individually to environmental conditions, generating plant assemblages by mere coincidence (Gleason 1926). Gleason questioned whether Clements' theory of climax communities goes too far by "pigeon-holing" assemblages into typical communities, indicating that there are often no clear and abrupt boundaries between distinctive climax communities (Gleason 1926). Instead, individual plants sort along gradients in environmental conditions according to their physiological tolerances. These environmental conditions may be correlated with geographic location, or controlled, modified or supplied by vegetation, but the presence of certain species does not exert a deterministic influence on the distribution of all other species (Gleason 1926). Following a Gleasonian view of communities, species composition would change gradually along an environmental gradient such as elevation as the abundance of species shifts individualistically (Vellend 2016).

Certainly, the Gleasonian view is not without criticisms, where some would argue that it is too far individualistic in its view of plants species (Callaway 1997), and ignores the importance of interactions among species (e.g. mutualism, facilitation, parasitism, etc.). This debate is still unresolved and remains evident in competing models that have since built on concepts proposed by Clements and Gleason (Fisher and Fulé 2004, Dyakov 2016). With a modern understanding of ecology, the Clements-Gleason dichotomy can be viewed as contrasting hypotheses regarding the relative strength of the influence exerted by biotic filters (e.g. interdependence of species) and abiotic filters (e.g. climatic or environmental variables) on the formation of plant assemblages. What are the relative strengths of the abiotic and biotic filtering effects, and to what extent are vegetation assemblages consistent and self-reinforcing? Understanding the processes and drivers that produce plant assemblages in mountain valley

bottom peatlands is an important research topic of interest and in the subject of my second

Chapter.

1.3.2 Challenges in the detection of plants

The ability to collect accurate species inventories is fundamental to instilling confidence

in inferences made based on empirical data. Such inferences often have major implications for

policy decisions affecting conservation of at-risk species (Banks-Leite et al. 2014, Spitale and

Mair 2017), invasive species monitoring (Regan et al. 2006), and land use management and

policy through environmental impact assessments (Garrard et al. 2015). One of the biggest

challenges in the detection of species by human observers is imperfect detection (i.e. when the

probability of detecting a species that is present in a surveyed area is less than 1).

The detection of species is rarely ever perfect, and failure to detect a species does not

necessarily ensure that it is absent (MacKenzie et al. 2002). For example, animals are mobile and

avoid areas where surveyors are sampling, making them challenging to census completely

(Nichols 1992). Consequently, there is a long and developed practice within animal ecology of

quantifying detection probabilities and producing statistical models capable of estimating true

populations based on these probabilities (MacKenzie et al. 2002). For instance, such is the case

with mark-recapture methods (Nichols 1992), or occupancy modelling (Campos-Cerqueira et al.

2017).

Despite being sessile organisms, plant species are not immune to imperfect detections

(Alexander et al. 1997). Yet statistical models and associated sampling designs to control for

imperfect detections have largely been restricted to studies in animal ecology until recently

(Chen et al. 2013). Researchers studying plants have rarely quantified and accounted for

imperfect detections in analyses (Dennett and Nielsen 2019). More recent studies on vegetation

surveys in the literature are demonstrating that imperfect detection of plants is ubiquitous and can be severe (Chen et al. 2013, Dennett and Nielsen 2019, Morrison et al. 2019). Commonly, imperfect detections arise from errors such as the misidentification of species (i.e., errors of commission) and from false absences from overlooking species present (i.e., errors of omissions; Dennett et al 2018).

These errors may be influenced by factors related to the sampling design (Moore et al. 2011), environmental factors (Ng and Driscoll 2015), or even plant traits themselves (Chen et al. 2013). While factors relating to sampling design are adjustable, environmental factors and plant traits are outside the control of investigators. For example, plant traits such as plant life stages and size (Chen et al. 2013), the presence of flower structures or flowering period (Ng and Driscoll 2015), which can be affected by environmental factors like elevation, may influence imperfect detections. However, sampling design elements, like having smaller study plots or quadrat sizes (Dennett et al. 2018) or increasing survey effort (Moore et al. 2011), can be fine-tuned to optimize detection probabilities and mitigate the influence of environmental factors and plant traits on imperfect detections within a study. The sources of imperfect detection in peatlands, and certainly in mountain valley bottom peatlands, are largely unstudied (Morrison 2016). The factors that influence imperfect detection in peatlands, and the optimal survey strategies for vegetation surveys in these ecosystems, is the subject of my third chapter

1.4 Thesis organization

My thesis follows a manuscript style with an introductory chapter, two data chapters, and a conclusion chapter:

Chapter 1 – "Introduction: Thesis context and literature". This chapter provided general context and literature for my thesis document.

Chapter 2 – "Assembly of plant communities in mountain valley bottom peatlands" is a case-study of the vegetation patterns and distributions of twenty valley bottom peatlands in the upper Bow River basin of Alberta's Rocky Mountains. My goal in this chapter was to describe and characterize the peatland vegetation communities along an elevation gradient in order to determine if the distribution of plant species is contingent on elevation, and to characterize how the distribution of plant species changes along an elevation gradient.

Chapter 3 – "Sources of imperfect detection in peatland vegetation surveys" is a study on the survey methods used to characterize the vascular plant occurrence data described in chapter 2. My goal in this chapter was to determine potential sources of detection errors in peatland vegetation surveys and to determine a best-practice survey strategy to minimize detection errors.

Chapter 4 – "Conclusion: Recommendations and future work". In this chapter I summarize the findings of chapter 2 and 3 and provide recommendations for stakeholder groups and directions for future research.

2 Assembly of plant communities in mountain valley bottom peatlands

2.1 Introduction

2.1.1 Chapter scope and context

Community ecologists are interested in what controls the distribution of species and which species co-occur under what conditions (Vellend 2016). The mechanism explaining the succession of plant species in a habitat is commonly illustrated using a filtering metaphor, whereby starting at the coarsest level: (1) biogeographical constraints exclude species from a community unable to reach it; (2) abiotic filters, the environmental constraints, exclude species capable of reaching the community but unable to tolerate the range of environmental conditions and resources provided; and lastly at the finest level (3) biological filters, including predation, competition, and other interspecific interactions, exclude species that cannot establish and co-exist with species already established in the community (Poff 1997, Keddy 2010, Kraft et al. 2014). Competition and interspecific interactions can be linked to concepts of fundamental and realized niches (Hutchinson 1957, Leibold 1995) where interactions with other species may expand (through mutualism, or facilitation, etc.) or contract (through competition, predation, or parasitism, etc.) the potential range of a given species (Mittelbach 2012).

Where the influence of biological filters is strong relative to environmental filters, we would expect to see consistent and self-reinforcing community composition. This idea that certain species will necessarily assemble into interacting communities that are compositionally consistent and self-reinforcing can be traced back to Frederic Clements (Clements 1916). In contrast, where the influence of biological filtering is weak, we may expect to see the distribution of species evidencing individualistic spatial patterns and little consistency in community composition. I trace the idea that biological filtering should be subordinate to

environmental filtering back to Henry Gleason, who asserted that species respond individually to

environmental conditions, generating plant assemblages in space almost by coincidence (Gleason

1926; Van Der Valk 1981).

The resulting Clements-Gleason dichotomy provided one of the greatest theoretical

debates in ecology in the early 20th century (Vellend 2016). This debate centred around

understanding the drivers of community assembly that produce the patterns of plant community

composition we observe along environmental gradients (Fig. 2.1). On the Clementsian side, we

predict that as we move along a strong environmental gradient, we should witness abrupt

changes in community composition as we transition from one self-reinforcing community to

another (Clements 1916). Whereas on the Gleasonian side, we predict that community

composition should shift gradually along strong environmental gradients, with no clear transition

thresholds and with the majority of species exhibiting individualistic relationships to the

environmental gradient (Gleason 1926).
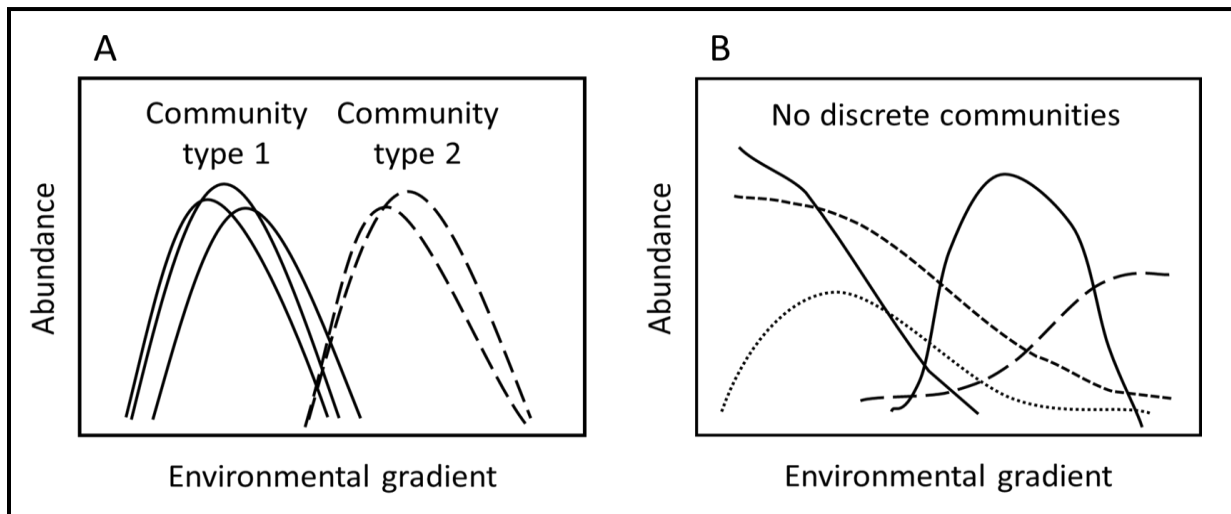
Figure 2.1. a) Clementsian hypothesis of communities showing abrupt transition in abundance
between climax community types 1 and 2 along an environmental gradient; b) Gleasonian
hypothesis of communities showing gradual changes in abundance of individual species along an
environmental gradient. Figure adapted from Vellend (2016).

12

Mountain ecosystems provide an excellent testing ground for these alternative hypotheses, since elevation is a strong environmental filter and is correlated with many abiotic and climatic parameters important in plant succession and species distributions (Pickett et al. 2009). For example, elevation influences factors like the amount of precipitation (Sanchez-Moreno et al. 2014), water table stability (Sanchez-Moreno et al. 2014), temperature (Wang et al. 2011), phenology (Piao et al. 2011), soil depth (Tol et al. 2013), and soil quality (He et al. 2016), which should be important in determining the distribution of plant species.

Moreover, there is insufficient knowledge about the role of environmental gradients in determining vegetation community composition, species richness and distribution observed in mountain peatlands (Chimner et al. 2010, Harbert and Cooper 2017). Although there have been studies on the processes that determine vegetation assemblages of peatlands in mountain ranges, many of them are conducted in mountain ranges outside of Canada such as in Colorado (Chimner et al. 2010, Harbert and Cooper 2017), in European (Sekulova et al. 2011, Jimenez-Alfaro et al. 2014) or in South American (Cooper et al. 2010) mountain ranges. To the best of my knowledge, there are no other studies in the Rocky Mountains of Alberta, Canada, particularly within the upper Bow River basin, that survey and characterize the vegetation assemblages of mountain valley bottom peatlands. Yet, Alberta's mountain valley bottom peatlands provide an important opportunity to study community assembly of plants along an elevation gradient. In addition, they provide an opportunity to study peatlands in the Rocky Mountains of a more northern latitude which may be important to our overall understanding of peatlands along an latitudinal gradient.

Further, the primary environmental gradients affecting vegetation composition and species richness are often strongly habitat-dependent (Sekulova et al. 2011) and may be unique

to different regions. For example, both Chimner et al (2010) and Sekulova et al (2011) found elevation to be the most important determinant of mountain peatland vegetation composition, whereas Harbert and Cooper (2017) found water chemistry to be most important in structuring the vegetation of peatlands. Other variables that were found to be important included pH (Chimner et al. 2010, Harbert and Cooper 2017) and concentrations of calcium ions in groundwater (Chimner et al. 2010). Determining the primary environmental gradients structuring vegetation composition in mountain valley bottom peatlands is critical to enhancing our understanding of these important ecosystems.

2.1.2 Chapter objectives

In this chapter, I describe and characterize Alberta's Rocky Mountain valley bottom peatland vegetation communities along an elevation gradient to reach the following research objectives: (i) *To determine if the distribution of plant species is contingent on elevation.*; (ii) *To characterize how the distribution of plant species changes along an elevation gradient.*

First, I wanted to determine if the distribution of plant species is contingent on elevation by answering the following research questions: (a) *Does community composition of mountain valley bottom peatlands change along an elevation gradient;* and (b) *Do there appear to be distinct communities that are sorted along elevation?* I predict that mountain valley bottom peatland community composition will change along an elevation gradient and that elevation will be the most important determinant of vegetation composition of these peatlands, similar to results from Chimner et al. (2010). If elevation explains vegetation composition, peatlands with similar elevations are likely to have more similar plant assemblages, revealing distinct communities sorted along elevation.

Second, I wanted to characterize how the distribution of plant species changes along an elevation gradient by answering the following research questions: (c) *Is the change in community composition along the elevation gradient abrupt or gradual?*; and (d) *Does the abundance of species change individualistically or are groups of species behaving similarly along the elevation gradient?* If the distribution of plant species is not primarily determined by the distribution of co-occurring plant species, the abundance of different species will change individualistically and gradually along the studied range of elevation and consequently community composition will change gradually (e.g. Whittaker 1956; Curtis 1959). Contrarily, if plant distributions are strongly codependent, community composition will change abruptly along the elevation gradient as one cohesive plant assemblage replaces another. I would also expect groups of species to have shared elevation optima.

2.2 Methods

2.2.1 Study area

Between May and June 2019, I selected 20 valley-bottom peatlands to include in my study using a combination of stakeholder consultation and site visitation. I selected sites of comparable size that had little to no direct anthropogenic disturbance and which spanned an elevation gradient of 1415 – 1959 meters above sea level (m a.s.l.), in the upper Bow River basin in Alberta's Rocky Mountains, Canada (Figure 2.2; detailed listing of sites including coordinates and elevations in Appendix A). The lower limit of continuous permafrost in the Albertan Rocky Mountains is approximately between 2180 – 2575 m a.s.l. (Harris and Brown 1982). Since my work was focused within the lower elevations where permafrost is discontinuous or absent, I did not detect any permafrost at my sites. Additionally, my peatlands form in relatively gentle slope

topography and my study systems were in valleys running mainly East to West (site images of

typical mountain valley bottom peatlands are also found in Appendix A).
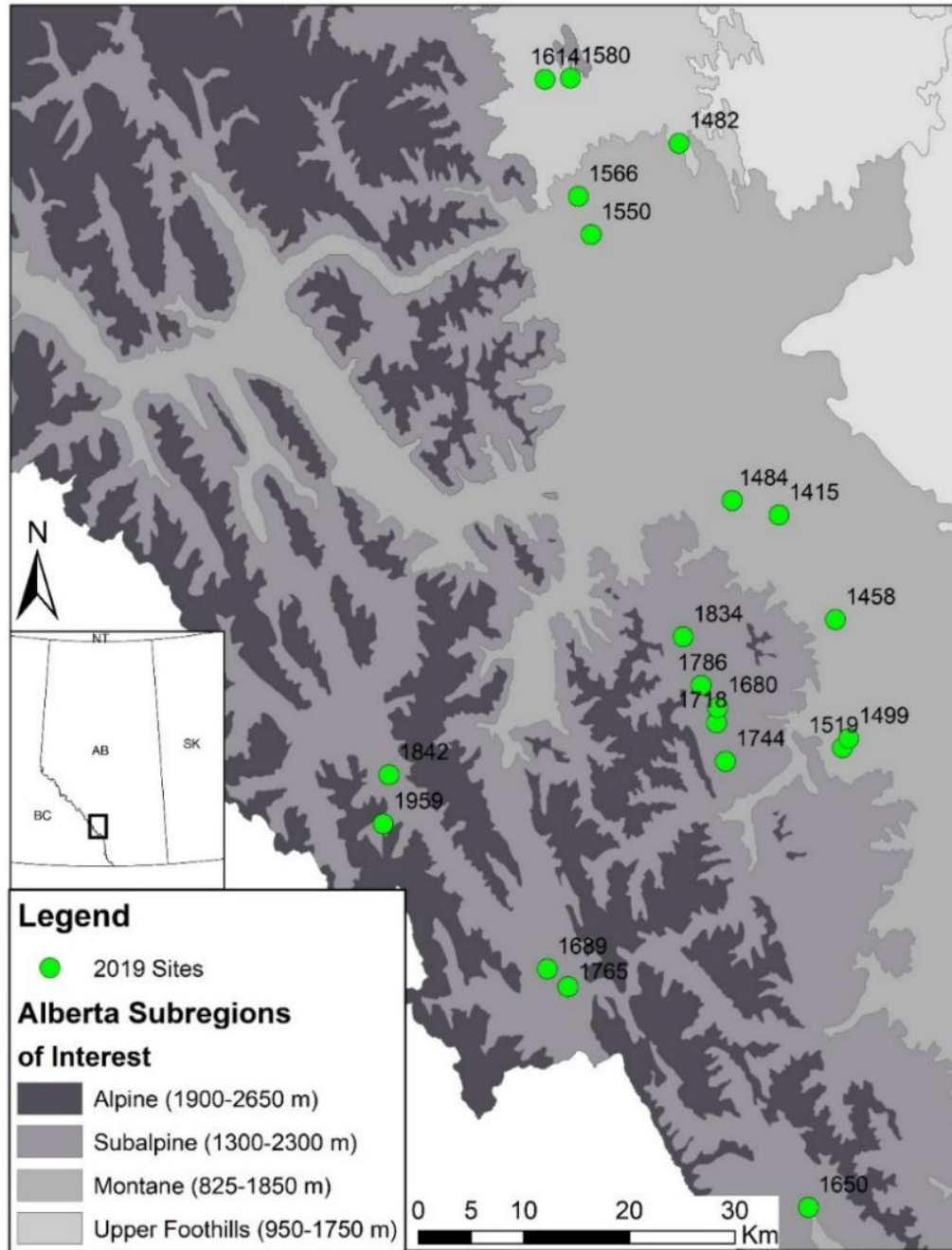
Figure 2.2. Map showing 20 valley-bottom peatland sites sampled between July and August 2019, spanning an elevation gradient between 1415-1959 m a.s.l. in the upper Bow River basin within Alberta's Rocky Mountains, Canada. Points indicate the location of peatlands and labels the elevation of each peatland.

2.2.2 Field methods

I carried out vegetation surveys where I identified vascular plants and mosses to the species level at each peatland between July 19 and August 12, 2019. Conventional vegetation surveys suffer from errors of omission that are biased toward certain site conditions or plant traits (Chen et al. 2013). To adequately capture the presence-absence of all vascular plant and moss species, I combined three surveying methods to obtain the data used in this study: transect surveys, quadrat surveys, and timed-walk surveys. Each of these methods has advantages and disadvantages but combined they should more comprehensively assess plant occurrences.

Transect survey

At each site, I established three parallel 50-meter long transects, 1-meter wide, spaced 50 meters apart, oriented perpendicular to any stream flow or parallel to any moisture gradient. Along each transect, I identified all tall shrubs (i.e. shrubs greater than 0.5 m in height) and trees to species level using a field guide by Johnson et al (1995). All plants species identifications were cross-referenced and standardized using the Integrated Taxonomical Information System (ITIS) database (Integrated Taxonomic Information System 2020).

Quadrat survey

I then placed five 1 m^2 quadrats along each of the three transects, such that they were spaced approximately 10 meters apart. Within each 1 m^2 quadrat, I identified all vascular plant species to species level using field guides by Johnson et al. (1995) and Moss and Packer (1983), and mosses as either *Sphagnum* moss or brown moss (henceforth "moss cover types"). I recorded relative percent cover of vascular plants, moss cover types, and other cover types such as cover of water and cover of bare ground at each quadrat following modified cover classes based on Peet et al (1998). All plants species identifications were cross-referenced and standardized using

the Integrated Taxonomical Information System (ITIS) database (Integrated Taxonomic

Information System 2020).

Timed-walk survey

I conducted using two independent observers, simultaneous 15-minute timed walk

surveys within my valley-bottom peatland sites to identify the vascular plant species

encountered. Afterward, I conducted a separate timed-walk survey to identify the moss species

encountered. These walks were meandering, contained within a 3.14 ha area that comprised a

100 m radius circle around the center of the middle transect. Thus, these timed walks included

the same environments as the quadrats and transect surveys. During these timed walks, I

recorded each species' time to first detection. For vegetation detected on the timed-walk surveys,

I identified all mosses and vascular plants to species level using field guides (Moss and Packer

1983, Vitt et al. 1988, Johnson et al. 1995). I cross-referenced and standardized all plant

identifications using the Integrated Taxonomical Information System (ITIS) database (Integrated

Taxonomic Information System 2020).

Covariate measurements

At each site, I recorded the GPS coordinates and the site's elevation (SXPro GNSS,

Geneq inc, Montreal, Quebec). At each quadrat (n = 15), I measured soil pH (FieldScout pH 400

Meter, Spectrum Technologies, Aurora, Illinois) and conductivity (HI 98331 Soil Test Direct

Soil Conductivity and Temperature Tester, Hanna Instruments, Laval, Quebec) to produce the

following: average site pH, minimum site pH, maximum site pH, average site conductivity,

minimum site conductivity, and maximum site conductivity. These covariates, pH and

conductivity, were selected because they are key edaphic parameters that influence vegetation

composition (Chimner et al. 2010, Harbert and Cooper 2017) and are also critical in classifying

peatlands according to the Alberta Wetland Classification System based on the defined critical thresholds in pH and conductivity summarized in Table 2.1 (Alberta Environment and Sustainable Resource Development (ESRD) 2015).

Table 2.1. Summary table of critical thresholds in pH and conductivity (mS/cm) for bog-fen differentiation according to the Alberta Wetland Classification System.

Peatland type	pH	Conductivity (mS/cm)
Bog	< 4.5	low
Poor fen	< 5.5	< 0.1
Moderate – rich fen	5.5 – 7.0	0.1 – 0.25
Extreme – rich fen	> 7.0	0.25 – 20

2.2.3 Statistical analyses

Data preparation

Maximum cover dataset

Since I wanted to assess the potential cover of species at a given elevation, assuming all other environmental conditions, like soil moisture, were optimal, I obtained the maximum cover value for each species of vascular plant or moss type recorded among all fifteen quadrats surveyed at each site (henceforth "maximum cover"). Thus, the cover at a site can exceed 100% because it reflects the maximum cover out of the 15 quadrats for each of the vascular plant species or moss types. I did this because my quadrats were arranged along the moisture gradient to capture the heterogeneity in environmental conditions in each site, but my sample unit was the individual peatland.

Occurrence dataset

The combination of the transect, quadrat, and timed-walk survey methods produced presence-absence data (henceforth "occurrence data") for both vascular plant and moss species

for each valley bottom peatland site. The species lists of vascular plant and moss species that I detected at each peatland site is reported in Appendix B.

Spatial autocorrelation

To confirm that any relationships I observed between vegetation distributions and site elevations were not simply a product of spatial autocorrelation, I tested whether geographic distances among sites might be confounded with elevation differences among sites. I measured concordance between these dissimilarity matrices with a Mantel test. I calculated the site geographic distance matrix using Euclidean distance among the recorded site coordinates. Similarly, I represented the difference in elevation among my sites with Euclidean distance.

I also used a Mantel test to evaluate whether there was significant concordance between the geographic distances among sites and the dissimilarity in vascular plant and moss species occurrences among sites because this could indicate significant spatial autocorrelation in vegetation composition. To represent vegetation composition, I used vascular plant and moss occurrence data and I calculated dissimilarity among my twenty valley-bottom peatlands using the Sørensen distance measure, as recommended by McCune and Grace (2002). Thus, I recalculated the geographic distance matrix using the Sørensen distance measure so that the matrices could be appropriately compared.

Last, I used another Mantel test to evaluate whether there was significant concordance between the differences in elevation among sites and the dissimilarity in vascular plants and moss species occurrence among sites, since this may indicate a relationship between the

differences in vegetation composition and the differences in site elevations, the environmental gradient of interest in this study. In both cases, I used the Sørensen distance measure.

I carried out all Mantel tests on dissimilarity matrices using PC-ORD 7.08 (McCune and Mefford 2016). All Mantel tests used an alpha of 0.05.

Elevation as a constraint on plant communities

To determine if the distribution of plant species is contingent on elevation specifically or other edaphic conditions like soil pH or conductivity (objective 1), I compared distance-based redundancy analysis (dbRDA) and non-metric multidimensional scaling (NMS) ordinations. I compared the results of these ordinations using both my maximum cover and my species occurrence data. I carried out all ordinations in PC-ORD 7.08 (McCune and Mefford 2016).

To model the maximum potential abundance of each cover type, I used the maximum cover dataset based on the fifteen quadrats surveyed at each of the twenty sites. To prepare my data for ordination, I transformed these maximum cover values using the $(2/\pi)\text{arcsine}(x^{1/2})$ (henceforth "arcsine square-root function") for compositional data, scaling them from 0 to 1. I also excluded species that were present in fewer than 10% of peatlands to reduce the effect of rare species on the ordinations.

To model species occurrence, I used the occurrence data of all vascular plant and moss species. Again, this combined all species I observed in my fifteen quadrats, species recorded along the three transects, and the species I detected during the timed walks at each site. I removed species that were present in fewer than 10% of sites to reduce the effect of rare species on the ordinations.

For both the maximum cover and occurrence data, I conducted a distance-based redundancy analysis (dbRDA) with elevation as the constraining variable to assess the degree of variance in community composition that could be attributed to elevation (Legendre and Anderson 1999). My distance measure was Bray-Curtis for maximum cover of vascular plants and moss types and the Sørensen distance measure for the occurrence of vascular plant and moss species. I tested the significance of the first eigenvalue using a Monte Carlo randomization test with 999 randomizations, using an alpha of 0.05.

To visualize the variation in community composition in a more exploratory context, I followed up with an unconstrained ordination analysis using the non-metric multidimensional scaling (NMS) ordination, which allowed me to investigate patterns of co-occurrence among sites in terms of vegetation composition, and then post-hoc, explore how covariates related to the variance in plant community composition represented by the NMDS ordination axes. Specifically, I examined the Pearson correlation coefficients between NMS axes scores for each site and: 1) site elevation, 2) average pH from the fifteen quadrats, 3) minimum pH from the fifteen quadrats, 4) maximum pH from the fifteen quadrats, 5) average conductivity from the fifteen quadrats, 6) minimum conductivity from the fifteen quadrats, and 7) maximum conductivity from the fifteen quadrats. I used Bray-Curtis as my distance measure for my maximum cover data and the Sørensen as my distance measure for my occurrence of vascular plant and moss species data. I determined the optimal number of dimensions by comparing 250 runs with real data to 250 runs with randomized data. All runs used random starting configurations.

Vascular plant assemblages and their indicators

      To determine if there appears to be distinct communities that are sorted by elevation

(objective 1), I used hierarchical cluster analysis and indicator species analysis to determine if

vascular plant species and moss types (*Sphagnum* spp. vs. brown moss) formed consistent

assemblages in valley-bottom peatlands and if certain species could be representative indicators

of these assemblages. I transformed these maximum cover values using the arcsine square-root

function for compositional data, scaling them from 0 to 1, as recommended for compositional

data by McCune and Grace (2002). Using this arcsine square-root transformed maximum cover

dataset, I conducted the hierarchical cluster analysis on PC-ORD 7.08 using Bray-Curtis as my

distance measure, and the flexible beta linkage method set at -0.25 to order my twenty sites

based on their similarity in maximum cover data of vascular plants species, moss cover types,

and other cover types such as cover of water and cover of bare ground (McCune and Mefford

2016).

      To find the optimal number of groups, I ran an indicator species analysis at each pruning

point of the cluster dendrogram produced by the hierarchical cluster analysis, and selected the

optimal pruning location as the number of groups that yielded the lowest average *P*-value for its

indicator species analysis. I then carried out indicator species analysis on the optimal number of

groups produced by the hierarchical cluster analysis to calculate an indicator value for each

species by taking the product of the species' relative abundance and constancy, multiplying by

100 and then using a Monte Carlo randomization test to assign a *p*-value. For each significant

indicator species (alpha = 0.05), I was interested in whether these species were easily detectable

or if they were rare or cryptic because this will help me evaluate their individual practicality as

indicators. I determined the average number of quadrats each indicator species was found in, the

average percent cover among the quadrats where the species was found and its standard deviation using the relative cover data averaged among the fifteen quadrats. I also calculated the average time to first detection of the species in minutes and the standard deviation using my recorded species' time to first detection from my 15-minute timed-walk dataset.

Individual species and elevation

To characterize how the distribution of plant species changes along an elevation gradient (objective 2), I modelled how individual species responded to the elevation gradient to examine if the community composition along the elevation gradient changes abruptly or gradually, and to observe if vegetation maximum abundance changes individualistically or if any groups of species were behaving similarly along the elevation gradient. I wanted to model the potential cover of a species at each elevation, assuming other environmental condition were optimal, so I again used the maximum cover dataset. I removed species that did not appear in at least half of the twenty sites to allow me to investigate trends within the species that were most dominant, and used the ggplot2 package to create LOESS curves with a confidence interval of 90%, smoothed using the locally-weighted scatterplot smoothing (LOESS) function in RStudio version 3.6.1 (R Core Team 2020). The LOESS method is useful because it fits a function weighing local datapoints more heavily which may improve estimates of the maximum abundances between my data points (Cleveland and Devlin 1988). To better visualize the trendlines of species with low percent cover values, I replotted the data after relativizing the maximum cover values by the maximum value observed among the twenty sites for each species and cover type.

Additionally, I wanted to model how vascular plant species particularly diagnostic of vegetation assemblage responded to the elevation gradient. Again, I created LOESS curves with a confidence interval of 90%, smoothed by the LOESS function using the ggplot2 package in

RStudio version 3.6.1 (R Core Team 2020). Since many of these species occur at low maximum cover values, I replotted the data after relativizing the maximum cover values by the maximum value observed among the twenty sites for my indicator species analysis group indicators.

2.3 Results

2.3.1 Geographic location is not confounded with elevation or vegetation composition

Euclidean distance among sites in terms of elevation and in terms of geographic location were not concordant (Mantel test, $r = 0.132$, $p = 0.1071$), revealing that the difference in elevation among my valley-bottom peatlands was not confounded with their geographic location. Further, I did not find evidence that spatial autocorrelation could explain patterns in vascular plant and moss species occurrence data, since vegetation composition was not concordant with geographic locations of my twenty valley-bottom peatlands (Mantel test, $r = -0.035$, $p = 0.4214$).

2.3.2 Elevation explains minimal variation in vegetation composition

I did not find strong support for the hypothesis that elevation could explain patterns in vascular plant and moss species occurrence data. Vegetation composition was not significantly concordant with elevation for my twenty valley-bottom peatlands (Mantel test, $r = 0.205$, $p = 0.0511$). More, elevation did not explain a large fraction of the variance in vascular plant maximum cover or the occurrence of vascular plant and moss species, based on my dbRDA analyses. These analyses yielded a single canonical axis each, which explained 7.7% of the variance in my vascular plant maximum cover data and 7.8% of the variance in my vascular plant and moss species occurrence data. However, the eigenvalues for these axes were marginally significant in both cases, with Eigenvalue = 0.012, $p = 0.0741$ in the case of maximum vascular plant cover and Eigenvalue = 0.010, $p = 0.0651$ in the case of vascular plant and moss species occurrence.

Conductivity and pH are associated with variance in vegetation composition

The optimal number of NMS dimensions for visualizing my arcsine square root transformed vascular plant maximum cover data was two, yielding a final stress of 15.107 after 29 iterations (Fig 2.3). The ordination solution explained 85% of the variance in my maximum cover data: 60.5% on the first axis and 24.5% on the second. Notably, the results agree with my dbRDA, as elevation was only weakly related to either axis (Table 2.2). Rather, the first axis was most related to average conductivity ($r^2 = 0.319$). The second axis was related to average conductivity ($r^2 = 0.280$) and soil pH ($r^2 = 0.270$; Table 2.2).
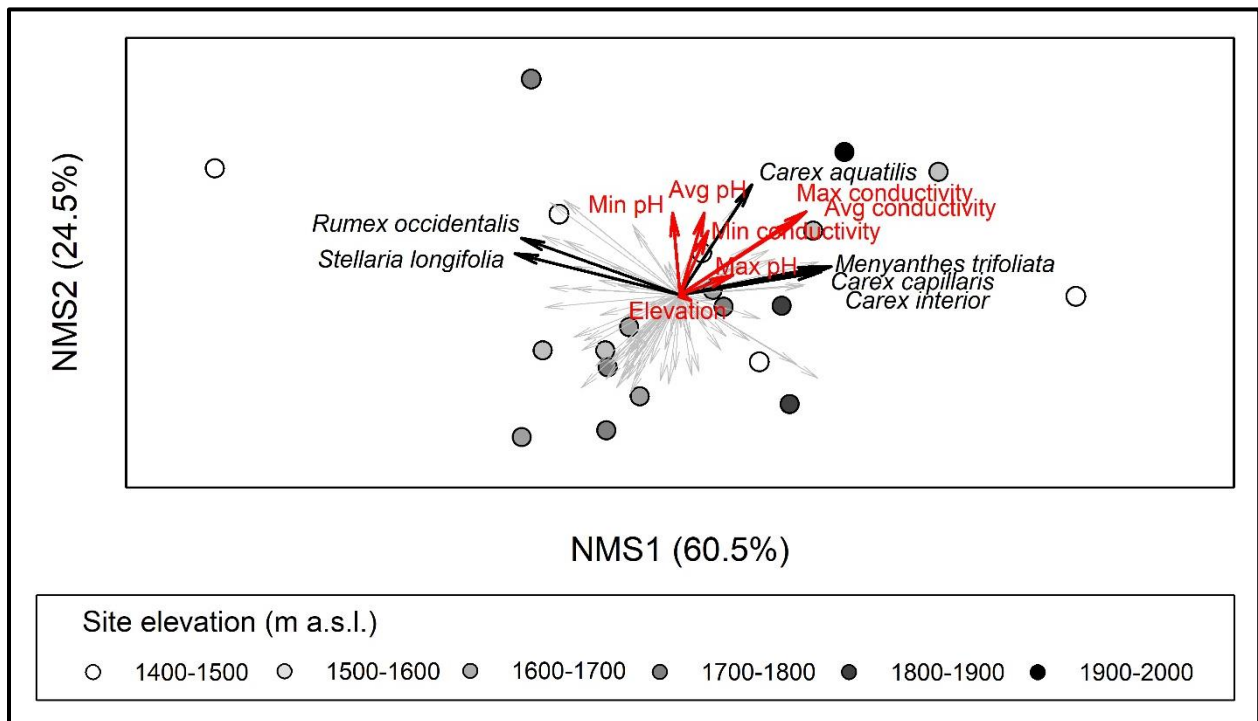
Figure 2.3. Two-dimensional solution for non-metric multidimensional scaling (NMS) ordination and vector biplot for maximum cover data of vascular plants. Sites are represented by circles ordinated on axes NMS1 and NMS2, with gray vectors representing all cover classes, black vectors representing cover classes with a r^2 cut-off ≥ 0.4, and red vectors representing environmental variables (no cut-off applied). Axes are scaled by the % variance explained.

The optimal NMS solution to visualize variance in the occurrence of vascular plants and mosses had three dimensions, with a final stress of 12.033 after 68 iterations (Figure 2.4). It explained 85.4% of the variance in vascular plant and moss occurrence: 44.9% on NMS1, 32.5% on NMS2, and 8.0% on NMS3. NMS1 was principally related to variance in conductivity, but also aligned with variation in pH, particularly maximum pH ($r^2 = 0.244$; Table 2.2b). NMS2 was not as well characterized by my soil measurements but was related to soil minimum conductivity ($r^2 = 0.183$; Table 2.2b). Neither NMS1 nor NMS2 were strongly related to elevation; however, NMS3 was strongly related to elevation ($r^2 = 0.464$; Table 2.2b), though this explained little variance in my vegetation occurrence data (8%).
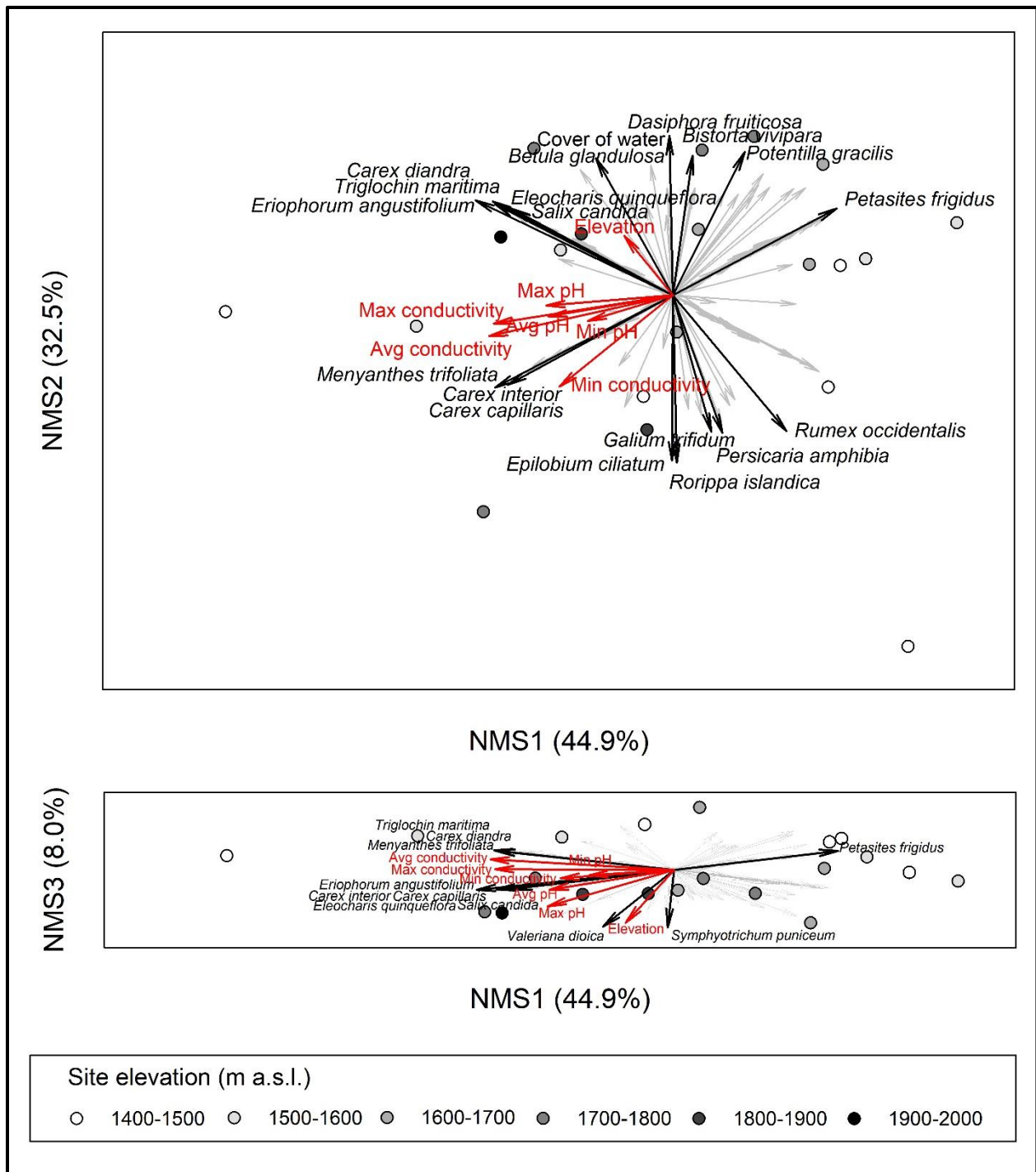
Figure 2.4. Three-dimensional solution for non-metric multidimensional scaling (NMS) ordinations and vector biplots for occurrence data of vascular plants and mosses. Sites are represented by circles ordinated on axes NMS1 and NMS2 (top panel) and on axes NMS1 and NMS3 (bottom panel), with gray vectors representing all cover classes, black vectors representing cover classes with a r^2 cut-off ≥ 0.4, and red vectors representing environmental variables (no cut-off applied). Axes are scaled by the % variance explained.

Table 2.2. Summary table of NMS axes Pearson correlation values to environmental variables for the: a) two-dimensional NMS ordination solution for vascular plant maximum cover data; and b) three-dimensional NMS ordination solution for occurrence of vascular plant and moss species.

a) NMS two-dimensional solution for maximum cover		
Environmental variables	**r^2 with NMS1**	**r^2 with NMS2**
Elevation	0.003	0.001
Average conductivity	0.319	0.280
Maximum conductivity	0.280	0.231
Minimum conductivity	0.016	0.164
Average pH	0.012	0.270
Maximum pH	0.056	0.016
Minimum pH	0.001	0.270
b) NMS three-dimensional solution for occurrence of vascular plants and mosses		
Environmental variables	**r^2 with NMS1**	**r^2 with NMS2**	**r^2 with NMS3**
Elevation	0.036	0.077	0.464
Average conductivity	0.516	0.036	0.018
Maximum conductivity	0.490	0.018	0.000
Minimum conductivity	0.196	0.183	0.011
Average pH	0.236	0.010	0.064
Maximum pH	0.244	0.002	0.221
Minimum pH	0.111	0.014	0.005

2.3.3 There are four distinct assemblages of vascular plants

The dendrogram (Fig. 2.5) representing the agglomerative clustering of vascular plant maximum cover among my 20 valley-bottom peatlands possessed moderate chaining (11.57%) and summarized a total sum of squares of 13.96. Based on indicator species analyses carried out at every pruning point, the optimal pruning location for this dendrogram was at 4 distinct groups (lowest mean $p = 0.0002$ for the maximum indicator values across all species). At this pruning point, there is 35.2% of information remaining in the dendrogram. Following this result, my NMS ordinations (Fig. 2.3 & 2.4) were replotted with each of their site points symbolized by their group membership as determined in the dendrogram (Appendix C). Moreover, I report the significant indicator species for each of the four groups in Table 2.3. Each of these species was typically identified within 5 min of surveying a plot where it occurred, though their average cover was low among quadrats where they occurred (<10%).
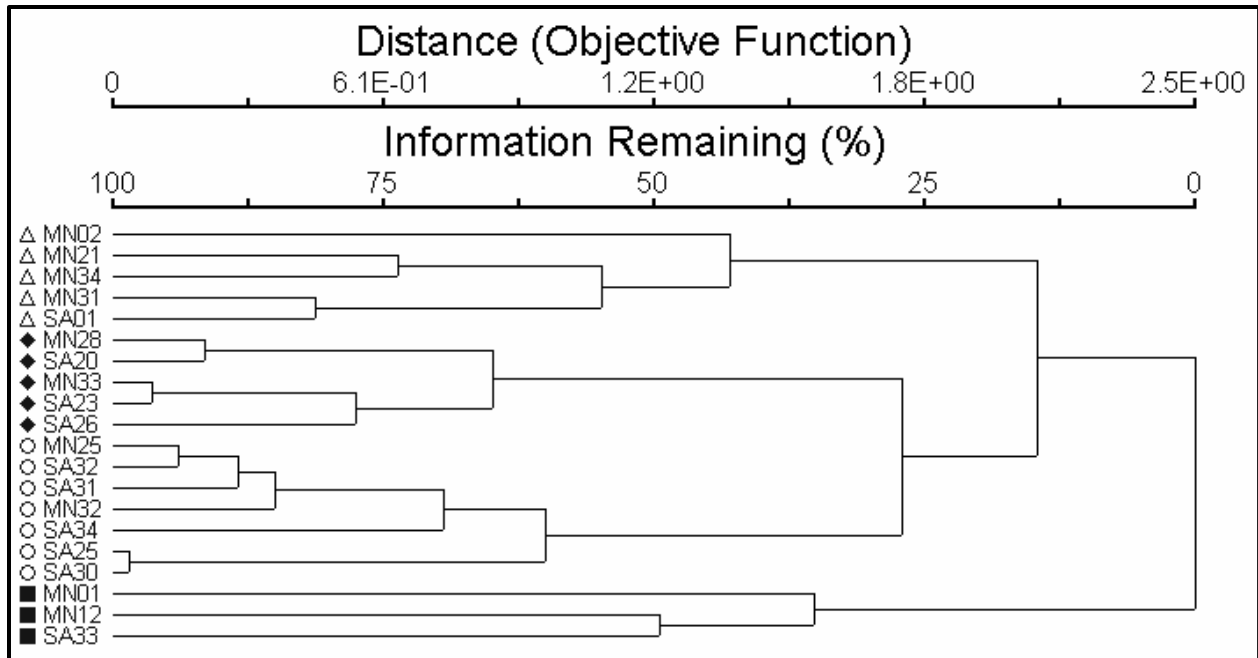
Figure 2.5. Hierarchical cluster analysis dendrogram showing the twenty valley-bottom peatland sites clustered optimally into the four distinct vegetation assemblages (group 1 in white triangles, group 2 in black diamonds, group 3 in black squares, and group 4 in white circles) based on their similarities in vegetation community composition. The letters in the site names indicate the Natural Subregion where the site was located, either SA for Sub-alpine or MN for montane. Dendrogram was pruned at 35.2% of information remaining, based on analysis of optimal number of groups (see Methods).

Table 2.3. Summary table of significant candidate indicator species/cover classes for each of the four distinct vegetation assemblages, with their respective observed indicator value (Obs. IV), p-value, N (the total number of sites where the species occurred out of 20 sites), the average number of quadrats (out of 15) in which the species was found at a site where it occurred, the average percent cover among in quadrats where it was found (%), n_1 (the total number of quadrats out of 300 in which the indicator species was detected) and its standard deviation (%), and the average time to detection during n_2 timed walks in which the indicator species was detected (minutes), n_2 (the total number of timed walks out of 40 during which the indicator species was detected), and its standard deviation (minutes).

Indicator species/ cover classes	Obs. IV	p-value	N	Average # of quadrats	Average % cover (%)	n_1	Standard deviation of average % cover (%)	Average time to detection (min)	n_2	Standard deviation of average time to detection (min)
Group 1										
Cover of bare ground	44.2	0.0384	5	2.0	2.90	10	2.23	n.d.	n.d.	n.d.
Carex capillaris	52.1	0.0436	7	4.7	4.02	33	4.82	3.56	12	4.24
Carex diandra	60.0	0.0302	3	5.3	3.03	16	1.53	1.16	7	2.09
Cover of water	44.9	0.0180	19	5.9	5.10	113	5.43	n.d.	n.d.	n.d.
Group 2										
Bistorta vivipara	58.4	0.0082	11	4.6	0.75	51	0.73	2.96	21	3.99
Sphagnum moss	62.1	0.0002	12	5.5	6.38	66	6.81	2.61	15	3.66
Group 3										
Epilobium ciliatum	54.9	0.0362	3	5.0	1.38	15	0.98	2.34	7	3.12
Galium trifidum	90.8	0.0028	4	3.8	1.33	15	1.29	3.48	4	5.33
Geum aleppicum	66.7	0.0140	2	5.0	3.75	10	4.51	2.62	9	2.04
Geum rivale	44.9	0.0196	13	5.8	3.48	76	3.00	2.68	27	4.05
Persicaria amphibia	66.7	0.0140	2	1.0	3.75	2	1.77	n.d.	n.d.	n.d.
Rorippa islandica	66.7	0.0140	2	2.5	0.80	5	0.27	2.25	4	1.41
Rubus arcticus	50.5	0.0034	17	8.2	1.36	140	2.48	3.18	33	4.00
Rumex occidentalis	78.2	0.0028	6	3.8	2.54	23	2.97	2.29	15	2.43
Stellaria longifolia	63.5	0.0088	15	3.0	1.63	45	4.22	4.58	21	3.62

Group 4										
Achillea millefolium	56.4	0.0200	8	3.4	0.89	27	0.55	2.83	22	3.13
Astragalus eucosmus	57.1	0.0136	7	3.3	2.04	21	1.82	4.38	7	3.66
Chamerion angustifolium	59.0	0.0142	4	5.1	3.26	13	3.94	4.02	21	4.80
Elymus trachycaulus	55.7	0.0306	5	3.0	2.36	14	1.69	4.69	13	5.05
Fragaria virginiana	51.2	0.0622	10	3.3	3.08	51	3.68	3.63	12	3.19
Petasites frigidus	57.1	0.0206	9	3.5	2.43	30	2.11	4.62	9	4.05
Potentilla gracilis	57.1	0.0136	4	2.8	2.14	14	1.25	2.96	13	3.33
Prosartes trachycarpa	71.4	0.0096	4	2.8	1.66	11	1.31	3.52	6	4.09
Salix maccalliana	58.1	0.0026	12	6.2	5.96	74	6.86	1.86	27	3.08
Vicia americana	71.4	0.0080	5	5.8	0.98	29	0.47	2.54	11	4.09

The four distinct assemblages of vascular plants can be classified into their peatland types according to their pH values, conductivities, covers of brown moss, *Sphagnum* moss, and water, compared to published ranges of values in the Alberta Wetland Classification System (Alberta Environment and Sustainable Resource Development (ESRD) 2015). The observed values are summarized in Table 2.4.

Table 2.4. Summary table of the minimum to maximum observed range in pH, conductivity (mS/cm), maximum brown moss cover (%) among quadrats, maximum *Sphagnum* moss cover (%) among quadrats, and maximum water cover (%) among quadrats, observed at n, the number of sites belonging to each group: a) Group 1; b) Group 2; c) Group 3; d) Group 4 as defined by the hierarchical cluster analysis dendrogram (Fig 2.7) pruned to its optimal number of groups by the indicator species analysis.

Variables	a) Group 1	b) Group 2	c) Group 3	d) Group 4
n	5	5	3	7
pH	7.30 – 7.86	6.12 – 7.72	6.98 – 7.76	6.34 – 7.57
Conductivity (mS/cm)	0.22 – 0.42	0.03 – 0.27	0.11 – 0.22	0.05 – 0.17
Max brown moss cover (%)	43.6 – 70.5	36.9 – 56.4	20.5 – 36.9	43.6 – 63.1
Max *Sphagnum* moss cover (%)	0 – 29.5	50 – 63.1	0	0 – 43.6
Max water cover (%)	10.1 – 70.5	17.7 – 36.9	0 – 33.3	6.4 – 33.3

Group 1 (Table 2.4a; n = 5) was the most basic, although it had considerable overlap among the groups (pH 7.30 - 7.86), and it also had the highest conductivity (0.22 mS/cm - 0.42 mS/cm) out of the four groups. Among the four groups, Group 1 sites had the greatest brown moss maximum covers within quadrats (43.6% - 70.5%) and the greatest water maximum covers within quadrats (10.1% - 70.5%), with less *Sphagnum* moss maximum covers within quadrats (0% - 29.5%). Based on these characteristics, Group 1 sites are likely extreme-rich fens (Alberta Environment and Sustainable Resource Development (ESRD) 2015).

Group 2 (Table 2.4b; n = 5) was the most acidic (pH 6.12 – 7.72) and had the lowest conductivity (0.03 mS/cm - 0.27 mS/cm) among the four groups. Among the four groups, Group 2 sites had the greatest *Sphagnum* moss maximum covers within quadrats (50% - 63.1%), were moderately wet (17.7% - 36.9% quadrat maximum cover of water) and had lower brown moss maximum covers within quadrats (36.9% - 56.4%). Consequently, I characterize Group 2 sites as poor fens (Alberta Environment and Sustainable Resource Development (ESRD) 2015).

Groups 3 (Table 2.4c; n = 3) and Group 4 (Table 2.4d; n = 7) appear to be intermediates of Groups 1 and 2. Sites belonging to Group 3 were slightly more acidic (pH 6.98 – 7.76) and less conductive (0.11 mS/cm - 0.22 mS/cm) compared to Group 1, but had substantially less brown moss cover and no *Sphagnum* spp. cover. Sites belonging to Group 4 had pH and conductivity values similar to Group 2, but brown and Sphagnum spp. moss cover more like Group 1. Although both Group 3 and Group 4 are likely moderate-rich fens, Group 3 with little moss coverage, is characterized more as a graminoid fen type, whereas Group 4 is more of a shrubby fen type (Alberta Environment and Sustainable Resource Development (ESRD) 2015).

2.3.4 Vascular plant species respond individualistically to elevation

Comparing the maximum cover of common vascular plant species (i.e. species present at > 50% of my 20 valley-bottom peatlands) to site elevation reveals that common species are responding individualistically to elevation (Fig. 2.6). The peaks in maximum cover of common vascular plant species are not occurring at shared elevations, whether their maximum cover is relativized (Fig. 2.6b) or not (Fig. 2.6a). Following the results of the NMS ordinations, the niche plots were replotted replacing elevation for average conductivity and average pH, which were relatively strongly correlated to the NMS axes, in Appendix D.
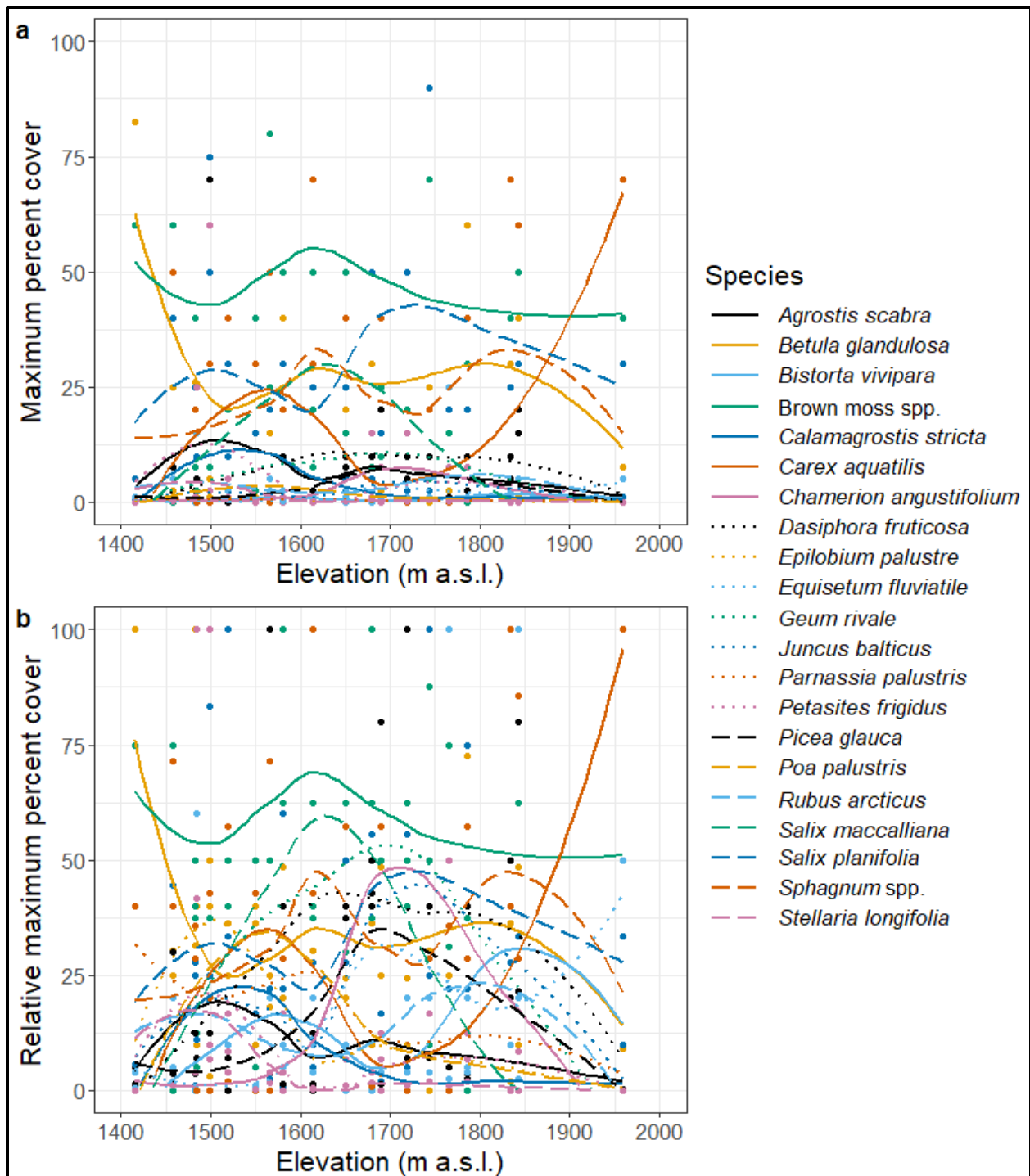
Figure 2.6. Species elevation niche plots for the 21 species present at >50% of sites showing a) their quadrat maximum percent cover values plotted against elevation (m a.s.l.) smoothed by the LOESS method; and b) showing their quadrat maximum percent cover values relativized by site maximum plotted against elevation (m a.s.l.) to increase visibility of trendlines of species with low percent cover values, smoothed by the LOESS method.

The species identified as significant indicators of the four vegetation assemblages tend not to be common. Only seven of 23 identified indicator species were present at 50% or more of my valley-bottom peatland sites and only 12 of 23 were present at 25% or more sites (Table 2.3). Interestingly, the elevations at which the maximum cover of these indicator species occurs do exhibit shared elevation optima (Fig. 2.7). The elevational optima are most clear when maximum quadrat-level cover is relativized by the maximum cover observed among my twenty sites (Fig. 2.8). For example, Group 4 indicators appear to reach maximum cover at about 1680 m a.s.l. (Fig 2.8d), whereas Group 2 indicators exhibit a shared maximum cover peak at about 1820 m a.s.l. (Fig. 2.8b). The pattern is not as clear without relativizing the maximum quadrat-level cover by the site maxima (Fig. 2.7), likely because the indicator species also tend to be present at low cover (Table 2.3).
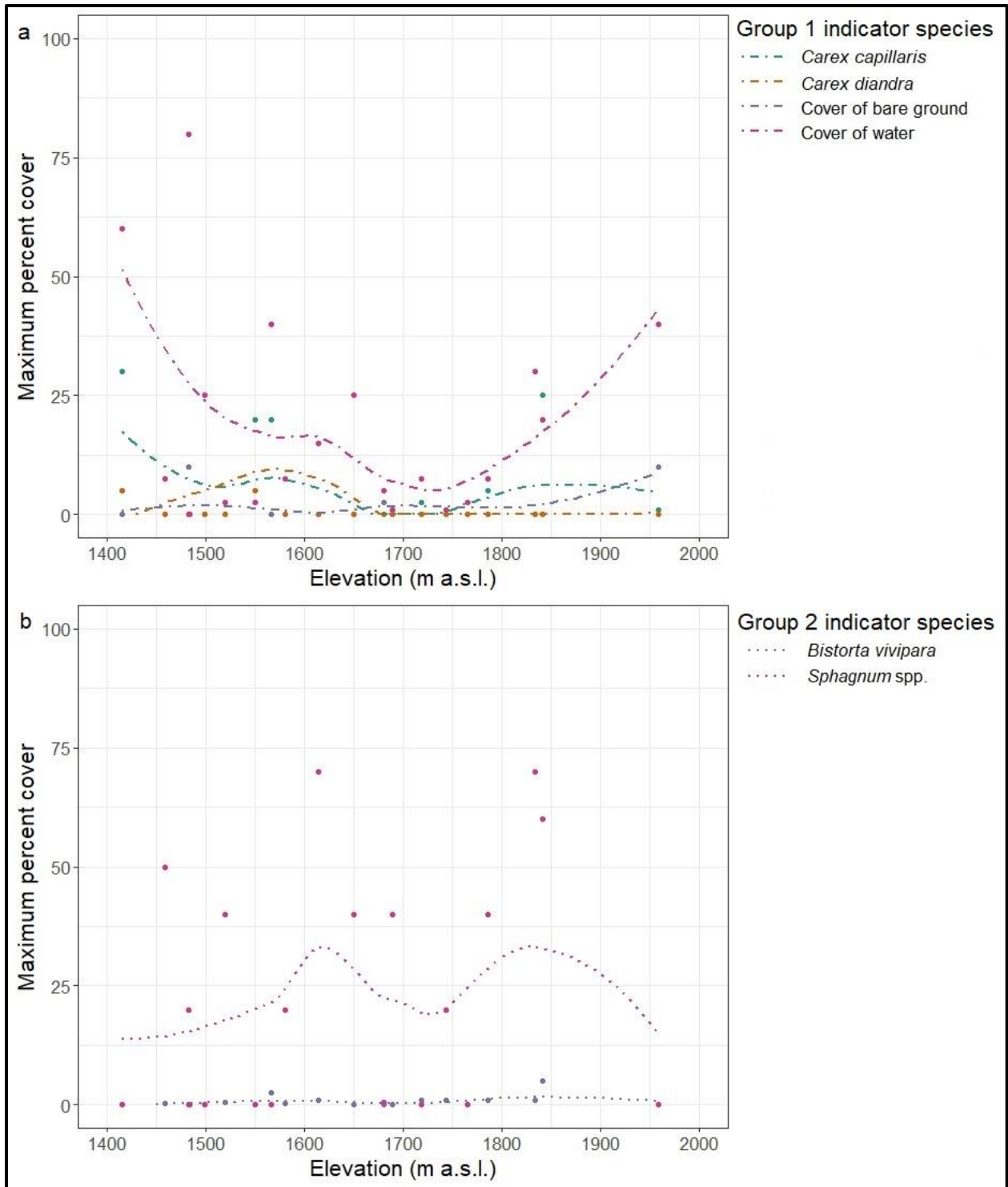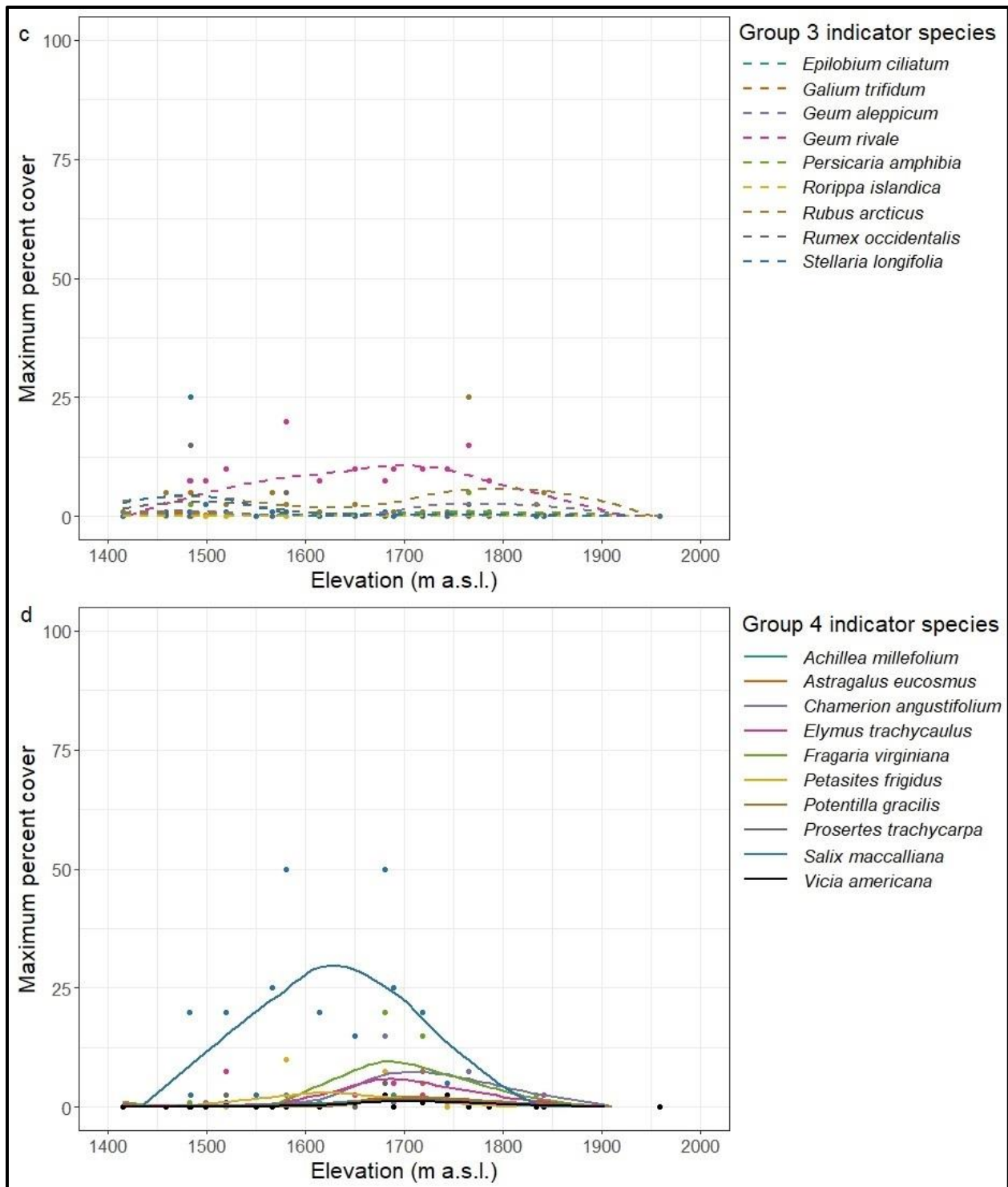
Figure 2.7. Species elevation niche plots for the significant indicator species of the four distinct assemblages comparing their quadrat maximum percent cover values plotted against elevation (m a.s.l.) smoothed by the LOESS method for: a) Group 1 in dot-dash lines, b) Group 2 in dotted lines, c) Group 3 in dashed lines, and d) Group 4 in solid lines
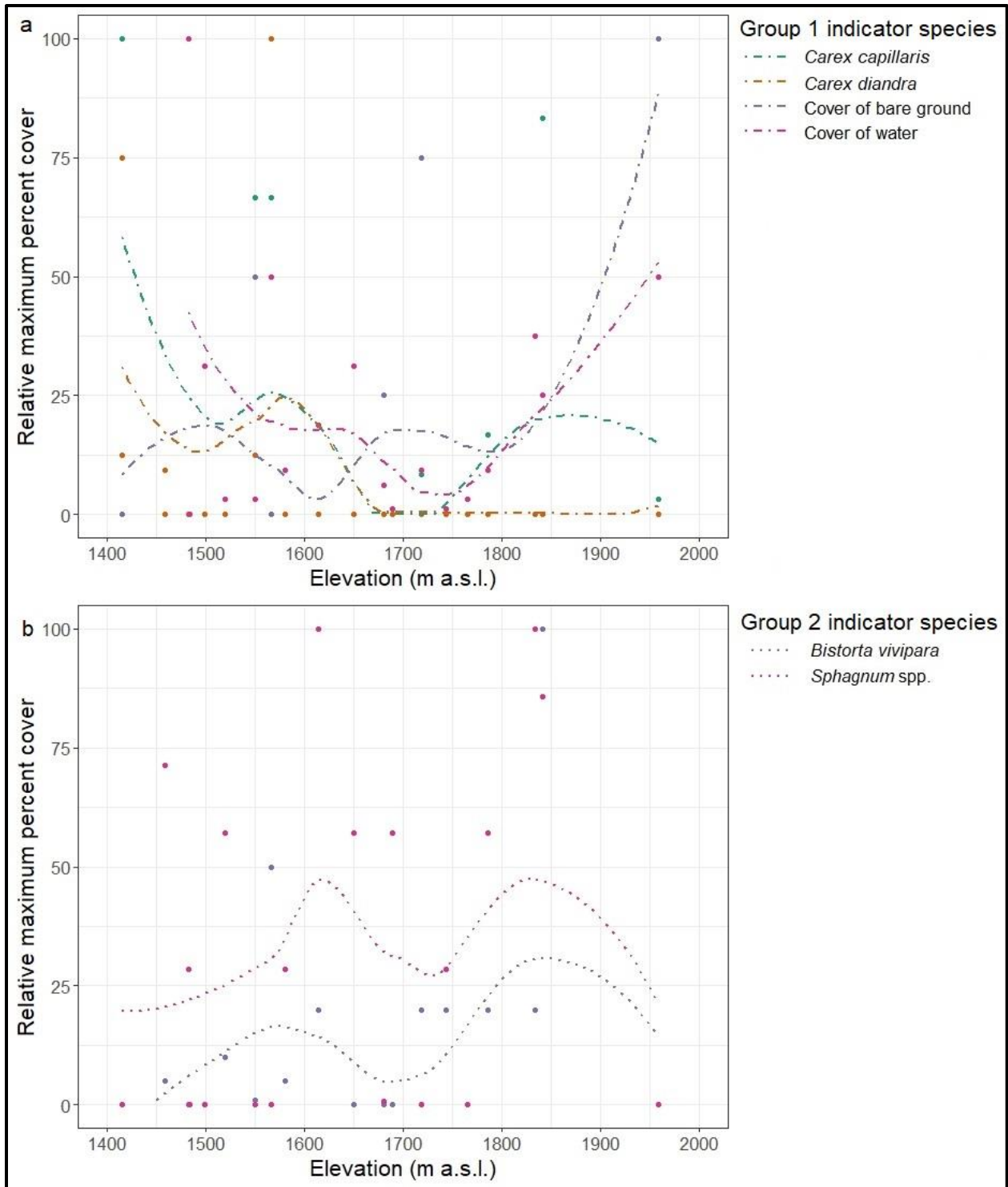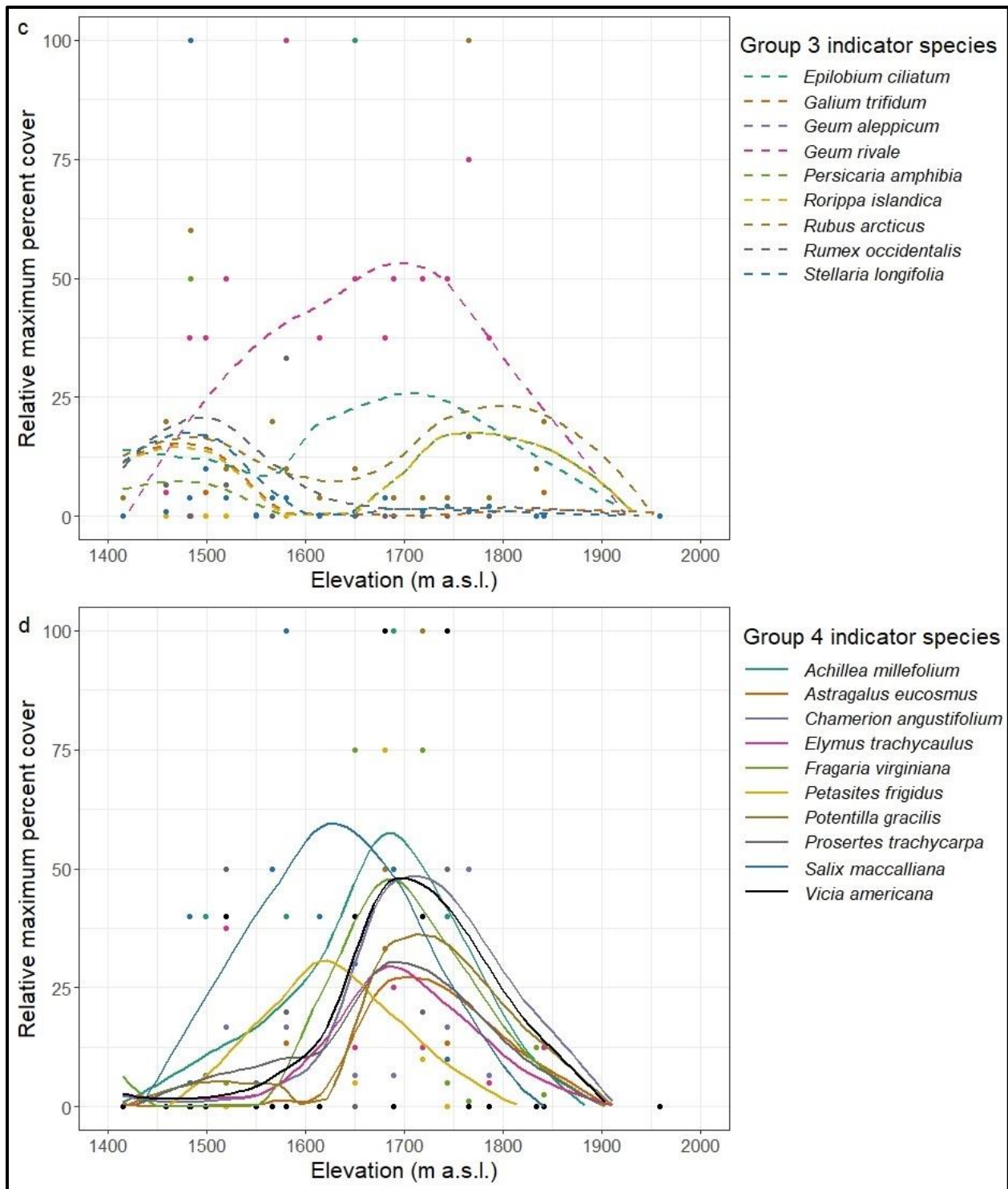
Figure 2.8. Species elevation niche plots for the significant indicator species of the four distinct assemblages comparing their quadrat maximum percent cover values relativized by site maximum plotted against elevation (m a.s.l.) to increase visibility of trendlines of species with low percent cover values, smoothed by the LOESS method: a) Group 1 in dot-dash lines, b) Group 2 in dotted lines, c) Group 3 in dashed lines, and d) Group 4 in solid lines.

41

2.4 Discussion

2.4.1 Environmental gradients explaining variation in vegetation composition

My first objective was to determine if vegetation composition changes along an elevation gradient and to determine if vegetation forms distinct assemblages sorted by elevation. I did identify distinct assemblages of co-occurring vascular plant and moss species, which formed four groups. Each group was identifiable by at least two statistically significant indicator species that demonstrated high fidelity and exclusivity to the group they were associated with (Table 2.3). Although these species occurred at low average percent covers ranging from a minimum of 0.75% to a maximum of 6.38% within quadrats, they were all typically identified within an average of 3.13 ± 0.94 minutes of the timed-walk survey. None of the species can thus be considered locally rare or difficult to identify, though very few were common across the whole suite of 20 peatlands I surveyed. This makes them practical indicators of their respective assemblages that may help surveyors better anticipate the co-occurring species that could be found in these mountain valley bottom peatlands, especially for surveys that are limited by time and human resources.

Contrary to my predictions, however, these groups were not sorted according to elevation. Elevation explained only minimal variation in vegetation composition among valley bottom peatlands. Each assemblage was present in at least one site in the Subalpine and one site in the Montane Natural Subregion, and elevation was not predictive of which group would occur in a peatland. Rather, the measured edaphic environmental variables, pH and conductivity, were more important drivers of variation in vegetation composition generally and were more predictive of which group would occur in a peatland than its elevation. That said, the indicator

species did evidence some degree of shared elevation optima when their maximum cover was plotted against elevation.

It is not surprising that soil pH and conductivity are important factors in predicting variation in vegetation community composition. Several other studies have concluded that soil pH is an important determinant of plant distributions in mountain peatlands (Chimner et al. 2010, Sekulova et al. 2011, Harbert and Cooper 2017). Chimner et al. (2010) also found that the concentration of ions in pore water was a key driver of vegetation composition, and this is likely captured by my measurements of conductivity. Soil conductivity and pH are also related to geomorphology (Cooper et al. 2010, Lemly and Cooper 2011), which dictates the water chemistry (Chimner et al. 2010, Lemly and Cooper 2011), and thus influences what plants will survive in a given peatland. Notably, pH and conductivity are key variables segregating among fen types and bogs, which have their own indicator species (Alberta Environment and Sustainable Resource Development (ESRD) 2015). Among the fen types, poor fens tend to be more acidic (pH < 5.5) and less conductive (conductivity < 0.1 mS/cm) than moderate rich fens (pH between 5.5 and 7.0; conductivity between 0.1 to 0.25 mS/cm) or extreme-rich fens (pH > 7.0; conductivity between 0.25 to 20 mS/cm), which are more alkaline, higher in conductivity, and can even be saline (Alberta Environment and Sustainable Resource Development (ESRD) 2015). Bogs are acidic (pH < 4.5) and generally low in conductivity (Alberta Environment and Sustainable Resource Development (ESRD) 2015). Plants are sorted by their ability to tolerate these conditions. For example, *Sphagnum* mosses and ericaceous species favour the acidic conditions of bogs and poor fens, whereas brown mosses and sedges tend to dominate moderate-rich and extreme-rich fens, favouring the more alkaline conditions (Alberta Environment and Sustainable Resource Development (ESRD) 2015). My four assemblages were categorized based

on these literature values and their significant indicator species where Group 1 was a extreme-rich fen, Group 2 was a poor fen, Group 3 was a graminoid moderate rich fen and Group 4 was a shrubby moderate-rich fen.

In terms of the low apparent importance of elevation in determining the distribution of plants in my study system, my results disagree with published studies by Naqinezhad et al. (2009) and Chimner et al. (2010). Instead, my results agree with studies by Sekulova et al. (2011), Lemly and Cooper (2011), Dyakov (2016), Harbert and Cooper (2017), who also found that other abiotic variables exerted greater influence than elevation on the distribution of peatland vegetation. Sekulova et al. (2011) suggests elevation might be a more important determinant of vegetation composition for higher altitude alpine peatlands, whereas pH had a greater role in structuring vegetation composition in subalpine peatlands in the West Carpathians, in Europe. Notably, all my twenty valley bottom peatlands were found either within the Subalpine or Montane Natural Subregions of the Albertan Rocky Mountains (Fig. 2.2). It is possible that if I had surveyed peatlands in the alpine region, elevation would have emerged as a more influential factor in determining vegetation community composition. Yet, in the Albertan Rocky Mountains, peatlands are exceedingly rare at elevations above the Subalpine Natural Subregion so I can only speculate about what factors might be important at such high elevations.

2.4.2 Relative strength of abiotic versus biotic filters

My second objective was to characterize how the distribution of plant species change along an elevation gradient. For the most common species (i.e. those that appear in at least half of the peatland sites), the change in community composition along the elevation gradient appears gradual. Vegetation cover for common species are individualistic in terms of their elevational niches. My findings thus support a more Gleasonian view of peatland plant communities, where

44

the effect of biotic filters is subordinate to the effect of abiotic filters in structuring my peatland communities (Gleason 1926). My results are in agreement with Dyakov (2016) who conducted a study of plant species distributions along an elevation gradient on Vitosha Mountain, in Western Bulgaria and found species curves of dominant vascular plant species along elevation to rarely exhibit symmetrical curves representing a single elevational optima, but more consistently found bimodal or complex species curves representing individualistic spatial patterns along each species' elevational niches.

Yet, for the subset of species that had high indicator values, there does appear to be some common elevation optima. Thus, although the primary drivers of vegetation composition appear to be more related to soil pH and conductivity in my study system and elevation only explains a weak, insignificant amount of the total variation in plant community composition, among the four distinct vegetation assemblages that I identified, I find some evidence that they may be sorted by elevation. However, this result relies on being very selective of the species I compare since the species with high indicator values are not ubiquitous or commonly distributed among my twenty peatlands, unlike my common species. Arguably, by comparing the most common species, this allows for more reliable conclusions regarding the trends of plant species distributions along an elevation gradient.

Group 1 indicator species appeared bimodal with peaks in maximum cover at the lowest and highest elevations I sampled, whereas Group 4 indicators appeared to peak in maximum cover between 1600 and 1700 m a.s.l. The two indicator species from Group 2 showed a common peak at around 1850 m a.s.l., suggesting that their optimal elevation might be slightly higher than those indicating Group 4. It is unclear from my study whether species within these assemblages are interacting to form consistent and self-reinforcing communities, or if these

45

patterns arise from a weaker effect of elevation in structuring these assemblages (see marginal

significance of the Mantel test between the concordance of elevation and patterns in vegetation

composition and the relatively strong correlation between elevation and the third NMS axis).

Perhaps increasing the number of sites sampled would yield sufficient statistical power to detect

a statistically significant influence of elevation on the distribution of plant and moss species in

my study system. However, it is clear from my study that elevation is not a primary determinant

of the distribution of plants and mosses in peatlands.

2.4.3 Future research

There is a strong need to locate, map, and characterize more valley bottom peatlands in

Alberta's Rocky Mountains. My study was limited by the need to locate many of these mountain

peatlands which reduced the number of sites I could survey. Critically, wetlands that are not

mapped cannot be studied, nor can they be conserved, and clearly these wetlands are important

habitat for a diversity of vascular plants and mosses.

In addition, knowledge of the abiotic gradients that structure these communities is

important to predict how climate change and other disturbances may affect the biodiversity,

health, and ecosystem services of these important peatland systems. Given that the specific

gradients that structure vegetation composition of my mountain peatlands are still not fully

understood, more local-scale environmental gradients and covariates such as site water table

stability, soil nutrients and properties, water chemistry, peat depth, slope, and aspect should be

analyzed with future surveys of vegetation in these mountain valley bottom peatlands. In

particular, the knowledge gaps regarding the water table stability of these mountain peatland

ecosystems provides important motivation for the continued study of these mountain valley

bottom peatlands. As climate change is expected to reduce the water availability supplied by

precipitation for wetland vegetation (Hauer et al. 1997), the water storage mechanisms by these peatlands and the role of groundwater in supplying the water balance of these systems to mitigate this change in water regime becomes an increasingly important research question. Further, aspect may also be an important consideration for future research since work by Danby and Hik (2007) observed an entire 1.0°C difference of soil temperatures between sites having a Northern aspect and sites having a Southern aspect. Aspect may also have a critical influence on the effects of climate change by determining the direction and magnitude of community composition change in mountain ecosystems (Danby et al. 2011). Overall, a better understanding of these environmental gradients and covariates will allow researchers to better predict and anticipate the changes to the underlying processes that may affect vegetation composition as a result of continued climate change. Improving our understanding of these mountain valley bottom peatlands is a critical investment to improve our conservation and decision-making ability in the upper Bow River basin area.

3 Sources of imperfect detection in peatland vegetation surveys

3.1 Introduction

3.1.1 Chapter context and scope

To prevent mismanagement of resources and poor decision making, imperfect detection caused by observer errors in species surveys must be limited (Dennett et al. 2018). Despite being sessile organisms, imperfect detection in vegetation surveys is ubiquitous (Morrison and Young 2016) and severe (Dennett et al. 2018). While the concept of imperfect detections is well established in animal surveys (MacKenzie et al. 2002), imperfect detections in plant surveys are seldom quantified and reported (Morrison and Young 2016). Notably, imperfect detections in plants are not limited to rare species but also occur with common species (Dennett et al. 2018), including those considered highly visible with distinct morphological features (Moore et al. 2011).

Imperfect detections include misidentifications of species (errors of commission) where a unique species is mistaken for one that is already accounted for in the plot, and false absences (errors of omission) where a species was present but was not seen (Dennett et al. 2018). These imperfect detections are most commonly quantified by comparing species lists between different observers, indicating the precision among estimates, rather than their accuracy (Morrison et al. 2019). This is because to indicate accuracy, species lists need to be compared with true values of species richness and occurrence at a site, which are rarely ever known with certainty (Morrison et al. 2019). Imperfect detections between species lists are reported quantitatively as pseudoturnover (Nilsson and Nilsson 1985), which ranges between 0 (where the list of recorded species between observers is identical) and 100 (where the list of recorded species between observers are entirely different). Pseudoturnover cannot distinguish between misidentifications

and false absences, as any inter-observer differences contribute equally to the pseudoturnover value.

Imperfect detections can be influenced by sampling design (Moore et al. 2011), environmental factors (Ng and Driscoll 2015), and plant traits (Chen et al. 2013). Errors from sampling design may be associated with the size of the study plots, quadrat size, or survey effort (Dennett et al. 2018). Errors may also be associated with environmental factors, such as elevation, which affects plant life stages (Chen et al. 2013), litter height (Ng and Driscoll 2015), and plant density and abundance (Dennett et al. 2018). Further, errors may be due to plant traits including plant size (Chen et al. 2013), or the absence of flowering structures (Ng and Driscoll 2015). Although environmental factors and traits of a study site cannot be controlled, errors associated with sampling design can be addressed with better sampling methods. For instance, including multiple visits and repeat observations (Kery et al. 2006, Bonneau et al. 2018), increasing search effort by increasing time spent at each site (Moore et al. 2011), or reducing quadrat sizes (Dennett et al. 2018) are potential ways to reduce imperfect detection in vegetation survey.

Though imperfect detections in plant surveys are gaining recognition, wetland plants are understudied compared with other terrestrial species. A recent review of 59 studies of imperfect detection in the literature indicated only two studies took place in wetland habitats (Morrison 2016): one in wet meadows and peat bogs (Lepš and Hadincová 1992), and the other in a sparsely wooded bog (Bråkenhielm and Qinghong 1995); subsequently followed by a study of imperfect detection in forested wetlands in Ohio (Morrison et al. 2019). To the best of my knowledge, no studies of imperfect detection, including studies on the environmental factors and functional traits that may affect imperfect detection of plant species, have been conducted in

mountain valley bottom peatlands. Certainly, none have been previously conducted in the Rocky Mountains of Alberta, where our understanding of peatland ecosystems is limited due to their remote location and unmapped status.

Understanding the extent of imperfect detentions in vegetation surveys of mountain peatlands and the methods to mitigate them is therefore an important issue since accurate measures of species richness and diversity are important in any vegetation assessment. This is particularly true for vegetation assessments conducted in remote locations where there is a direct trade-off between the intensity of each survey and the number of sites that can be surveyed. Thus, determining an optimal survey strategy for studying valley bottom peatlands in mountain habitats is critical to characterizing their condition and biodiversity value. More, any inferences around diversity-elevation patterns and the consistency of community composition along an elevation gradient (Chapter 2) relies on an accurate estimate of vegetation richness. The results of this chapter will therefore be pertinent to any future research into peatland vegetation richness and diversity.

3.1.2 Chapter objectives

In this chapter, I examine the quadrat-transect and timed-walked survey methods used to survey vascular plants to meet the following research objectives: (i) *To determine potential sources of imperfect detection in peatlands*; (ii) *To determine a best-practice and optimal survey strategy to minimize false absences in peatland vegetation surveys*.

First, I wanted to determine the potential sources of imperfect detections during timed-walk surveys in peatlands by answering the following research question: (a) *What functional traits and site-specific variables influence detectability of vascular plant species in peatlands?* Based on prior work by Dennett and Nielsen (2019), I expect that functional traits and site-

specific variables such as the cover of forbs, shrubs, graminoids, and trees, variables that

increase visual or physical obstruction, and the site species richness of vascular plants are

potential variables that could influence detectability of vascular plant species. This is because

errors are known to be more common in habitat with a greater plant density and abundance,

which can obstruct visibility and lead to errors of omission (Dennett et al. 2018). Such errors

may be more common for cryptic, rare, or inaccessible species (Dennett and Nielsen 2019),

which are more likely to occur in wetlands with higher total plant richness. Additionally, having

a greater number of species present at a site may increase the likelihood of misidentifications

(i.e. errors of commission).

Second, I wanted to determine a best-practice and optimal survey strategy to minimize

false absences in peatland vegetation surveys by answering the following question: (b) *What is*

the minimum survey time required to achieve <10% errors of omission? I predict that errors of

omission will decrease with increased survey time as increasing survey effort has been found in

previous studies to limit imperfect detection in vegetation surveys (e.g. Moore et al. 2011). In

addition, I examine the success of my survey methods, examining both their detections and

missed detections and answering the following question: (c) *Do my survey methods exhibit bias*

in failing to detect species of a certain growth form over others? I predict that both timed-walk

and quadrat-based survey methods will yield greater errors of omission of graminoid growth

forms, based on prior work by Chen et al. (2013) where graminoids were found to have the

lowest detection probabilities among forbs, shrubs, and trees due to higher probabilities of false

absences.

3.2 Methods

3.2.1 Study area & field methods

Between July 19 and August 12, 2019, I conducted vegetation surveys in twenty valley-bottom peatlands in the upper Bow River basin in Alberta's Rocky Mountains. Site selection and geographic position are described in Chapter 2.2.1 and a site list including coordinates, elevations, and site areas are in Appendix A. These peatlands were standardized to be of comparable size, and similar in aspect and slope (gentle slope topography in valleys mainly running East to West), but spanned an elevation gradient from 1415 – 1959 m a.s.l.

At each site, I identified vascular plants following a quadrat-transect survey design described in Chapter 2.2.2 to collect relative cover of vascular plant species within quadrats along transects and generate a species list. The active search times for each of the 15 quadrats per site (i.e. the time spent locating species within quadrats, but not including time spent to set-up quadrats, identify species using field guides, etc.) were recorded using a stopwatch. This was conducted to comment of the relative efficiency of the quadrat survey method to identifying vascular plants compared to the timed-walk survey method used in this study. Subsequently, I conducted 15-minute timed walks at each peatland to identify vascular plant species encountered. This order in survey method was consistent among sites and was implemented to prevent inadvertent trampling of quadrats during timed walks. Also, it ensured that I remained consistent among my sites, in case there was a priming effect of doing one survey method before the other, and preserved the site-to-site comparability, which was needed for Chapter 2. The 15-min timed walks by myself (CL) and independent observer with equivalent training and background in peatland vegetation surveys (MB) were constrained to a 3.14 ha area that comprised a 100 m radius circle around the center of the middle transect. For the timed walk

survey, MB and CL, simultaneously recorded the time to first-detection for each vascular plant

species encountered at the site to generate two independent observations of the species present

and their respective time to first-detection. Both observers identified all vascular plants to species

level, following taxonomy in Moss and Packer (1983), Vitt et al. (1988), and Johnson et al.

(1995). I later cross-referenced and updated all plant identifications, using the Integrated

Taxonomical Information System (ITIS) database (Integrated Taxonomic Information System

2020).

Henceforth, "quadrat-transect survey" refers to the combined data from the quadrat and

transect surveys; "quadrat survey" refers to only data from the quadrats; and timed-walk survey

refers to the 15-minute timed walk survey for vascular plants and the related occurrence and time

to first detection data.

Where possible, I also collected at least ten leaf samples spread across multiple plants for

each shrub species present at each site, selecting for whole, fresh leaves with access to the sun

and with no signs of pathogens or damage by insects. Using a leaf scanner (LI-3000A Portable

Area Meter and LI-3050A Transparent Belt Conveyer Accessory, LI-COR, Lincoln, Nebraska), I

recorded and calculated the mean leaf surface area for each shrub species. After, I dried the leaf

samples in a drying oven at 80°C for at least 24 hours to reach a constant weight, and then

gravimetrically determined the total dry mass on an analytical balance with 0.001 g accuracy

(MS204S Analytical Balance, Mettler Toledo, Columbus, Ohio). Using these values, I calculated

the specific leaf area (SLA) for each species of shrub present.

3.2.2 Statistical analyses

Pseudoturnover

I wanted to determine if vegetation cover by growth form, total richness of vascular plants, or the specific leaf area of shrubs influenced detectability of vascular plant species in peatlands (objective 1). Thus, I needed to quantify pseudoturnover and errors of omissions between the two independent observers, MB and CL using the species lists generated by the timed-walk surveys for vascular plants. I calculated pseudoturnover for each minute of the 15-minute timed walk for both observers using the equation from Nilsson and Nilsson (1985):

$$pseduoturnover = ((S_a + S_b)/(S_{aa} + S_{bb})) \times 100,$$

where S_a is the number of unique species recorded by MB not recorded by CL, S_b is the number of unique species recorded by CL not recorded by MB, S_{aa} is the total number of species recorded by MB, and S_{bb} is the total number of species recorded by CL.

Modelling pseudoturnover with functional traits and site-specific variables

I used a model competition framework to test among alternative general linear models predicting pseudoturnover using variables related to richness, growth form and visual or physical obstruction to determine which of these variables most influence the detectability of vascular plants in peatlands (objective 1). I tested the models using pseudoturnover calculated at three separate timepoints: 5 minutes, 10 minutes, and 15 minutes into the timed-walk survey for vascular plants, to determine if increasing the survey time would influence which function traits or site-specific variables contributed to pseudoturnover.

For each timepoint, I had one null model (intercept only) and nine hypothesized models using the predictors of pseudoturnover: 1) mean specific leaf area (SLA) of shrubs 2) mean forb

cover, 3) mean graminoid cover, 4) mean shrub cover, 5) mean tree cover, 6) site species richness, 7) visual obstruction to observers (i.e. mean forb cover + mean graminoid cover), 8) physical obstruction to observers (i.e. mean shrub cover + mean tree cover), 9) a fully saturated model that included all hypothesized terms (i.e. mean specific leaf area of shrubs + mean forb cover + mean graminoid cover + mean shrub cover + mean tree cover + site species richness). I calculated the mean SLA of shrubs by taking the average of the SLA values among the shrub species present at each site. I prepared mean forb cover, mean graminoid cover, mean shrub cover, and mean tree cover, using the quadrat survey data where each species was renamed by their growth form (i.e. forb, graminoid, shrub, or tree) and averaged to calculate a per site value for each variable. Finally, I obtained a value for site species richness from the combined data from all survey methods (i.e. transect-quadrat survey, timed walk survey for vascular plants, and timed walk survey for mosses) which produced a species lists in the form of occurrence data.

I conducted a separate Akaike information criterion corrected for small sample size (AICc) model competitions at each of the three timepoints using the "AICc" function in the "MuMIn" package (Barton 2020) and an alpha value of 0.05 to evaluate the significance of the best supported general linear model of the hypothesized models using R version 3.6.3 (R Core Team 2020).

Minimizing errors of omission

Since I needed to determine the minimum survey time required to achieve less than 10% errors of omission (objective 2), I made species accumulation curves for each valley-bottom peatland site based on: 1) the abundance data of vascular plant species from the quadrat survey approach; and 2) the average time to first detection of vascular plant species between two independent observers, MB and CL, and the occurrence data from the timed walk survey

approach. To smooth the curves, I used the average species richness (S mean) values calculated

by EstimateS 9.1.0 (Colwell 2013) to visualize the number of vascular plant detections as the

number of quadrats or survey time increased. S mean is the estimated species richness of the site

removing the influence of quadrat or minute interval order by shuffling the quadrat or minute

interval order for 100 permutations and then computing the average richness of the 100 different

runs. With the quadrat surveys, for each site I plotted the cumulative number of species observed

with each additional quadrat (n = 15 quadrats). With the timed walks, for each site I plotted the

cumulative number of species observed over one-minute intervals (n = 15 minutes). For species

observed by both observers during the timed-walks, I used the average time to detection. I then

determined the point at which the species richness observed from the 15-minute timed-walks

plateaus and calculated the minimum survey time required to minimize errors of omission to

10% at each of my twenty valley bottom peatland sites.

Comparison of survey approaches

I wanted to compare the quadrat survey approach with the timed-walk survey approach,

to comment on their respective ability to detect vascular plant species in valley-bottom peatlands

and to better understand their respective advantages and disadvantages (objective 2).

First, I used EstimateS 9.1.0 to obtain non-parametric estimators of "true" species

richness based on the frequency of rare species for both the quadrat survey approach and timed-

walk survey approach (Colwell 2013). Specifically, for the quadrat survey approach, since I had

abundance-based data, I determined the Chao index for abundance data (Chao1) (Chao 1987),

the abundance-based coverage estimator (ACE) (Chazdon et al. 1998, Chao et al. 2000), and the

first-order Jackknife (Jack1) (Burnham and Overton 1978, 1979, Heltshe and Forrester 1983,

Smith and van Belle 1984); and for the timed-walk survey approach, since I had incidence-based

(i.e. occurrence) data, I determined the Chao index for occurrence data (Chao2) (Chao 1984, 1987), the incidence-based coverage estimator (ICE) (Chazdon et al. 1998, Chao et al. 2000), and the first-order Jackknife (Jack1) (Burnham and Overton 1978, 1979, Heltshe and Forrester 1983, Smith and van Belle 1984).

Using a range of estimators is recommended because each index varies in their bias (Gwinn et al. 2015) and has their own advantages depending on the type of data. The abundance-based and incidence-based Chao indices (Chao1 & Chao2) consider the number of rare species in my species lists that only appear once or twice and extrapolates how many species are likely even more rare to estimate the "true" species richness of the sites (Chao 1984, 1987). The abundance-based and incidence-based coverage estimators (ACE & ICE) use the same approach as the Chao indices, but considers species that occur one to ten times in estimating "true" richness (Chazdon et al. 1998, Chao et al. 2000). The first-order Jackknife (Jack1) estimate examines the sampling progress by determining the number of species that could have been missed if fewer quadrats or minute intervals were surveyed and estimating the number of missing species from the actual set of quadrats or minute intervals (Burnham and Overton 1978, 1979, Heltshe and Forrester 1983, Smith and van Belle 1984). I compared these non-parametric estimators of "true" richness to each site's observed vascular plant richness measured using the quadrats and the timed walks to determine the success of each survey method in capturing the "true" richness.

In addition, I wanted to examine the differences between the quadrat-transect survey approach and the timed-walk survey approach in terms of their respective missed detections. I compared the combined quadrat-transect survey approach and the timed-walk survey approach by visualizing the missed vascular plant species detections for each approach, grouped to their

57

growth form (i.e. forb, graminoid, shrub, or tree), in stacked-bar charts. I determined if one survey approach was preferentially missing detections of a growth form group by using a two-way ANOVA, and an alpha of 0.05 to compare the proportion of missed detections between the two survey approaches in RStudio version 3.6.1 (R Core Team 2020).

Equally, I wanted to examine the difference between the quadrat-transect survey approach and the timed-walk survey approach in terms of which vascular plant species they were consistently detecting or missing. I was interested in the kinds of detections each survey approach was making, and to determine if there were any particularly faithful species that were being detected by one survey method consistently over the other. I used an indicator species analysis to determine if there were any species significantly (alpha = 0.05) associated with one of the two survey approaches, using PC-ORD 7.08 (McCune and Mefford 2016). The indicator species analysis calculates an indicator value for each species by taking the product of the species' faithfulness to a particular survey approach and exclusivity to that survey approach, multiplying by 100 and then using a Monte Carlo randomization test to assign a p-value.

3.3 Results

3.3.1 Site species richness of vascular plants influences pseudoturnover for short survey times

Mean pseudoturnover between the two independent observers, MB and CL, among my twenty sites (n = 20) at the end of their 15-minute timed walk surveys was approximately 23.95% ± 10.39% (standard deviation). Of the nine hypothesized models, only site species richness influenced pseudoturnover during the timed-walk survey for vascular plants, but only at the 5 minute survey durations (multiple r^2 = 0.205, AICc = 136.837), although the null model (intercept only) also had substantial support in predicting pseudoturnover after 5 minutes (AICc

= 137.669; Table 3.1a). In contrast, none of the nine hypothesized models were better than the null model (intercept only) at predicting pseudoturnover at 10 minutes (Table 3.1b) and 15 minutes (Table 3.1c) of survey time. Even though models using vascular plant species richness received substantial support given the data (ΔAICc = 1.782 and 0.577, for 10 and 15 minutes, respectively), the models were weak predictors of pseudoturnover (multiple r^2 = 0.094 and 0.147 at 10 and 15 minutes, respectively). Overall, the influence of vascular plant richness at a site on pseudoturnover in timed walk surveys becomes negligible within 10 min of survey effort.

Table 3.1. General linear models relating pseudoturnover to site-specific variables representing different conditions of the search environment ($n = 20$) at survey times: a) 5 minutes; b) 10 minutes; and c) 15 minutes. The K penalty per parameter, AICc values, delta AICc (ΔAICc) values, and AICc weights are listed for each hypothesized model.

a. *Pseudoturnover calculated at 5 minutes*

Hypothesized models	K	AICc	ΔAICc	AICc weights
Null (intercept)	0	137.669	0.832	0.252
SLA of shrubs (mean specific leaf area)	1	141.394	4.557	0.039
Mean forb cover	1	138.825	1.988	0.141
Mean graminoid cover	1	141.398	4.561	0.039
Mean shrub cover	1	141.401	4.564	0.039
Mean tree cover	1	139.538	2.701	0.099
Site species richness of vascular plants	1	136.837	0.000	0.382
Visual obstruction (mean forb + mean graminoid cover)	2	145.738	8.901	0.004
Physical obstruction (mean shrub + mean tree cover)	2	146.391	9.554	0.003
Fully saturated model with above terms	6	218.008	81.171	0.000

b. *Pseudoturnover calculated at 10 minutes*

Hypothesized models	K	AICc	ΔAICc	AICc weights
Null (intercept)	0	129.468	0.000	0.399
SLA of shrubs (mean specific leaf area)	1	133.213	3.745	0.061
Mean forb cover	1	133.031	3.562	0.067
Mean graminoid cover	1	133.928	2.459	0.117
Mean shrub cover	1	131.889	2.420	0.119
Mean tree cover	1	133.116	3.647	0.064
Site species richness of vascular plants	1	131.250	1.782	0.164
Visual obstruction (mean forb + mean graminoid cover)	2	138.584	9.115	0.004
Physical obstruction (mean shrub + mean tree cover)	2	138.749	9.280	0.004
Fully saturated model with above terms	6	211.084	81.616	0.000

c. *Pseudoturnover calculated at 15 minutes*

Hypothesized models	K	AICc	ΔAICc	AICc weights
Null (intercept)	0	127.448	0.000	0.389
SLA of shrubs (mean specific leaf area)	1	131.163	3.715	0.061
Mean forb cover	1	130.813	3.365	0.072
Mean graminoid cover	1	131.163	3.715	0.061
Mean shrub cover	1	131.149	3.700	0.061
Mean tree cover	1	131.197	3.748	0.060
Site species richness of vascular plants	1	128.025	0.577	0.292
Visual obstruction (mean forb + mean graminoid cover)	2	137.705	10.257	0.002
Physical obstruction (mean shrub + mean tree cover)	2	138.065	10.616	0.002
Fully saturated model with above terms	6	203.655	76.207	0.000

3.3.2 Survey approaches did not capture all species present

Species accumulation curves for the quadrat survey of vascular plants at each of the twenty sites passed the inflection point but did not plateau, suggesting more quadrats are likely required to capture the full complement of vascular plant species at each site (Fig. 3.1). On the contrary, using visual examination of the species accumulation curves for the 15 minute timed-walk for vascular plants based on the average time to first detection between two independent observers and their combined occurrence data, each accumulation curve passed the inflection point and beings to plateau approximate between 2 – 5 minutes of survey time, suggesting that a sufficient survey time was completed to capture the full complement of vascular plant species at each site that could be detected using this survey method (Fig. 3.2).

Based on my species accumulation curves from the timed-walk surveys, when solving for the minimum survey time required to minimize errors of omission to 10% (i.e., to capture 90% of species present), the minimum survey time averaged among my twenty sites (n = 20) to approximately 9.35 minutes ± 3.47 minutes (standard deviation).

These findings are further supported by comparing the observed species richness of each survey method with their non-parametric estimators of "true" richness (Table 3.2). The observed species richness for the quadrat survey approach captured an average of 85.9% of the ACE estimate, 77.1% of the Chao1 estimate, and 77.3% of the Jack1 estimate of "true" richness. Whereas, the observed species richness for the timed-walk survey approach captured among my twenty sites an average of 99.3% of the ICE estimate, 99.3% of the Chao2 estimate, and 98.3% of the Jack1 estimate of "true" richness.

Despite plateauing species accumulation curves with the timed walk surveys, when I compared the species richness observed by combining the quadrat-transect survey and the timed-

61

walk survey approaches, I found that the timed-walks failed to capture all species present. In other words, there were some vascular plant species that were only detected by the quadrat survey approach. The reverse was also true: some vascular plant species were only detected by the timed-walk surveys, resulting in turnover between the two survey methods. However, because the quadrat-transect surveys did not achieve a plateau in species richness after the 15 quadrats, it is not possible to say definitively whether additional quadrats would have eventually captured all the species that were detected by the timed-walk surveys. If that were the case, the timed-walk survey estimates of vascular plant richness would represent a nested subset of the species detected by the quadrat-transect method.
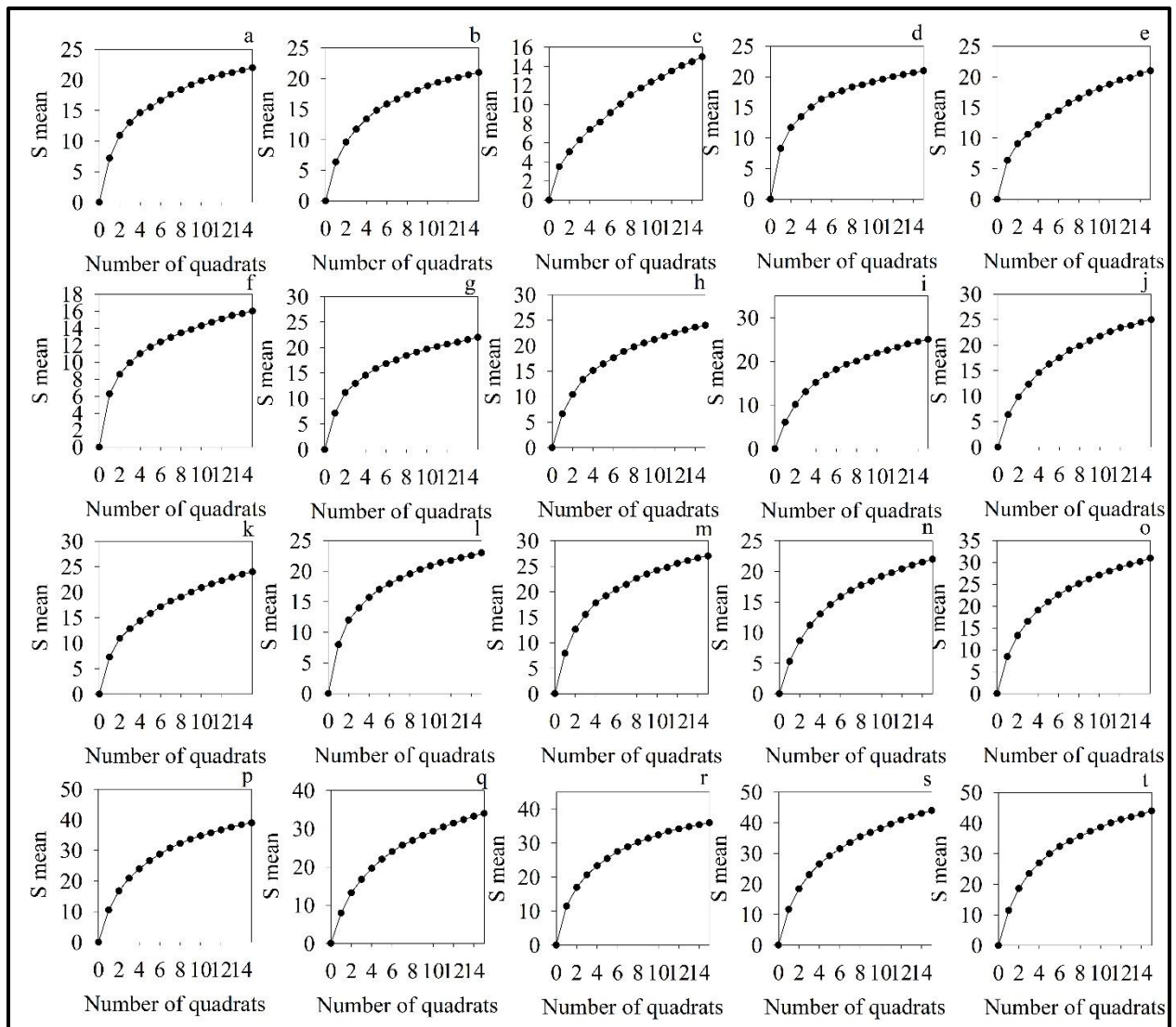
Figure 3.1. Species accumulation curves of vascular plant detections for the quadrat survey approach plotting S mean, the average number of species over 100 randomized shuffles of quadrat order as the number of quadrats (n = 15) increases for each of the 20 valley bottom peatland sites, ordered by increasing vascular plant species richness: a) MN33; b) MN02; c) SA01; d) SA20; e) MN28; f) MN34; g) SA32; h) MN22; i) MN31; j) MN21; k) MN01; l) MN32; m) SA26; n)SA33 o) SA23; p) MN25; q) SA34; r) SA31 s) SA30; t) SA25.
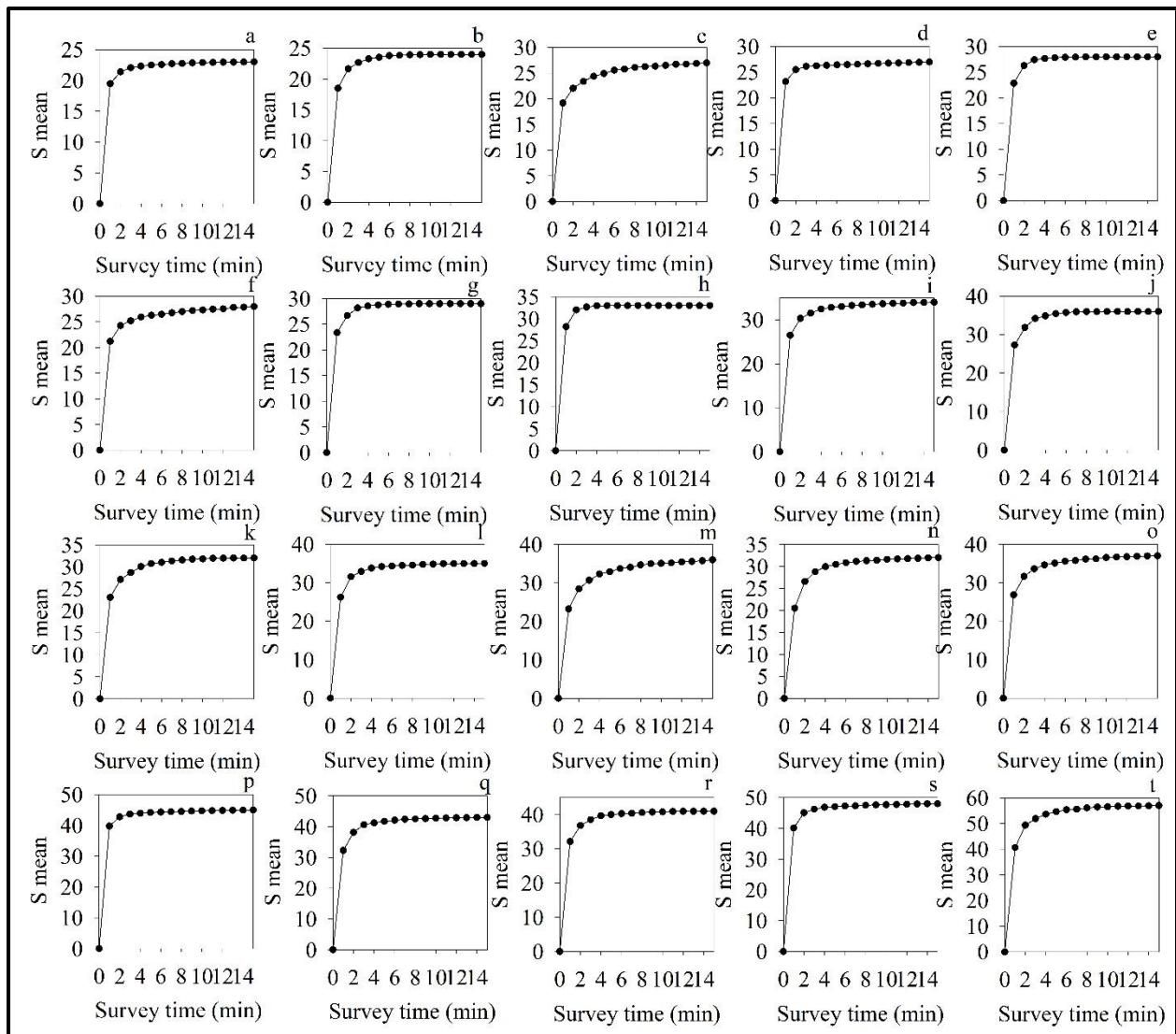
Figure 3.2. Species accumulation curves of vascular plant detections for the 15 minute timed-walk survey approach plotting S mean, the average number of species over 100 randomized shuffles of minute-interval order as the survey minute-intervals (n = 15) increases, based on the average time to first detection between two simultaneous, independent observers, for each of the 20 valley bottom peatland sites, ordered by increasing total vascular plant species richness: a) MN33; b) MN02; c) SA01; d) SA20; e) MN28; f) MN34; g) SA32; h) MN22; i) MN31; j) MN21; k) MN01; l) MN32; m) SA26; n)SA33 o) SA23; p) MN25; q) SA34; r) SA31 s) SA30; t) SA25.

64

Table 3.2. Summary table of vascular plant species richness estimates comparing the combined species richness (S) observed between the quadrat-transect survey and timed-walk survey, and the species richness estimates for a) quadrat survey: species richness (S) observed, mean abundance-based coverage estimator (ACE mean), mean abundance-based Chao index (Chao1 mean), and mean first-order Jackknife (Jack1 mean) calculated from vascular plant abundance data from 15 quadrats; and b) timed-walk survey: species richness (S) observed, mean incidence-based coverage estimator (ICE mean), mean incidence-based Chao index (Chao2 mean), and mean first-order Jackknife (Jack1 mean) calculated from vascular plant occurrence data over 15 minutes of timed-walk surveys, where the time at detection was averaged between two simultaneous independent observers.

Site	Combined survey method S observed	a) Species richness estimates calculated from quadrat survey				b) Species richness estimates calculated from timed-walk survey			
		S observed	ACE mean	Chao1 mean	Jack1 mean	S observed	ICE mean	Chao2 mean	Jack1 mean
MN33	27	22	23.89	23.12	27.6	23	23	23	23
MN02	27	21	23.61	25	26.6	24	24	24	24
SA01	30	15	19.34	22.99	21.53	27	27.38	27.47	27.93
SA20	32	21	22.34	25.49	25.67	27	27.32	27	27.93
MN28	32	21	23.63	23.66	28.47	28	28	28	28
MN34	34	16	18.82	20.5	20.67	28	29.02	29.87	29.87
SA32	34	22	24.44	27.99	27.6	29	29	29	29
MN22	36	24	26.06	28	30.53	33	33	33	33
MN31	36	25	28.15	31.24	32.47	34	34.34	34	34.93
MN21	36	25	29.59	42.97	33.4	36	36	36	36
MN01	36	24	25.78	28.5	32.4	32	32	32	32
MN32	39	23	29.24	27.16	28.6	35	35	35	35
SA26	40	27	30.43	36.99	33.53	36	36.74	36.93	37.87
SA33	41	22	24.98	24.25	28.53	32	32.24	32.47	32.93
SA23	42	31	49.49	40.99	40.33	37	37.3	37.16	37.93
MN25	47	39	43.8	70.96	50.2	45	45.33	45	45.93
SA34	48	34	40.81	46.23	45.2	43	43.23	43	43.93
SA31	55	36	42.88	43.99	43.47	41	41	41	41
SA30	58	44	53.54	59.11	58	48	48.34	48	48.93
SA25	62	44	51.36	84.47	58.93	57	57.28	57.47	57.93

3.3.3 Some bias in detections and missed detections of survey approaches

Growth form bias in survey approaches

The quadrat-transect survey approach, compared to the timed-walk survey approach, had more overall missed detections over the twenty peatland sites and in general detected fewer species than the timed-walk survey approach (Fig. 3.3a). There was also a bias in detection of one or more growth forms of one survey method compared to the other as determined by a significant interaction effect between the survey approach and the growth forms (Fig 3.3b; Two-way ANOVA, $F_{3,152} = 14.162$, $p = 3.46 \times 10^{-8}$).
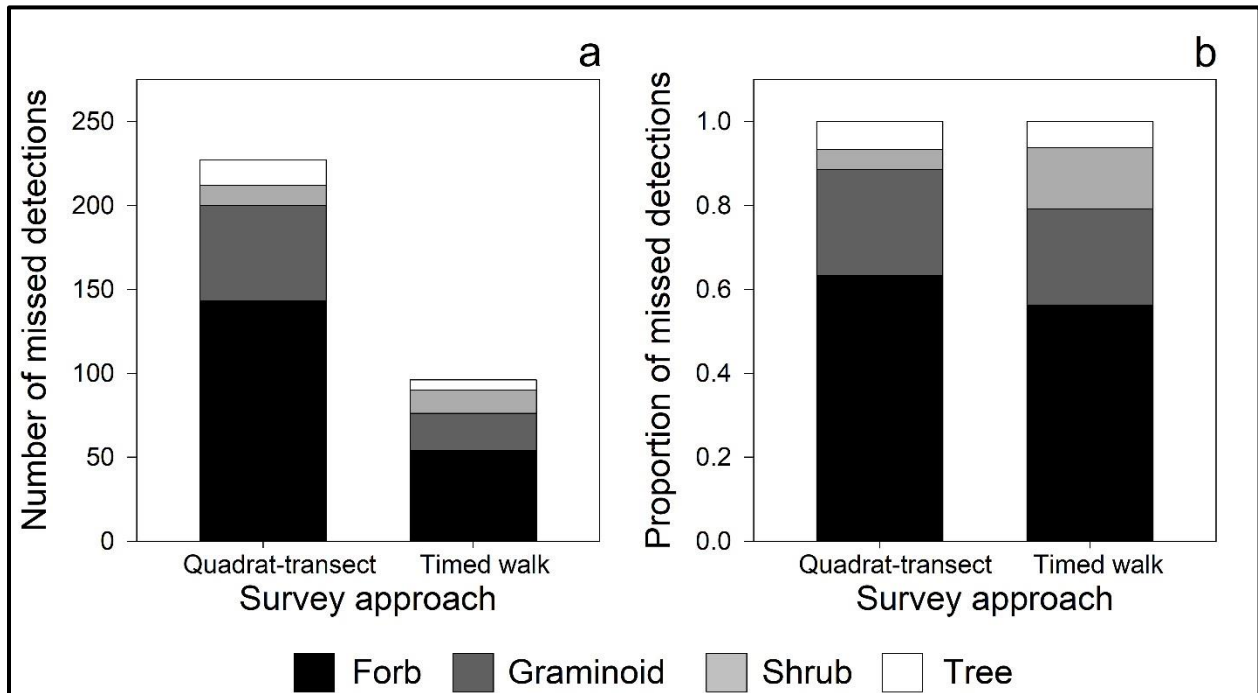
Figure 3.3. a) Stacked bar graph showing the total number of missed species detections for the quadrat-transect and timed walk survey approaches over 20 sites; and b) stacked bar graph showing the proportion of total missed species detections for the quadrat-transect and timed walk survey approaches over 20 sites. Missed species detections are grouped by their growth forms where black represents forb, dark gray represents graminoid, light gray represents shrub, and white represents tree.

Limited species bias between the two survey approaches

Indicator species analysis of the detections by the two survey approaches determined two significant indicators of the timed-walk survey approach: *Arnica chamissonis* (observed indicator value = 38.5, *p* = 0.0472) and *Pedicularis groenlandica* (observed indicator value = 55.6, *p* = 0.0216) out of 147 species total. There were no statistically significant indicator species for the quadrat-transect survey approach. Overall, this suggests that other than the two species which were consistently found by the timed-walk survey approach and typically missed by the quadrat-transect survey approach, there was no consistent species bias between the two survey approaches. The turnover in vascular plants identified by the two survey methods was not consistent, from one site to another.

3.4 Discussion

3.4.1 Sources of imperfect detections in peatlands

My first objective was to determine potential sources of imperfect detections in peatland vascular plant surveys. I examined nine hypotheses representing how growth forms, visual or physical obstruction, and total species richness might predict pseudoturnover. I did not observe any influence of vascular plant coverage (i.e. mean forb cover, mean graminoid cover, mean shrub cover, or mean tree cover) on pseudoturnover. This was contrary to Dennett and Nielsen's (2019) study of boreal forest surveys which concluded that, surprisingly, increased total vascular plant cover actually reduced pseudoturnover, possibly due to increased cautiousness by observers. Instead, I found that the site's species richness of vascular plants was the best predictor of pseudoturnover during brief (5 minutes) timed-walk surveys, though the importance of species richness diminished with increased survey time. This suggests that vascular plant richness was predictive of pseudoturnover simply because when there are more species to

identify it takes longer to detect them all, and the two independent observers were encountering the species in a unique order during their timed-walk surveys. If time was a constraint, this alone could account for greater species list overlap between the two observers at sites with lower vascular plant richness. Alternatively, a site with higher total species richness of vascular plants may have a greater number of rare species or species growing at low densities, which Dennett et al. (2018) demonstrated have lower detection probabilities. This could also explain higher errors of omission and pseudoturnover in sites with higher vascular plant richness.

Collectively, my results provide strong evidence that 15 minutes timed-walk surveys are sufficient in duration and that longer surveys would not increase observed vascular plant richness. First, for surveys > 10 minutes, pseudoturnover was no longer best predicted by species richness. Second, when the detections by the two observers were combined, there was extremely high agreement between observed and non-parametric estimators of "true" richness. Third, the combined species accumulation curves plateaued within about 10 minutes and suggest that survey time was not limiting the observed richness of vascular plants.

In general, even after 15 minutes, the pseudoturnover in my timed-walk surveys remained on average 23.95% ± 10.39% (standard deviation). Thus, there must be other variables contributing to pseudoturnover, as none of my hypothesized models were strongly predictive of pseudoturnover. Dennett and Nielsen (2019) observed an increase total pseudoturnover at sites with more structurally complex vegetation (i.e. greater horizontal cover and mean transect cover) likely due to increased distractions at these sites with more complex understories. It is possible that horizontal cover similarly influences pseudoturnover in my peatland sites. However, since I did not measure this site-specific variable in my study, horizontal cover should be considered in future studies of imperfect detections in peatlands.

Pseudoturnover could also be determined by variables related to sampling design and survey methods, rather than growth form and cover-related variables. Observer background and experience (Morrison and Young 2016, Morrison et al. 2019), and observer fatigue (Moore et al. 2011, Morrison and Young 2016) have been documented in some studies to influence detectability. In my study I attempted to control for this by ensuring the observers had equivalent training, identification experience and familiarity with species present within my peatland sites. However, trampling of sites by observers was noted by Morrison et al. (2019) as a potential source of error in their study on pseudoturnover in the sampling of vegetation in forested wetlands in Ohio. Specifically, trampling by one observer made it more difficult for the other to see some herbaceous species (Morrison et al. 2019). Since trampling of sites is unavoidable in timed-walks, it is a plausible potential source of error in the timed-walk surveys conducted in my study. Future studies of imperfect detections in peatlands should consider investigating such potential sources of error.

3.4.2 Pseudoturnover is ubiquitous and can be severe

Pseudoturnover values involving vegetation surveys conducted by two observers reported in the literature range between 11.4% and 33.4% across a diverse set of habitat types, and average 18% (calculated from: Nilsson and Nilsson 1985; Lepš and Hadincová 1992; Scott and Hallam 2002; Kercher et al. 2003; Gray and Azuma 2005; Burg et al. 2015; values summarized in Morrison 2016). Average pseudoturnover between my two independent observers among my twenty sites fell within this range at 23.95% ± 10.39% (standard deviation) for the 15-minute timed-walk survey. This pseudoturnover value is very similar to the 24% reported in a study conducted mainly in grasslands and woodlands of the UK by Scott and Hallam (2002). Among eleven sites, Scott and Hallam (2002) found an average of 92 species per site, although this value

included mosses and lichens in addition to vascular plants. For comparison, my twenty sites average approximately 44 vascular plant species per site. This demonstrates the level of pervasiveness and the severity of imperfect detections that can exist in vegetation surveys and makes clear the value in having two, independent observers complete timed-walk surveys simultaneously. Not only do they provide safety for one another in remote field locations like the mountain peatlands I studied, but by combining their observations, I reduced errors of omission and maximized detections of vascular plant species, evidenced by the plateauing species accumulation curves. Species missed by one observer were fortunately caught by the other.

3.4.3 Combination of survey approaches

There are a variety of advantages and disadvantages associated with the quadrat and timed-walk survey approaches. For the timed-walk survey, my species accumulation curves based on the average time to detection of vascular plant species between two independent observers and their combined species occurrence data (Fig 3.2) shows that this method was very efficient in its ability to capture the majority of species at a given site. This is unsurprising because restricted survey times of up to 20 minutes are well established methods in monitoring protocols such as with surveys conducted by the Alberta Biodiversity Monitoring Institute (Zhang et al. 2014). However, Zhang et al. (2014) suggests that imperfect detections through errors of omission still remain after 20 minutes of survey time and recommended the use of unrestricted and longer survey times. In my study, the strongly plateauing species accumulation curves and high agreement between observed richness and estimated "true" richness values suggests that additional survey time was unlikely to result in notably higher richness measurements. In most cases, a cursory 5-minute survey will likely detect the majority of

species. However, if the goal is to collect a comprehensive species list, it is recommended that survey times should be at least 9 minutes in length.

In contrast, the quadrat survey approach was less efficient at measuring vascular plant richness. For comparison, the deployment and takedown for each of the required transects and quadrats takes approximately 25 minutes, and a total of approximately 30 minutes of active search time is required to identify vegetation within all 15 quadrats. This does not include time taken to look-up unfamiliar species within field guides or travel time to walk between transects. Consequently, a conservative estimate of the time required to complete the quadrat survey approach per site is approximately 105 minutes (or 1 hour and 45 minutes), compared to the 15 minutes required by the timed-walk survey approach. In addition, my sampling adequacy analyses reveal that I need more than 15 quadrats per peatland to accurately capture vascular plant richness. Overall, estimates of vascular plant richness obtained from the quadrat-transect surveys were consistently lower than those obtained by the timed-walks. The timed-walk surveys require little equipment and can be advantageous for sites that are difficult to access (e.g. some of my sites in the mountains that require long uphill hikes of up to 3 kilometers one-way). Whereas the quadrat survey approach does require extra equipment, quadrats may eliminate any potential errors associated with site trampling since extra time is taken to arrange quadrats and observers take care not to step within quadrats.

However, one of the biggest considerations for choosing one survey approach over another would come from the research questions that need to be answered and the kinds of data they require. The timed-walk surveys provide presence-absence (i.e. occurrence data) and may be favourable if objectives are to simply record species inventories, locate focal species, or measure general richness. The quadrat survey approach, however, would provide relative

abundance, enabling more fulsome calculations of biodiversity and evenness. Further, the quadrat approach can yield greater repeatability and more sensitive change detection if permanent plots are established and multiple visits of a site are conducted. For example, Vittoz and Guisan (2007) in their study of alpine meadows in the Swiss Alps, warn that occurrence data of species is insufficient to meet monitoring objectives. Cover estimates were determined to be necessary to allow for subsequent interpretations, such as species turnover (Vittoz and Guisan 2007).

Based on my analysis of the quadrat-transect survey approach with the timed-walk survey approach (Fig. 3.3), there does appears to be some preferential missed detections among shrub growth forms in my peatlands, where the quadrat-transect survey approach identified a higher richness of shrubs than the timed-walk survey approach. This contradicts the findings of Chen et al. (2013) who report a bias towards missed detections of graminoid growth forms in their study of vascular plant detection in mountainous sites of Switzerland. My results also differ with Dennett and Nielsen's (2019) study on *Carex* spp. detection in northeastern boreal Alberta, which evaluated the detection of forbs, graminoids, shrubs and tree growth forms, and found no bias in the detectability among growth forms.

It is also important to note that both survey approaches identified species of vascular plants not identified by the other. Notably, the timed-walk survey approach also consistently identified two species which was typically missed by the quadrat-transect survey approach: *Arnica chamissonis*, the Chamisso arnica, and *Pedicularis groenlandica*, the elephanthead lousewort. *Arnica chamissonis* is a perennial, with solitary stems 20 – 80 cm tall, with lanceolate leaves and several flower heads with pale yellow ray flowers (Moss and Packer 1983, Johnson et al. 1995). *Pedicularis groenlandica*, is a perennial, with clustered stems 30 – 50 cm tall, fern-

like lanceolate leaves and with many reddish purple flowers resembling the head and trunk of an elephant (Moss and Packer 1983, Johnson et al. 1995). Both species appear in low average percent cover when found in quadrats. *Arnica chamissonis* appeared in 5 out of 300 total quadrats among twenty sites with an average relative percent coverage of about 2.95% and *Pedicularis groenlandica* appeared in 16 out of 300 total quadrats among twenty sites with an average relative percent coverage of about 1.53%. It is possible that the timed-walk survey approach had a greater success in locating these species because these species are rare within my peatlands and appear in clumped spatial distributions at these sites. Stems are few and solitary which are more likely to be detected on a walk than be included in a randomly thrown quadrat along transects. Similarly, I would expect species that are rare, or have clumped, heterogenous spatial distributions to be better detected by the timed-walk survey approach, whereas species that are more common and have homogenous spatial distributions are possibly more likely to be detected by the quadrat-transect approach. Using more quadrats would potentially yield higher richness estimates based on my species accumulation curves, so eventually all species would be found that were also found in the timed walks. In contrast, timed walks had plateaued, so additional survey time was unlikely to result in more detections. The quadrat-transect approach may also be more beneficial to identifying small and cryptic species, or to differentiate subtle differences between species because surveyors are forced to focus on a small patch in greater detail. The hypotheses addressed here could possibly account for the errors of omission committed by each survey approach and explain the difference of the combined vascular plant species richness value and the observed species richness by each survey approach (Table 3.2).

Given these potential biases that individual survey approaches may introduce, it is strongly recommended that multiple survey approaches be employed whenever possible in future

studies to ensure robust measurements of species richness and diversity. Should only one survey method be employed, the timed-walk survey is likely the best option because it is more efficient and have reduced errors of omission compared to the quadrat-transect approach, with the caveat that the research isn't focused on woody vegetation. Ultimately, the use of multiple survey approaches in my Chapter 2 study ensured accurate inferences on diversity-elevation patterns and the consistency of community composition along an elevation gradient by accounting for each survey approaches' potential to commit imperfect detections. Nevertheless, irrespective of the survey approach chosen, imperfect detections are characteristic of methods employing observers in vegetation surveys. Consequently, all vegetation studies using observers are strongly encouraged to quantify and report imperfect detections with their results.

3.4.4 Future work

Future work in peatlands should investigate more sources of imperfect detection, especially but not limiting to, the functional traits or site-specific variables that may affect detectability in vegetation surveys. More research on the strategies to reduce false absences, misidentifications and pseudoturnover, such as repeated measurements, will build towards creating a best practice strategy for sampling vegetation in peatlands. In addition, there are opportunities to study the effect of site trampling in timed walks which may reduce detection probabilities, and to investigate any priming effect of available species which may increase detection (i.e. an increase in detection probability based on having already detected a species in a previous survey method when multiple survey methods are employed at a site). Further, recent work by Morrison et al. (2019) suggests investigating the individual contributions of false absences, misidentifications, and cautiousness in contributing to pseudoturnover is a worthy endeavour. Certainly, more attention to the pervasiveness and severity of imperfect detection in

vegetation surveys is needed, especially as the role of plants as indicators of climate change and

changing ecosystem conditions continues to be an important part of monitoring and conservation

programs.

4 Conclusion: Recommendations and future work

4.1 Key findings

The goals of this thesis were to 1) describe and characterize the mountain valley-bottom peatland vegetation communities along an elevation gradient in order to determine if the distribution of plant species is contingent on elevation, and to characterize how the distribution of plant species changes along an elevation gradient (Chapter 2); and to 2) determine potential sources of detection errors in peatland vascular plant surveys and determine a best-practice and optimal survey strategy to minimize detection errors (Chapter 3).

In Chapter 2, I determined that vegetation in my mountain valley bottom peatlands formed four distinct assemblage groups, but these groups were not sorted according to elevation. Rather pH and conductivity were more important factors in predicting variation in my vegetation community composition. In addition, I found evidence of the effect of biotic filters being subordinate to the effect of abiotic filters in structuring my peatland communities, supporting a Gleasonian view of communities along an elevation gradient. This work generated a comprehensive species lists for vascular plants and moss species found in Appendix B, and determined significant indicator species for each assemblage group which may assist future observers to better anticipate the co-occurring species they may observe in mountain valley bottom peatlands in the upper Bow River basin.

In Chapter 3, I identified site species richness of vascular plants as a potential predictor of pseudoturnover at low survey times and reinforced the idea that pseudoturnover is ubiquitous and can be severe in vegetation surveys involving observers. Therefore, I recommended that all studies that employ human observers in vegetation surveys should aim to quantify and report their pseudoturnover values with their results. Although I determined that the timed-walk survey

approach was more efficient than the quadrat-transect survey approach in detecting vascular plant species, the quadrat-transect survey approach is not without merits. However, I suggested the use of a combination of survey approaches as a best practice to account for the imperfect detections that having only one individual observer or using only one survey approach presents. In general, I demonstrated that by using a combination of survey approaches in my survey methods, this provided added confidence to my findings in Chapter 2 by ensuring accurate measures of vegetation diversity.

4.2 Future work

In addition to the recommendations for future work contained within each data chapter, there are additional research topics and opportunities that can build off my work presented in this thesis in a general sense. First, I expect species lists to assist with remote-sensing research at some of my peatland sites, by providing the needed ground-truthing to verify occurring species and relative estimates of vegetation coverage. Second, it is important to understand the role of peatland vegetation in structuring hydrological regimes (and vice versa), to improve our ability to predict and anticipate future changes to both peatland ecosystems and water security in the region with a changing climate. In addition, researching the role of beavers in influencing the hydrology of these systems is also important to develop a holistic understanding of these mountain peatlands. Third, it is critical to investigate the role of slope and aspect in influencing plant communities in mountain peatlands, in addition to studying other mountain processes. Further, locating higher elevation peatlands will be important to understanding the role of permafrost in structuring mountain peatland vegetation communities. Last, recent work in the Rooney Lab characterized avian species richness elevational patterns in many of my valley bottom peatlands (Reynolds 2020). Given that peatlands are critical breeding habitats (Warner

and Asada 2006), staging areas and feeding grounds for many avian species (Minayeva and Sirin 2012), determining the relationships between co-occurring plant species and avian species is a worthy endeavor to better understand mountain valley bottom peatlands' ability to support avian diversity, including birds that are identified as vulnerable or at risk in Alberta.

4.3 Recommendations for stakeholders

My research emphasizes a need to map and characterize Alberta's mountain valley bottom peatlands because notably, unmapped peatlands cannot be studied, nor can they be conserved. Without a complete inventory of these mountain valley bottom peatlands and the species that occupy them, key decisions regarding land-use and resource extraction (i.e. logging) cannot be made with a complete understanding of their implications to rare or at-risk species of plants and animals, and to the hydrology of these complex ecosystems. Research conducted in the present will also be especially important as baseline data to study the future effects of climate change on communities and biodiversity of plant species. Thus, it is highly recommended that more mountain valley bottom peatlands are located, added to the Alberta Merged Wetland Inventory (Alberta Environment and Parks 2018), and surveyed for their plant occurrence and abundances.

It is also recommended that researchers conduct more studies in this region, building on the work presented here and by others to better our collective understanding of these important mountain valley bottom peatlands. First, future studies of mountain valley bottom peatlands should include and take into consideration the influence of more environmental covariates, such as water chemistry, soil nutrients, water table depth, peat depth, slope and aspect, in explaining variance among vegetation community composition of mountain valley bottom peatlands. Second, future studies should consider redundancy in sampling designs, such as repeated

measurements and multiple survey methods to reduce the amount of errors of omissions, errors of commissions, and pseudoturnover. To ensure a robust measurement of species richness, future studies could employ a 15-minute timed-walk survey to act as a benchmark or quality assurance and assess the sufficiency of the number of quadrats deployed, taking into consideration the potential effect of trampling in reducing detectability of some species. For example, should the total number of species captured by quadrats be fewer than the number of species detected during the timed-walk survey, additional quadrats could be deployed.

Mountain valley bottom peatlands within the upper Bow River basin are habitats for a large diversity of plants. Overall, I found a total of 147 vascular plant species and 31 moss species among my twenty mountain valley bottom peatlands. Species lists are found in Appendix B. Although I did not identify any plant species with at-risk conservation statuses or have populations that are currently being tracked by the Albertan government, I did identify three species (*Carex trisperma*, *Eleocharis quinqueflora*, and *Salix alaxensis*) which are identified by the Alberta Conservation Information Management System (ACIMS) to be of S3 Ecological Community Conservation Rank meaning they are rare (i.e. 100 or fewer occurrences) and are potentially vulnerable to extirpation because of restricted ranges, relatively small population sizes, or other factors (Alberta Parks 2019). Still, these plant communities support many avian species which have been identified as either sensitive to habitat change, potentially at-risk, or at-risk in Alberta and threatened in Canada (Reynolds 2020). Thus, local watershed stewardship groups have an important role to play in advocating for the protections of these mountain valley bottom peatlands, by providing public awareness and engagement and by giving advice to decision makers.

As climate change increases the risks of drought and flooding events, it is increasingly appropriate to consider these mountain peatlands as important assets capable of mitigating these risks. The deadly Calgary flood of 2013 resulted in $6 billion in financial losses and property damage across southern Alberta – a cost shared among individuals, private companies, insurers, and taxpayers of the City of Calgary, the Government of Alberta, and the Government of Canada (The City of Calgary 2020a). In Calgary's Flood Resilience Plan, a planned increase in built infrastructure like reservoirs, dam gates and flood barriers is identified as a solution to upstream flood protections (The City of Calgary 2020b). Yet, mountain valley bottom peatlands are missing from the picture. It is estimated that the annual benefit of water regulation provided by each hectare of peatland is about $886 in 1998 dollars (i.e. $1414.77 when converted to 2020 dollars) which translates to annual water regulation benefits provided by Alberta's peatlands to be approximately $9.14 billion in 1998 dollars (i.e. $14.595 billion when converted to 2020 dollars) based on the inventory of peatlands in 1996 (Wilson et al. 2001). However, peatlands are continually threatened and destroyed by anthropogenic disturbances such as logging, which costs the government in lost water regulation benefits (not to mention the economic benefits peatlands provide in sequestering carbon, biodiversity, ecotourism, etc.) Therefore, I would recommend the City of Calgary, and the Government of Alberta to consider the role mountain valley bottom peatlands have in a holistic solution to reducing the downstream flood risks on the Bow River, but also, it's roles in providing baseflows during droughts. I would also recommend the Government of Alberta to consider protecting more of these important ecosystems for the immensely important ecosystem benefits they provide.

4.4 Final remarks

Around the world, the destruction of wetlands is increasing. During my time studying my peatlands, I've heard anecdotes and news about mangroves being destroyed to build luxury hotels, urban wetlands being paved over for warehouses, and ancient peatlands decimated to harvest surrounding trees. Yet, these wetlands are irreplaceable and critical in the ecological services they provide. Without radical, determined, and an abrupt change to the way we view our natural world and to our environmental and resource policies, we will lose our fight against climate change. We must vote for politicians that are committed to scientific decision making, for leaders that take climate change seriously and listen to scientists, and for representatives that will champion the protection of our valuable ecosystems.

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Appendix A

Table Appendix A1. Summary table of twenty valley bottom peatlands sites, their locations by Universal Transverse Mercator coordinate system with UTM Easting, UTM Northing, and UTM Zone values, elevations (m a.s.l.) and site area (m²) located in the upper Bow River basin within Alberta's Rocky Mountains, Canada.

Site	Location	UTM Easting	UTM Northing	UTM zone	Elevation (m a.s.l.)	Site area (m²)
MN02	Jumpingpound Demonstration Forest, AB	653882.7	5656867	11U	1415	118626.5
MN28	Moose Loop Trail, Bragg Creek, AB	659483.7	5647116	11U	1458	395159.6
MN21	Horse Lake, AB	643425.8	5691808	11U	1482	545713.4
MN01	Sibbald Lake Provincial Campground, AB	649432.6	5658408	11U	1484	779302.0
MN22	McLean Creek, AB	661066.9	5635818	11U	1499	36930.1
MN25	Silvester Creek, AB	660430.1	5634893	11U	1519	93130.2
MN34	Trappers Hill Campground, AB	635319.7	5682942	11U	1550	69091.1
MN31	Bighorn No. 8, AB	634002.0	5686519	11U	1566	311772.6
MN32	Waiparous Valley Road, AB	632955.9	5697700	11U	1580	57532.6
MN33	Waiparous Valley Road, AB	630543.9	5697527	11U	1614	91900.5
SA34	Alberta 40, AB	658419.2	5591327	11U	1650	39958.5
SA25	Powderface Trail, AB	648486.0	5638392	11U	1680	209633.0
SA32	Elkwood Campground, AB	633050.9	5613248	11U	1689	185524.1
SA30	Powderface Trail, AB	648468.9	5637001	11U	1718	51788.2
SA31	Powderface Trail, AB	649411.1	5633390	11U	1744	15031.4
SA33	Boulton Creek Campground, AB	635069.0	5611620	11U	1765	10022.9
SA23	Powderface Trail, AB	646915.9	5640528	11U	1786	22399.0
SA20	Powderface Trail, AB	645066.4	5645087	11U	1834	12467.1
SA26	Peter Lougheed Provincial Park, AB	617543.0	5631227	11U	1842	809911.4
SA01	Peter Lougheed Provincial Park, AB	617123.6	5626575	11U	1959	887949.1

Figure Appendix A1. Site images of typical mountain valley bottom peatlands located in the Montane Natural Subregion: MN01 (top left panel) and MN25 (top right panel); and typical mountain valley bottom peatlands located in the Subalpine Natural Subregion: SA20 (bottom left panel) and SA32 (bottom right panel).

Appendix B

Table Appendix B1. Presence-absence of species (indicated by black dots) grouped by growth form: 1) forb species; 2) graminoid species; 3) shrub species; 4) tree species; and 5) moss species; surveyed between July 19 - August 12, 2019 across twenty valley-bottom peatland sites: MN02, MN28, MN21, MN01, MN22, MN25, MN34, MN31, MN32, MN33, SA34, SA25, SA30, SA31, SA33, SA23, SA20, SA26, and SA01 in the upper Bow River basin within Alberta's Rocky Mountains, Canada. Species names and authorities were standardized using the Integrated Taxonomical Information System (ITIS) database (accessed on January 16, 2020). Significant indicators are denoted by (*#) where the # represents the indicator species group number to which it belongs (see Chapter 2 Table 2.3).

1) Forb species																				
Latin name and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Achillea millefolium L. (*4)				•	•	•		•	•	•	•	•	•	•	•		•		•	
Allium schoenoprasum L.													•							
Antennaria luzuloides Torr. & A. Gray														•	•					
Antennaria microphylla Rydb.												•	•	•						
Anthoxanthum nitens (Weber) Y. Schouten & Veldkamp				•								•		•					•	
Apocynum androsaemifolium L.														•						
Arnica chamissonis Less.		•	•		•	•		•	•	•		•	•				•			
Astragalus americanus (Hook.) M.E. Jones												•		•	•					
Symphyotrichum boreale (Torr. & A. Gray) A. Löve & D. Löve	•		•	•	•		•		•					•			•			•
Astragalus canadensis L.												•								
Aster L.											•					•		•		
Astragalus eucosmus B.L. Rob. (*4)										•		•		•	•					
Astragalus L.		•			•							•								
Bistorta vivipara (L.) Delarbre (*2)		•			•	•	•	•	•			•		•	•		•	•	•	•
Campanula rotundifolia L.								•	•			•	•	•						
Castilleja miniata Douglas ex Hook.														•	•		•			

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Castilleja raupii Pennell											●		●	●		●	●	●
Cerastium nutans Raf.																●		
Chamerion angustifolium ssp. angustifolium (L.) Holub (*4)			●	●	●			●		●	●	●	●	●	●	●	●	●
Chrysosplenium tetrandrum Th. Fr.			●	●														
Cirsium arvense (L.) Scop.										●			●		●			
Cirsium foliosum (Hook.) DC.													●					
Comarum palustre L.		●																
Delphinium glaucum S. Watson				●		●				●		●	●					
Epilobium ciliatum ssp. glandulosum (Lehm.) Hoch & P.H. Raven (*3)			●	●				●					●		●			
Epilobium palustre L.			●	●	●	●	●	●	●		●		●	●		●		●
Equisetum fluviatile L.	●		●		●		●	●	●	●	●	●	●	●	●	●	●	●
Equisetum scirpoides Michx.	●						●			●	●					●	●	●
Erigeron acris L.							●											
Erigeron glabellus Nutt.											●							
Eriophorum angustifolium Honck.	●					●									●	●		●
Erysimum cheiranthoides L.				●														
Fragaria vesca L.				●				●									●	
Fragaria virginiana Duchesne (*4)				●			●	●			●	●	●		●	●	●	●
Galium boreale L.				●				●			●		●	●				
Galium L.		●				●			●		●							
Galium trifidum L. (*3)				●	●	●	●							●		●		●
Galium triflorum Michx.											●							
Geum aleppicum Jacq. (*3)				●	●				●					●		●	●	●
Geum L.															●			
Geum rivale L. (*3)			●	●		●	●		●	●	●	●	●	●		●	●	●
Geum triflorum Pursh											●							
Heracleum sphondylium ssp. montanum (Schleich. ex Gaudin) Briq.				●														

Species																			
Lythrum salicaria L.											•								
Maianthemum canadense Desf.											•								
Menyanthes trifoliata L.	•					•							•						
Mertensia paniculata (Aiton) G. Don				•								•							
Mitella nuda L.		•				•			•	•	•		•	•		•	•		
Packera indecora (Greene) Á. Löve & D. Löve									•				•			•			
Packera paupercula (Michx.) Á. Löve & D. Löve	•					•				•	•	•						•	•
Parnassia palustris L.	•	•	•			•	•	•		•	•	•		•	•	•	•	•	•
Pedicularis groenlandica Retz.	•	•	•	•		•	•	•	•		•	•		•	•	•	•	•	•
Persicaria amphibia (L.) Delarbre (*3)				•													•		
Petasites frigidus var. sagittatus (Banks ex Pursh) Chern. (*4)		•		•	•		•	•	•		•	•	•		•	•	•	•	•
Platanthera hyperborea (L.) Lindl.	•	•	•	•	•	•	•	•			•	•		•	•	•	•		•
Potentilla gracilis Douglas ex Hook. (*4)		•				•			•			•		•	•	•		•	•
Potentilla norvegica L.				•															
Primula pauciflora var. pauciflora (Greene) A.R. Mast & Reveal						•		•						•		•		•	
Prosartes trachycarpa S. Watson (*4)						•			•			•		•	•				
Pyrola asarifolia Michx.	•		•				•			•				•	•		•	•	•	•
Pyrola L.			•																
Ranunculus gmelinii DC.		•																	
Ranunculus L.														•					
Rhododendron groenlandicum (Oeder) Kron & Judd									•						•				
Ribes triste Pall.									•					•					
Rorippa islandica (Oeder) Borbás (*3)				•										•		•			
Rubus arcticus ssp. acaulis (Michx.) Focke (*3)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Rubus pubescens Raf.			•						•				•		•		•	•	•
Rumex occidentalis S. Watson (*3)		•	•	•	•	•			•		•			•			•		
Scutellaria galericulata L.				•															
Senecio eremophilus Richardson				•															

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Senecio vulgaris L.								●												
Solidago canadensis L.												●								
Solidago spathulata DC.												●								
Sonchus asper (L.) Hill						●						●								
Stellaria longifolia Muhl. ex Willd. (*3)		●	●	●	●	●	●	●	●	●	●	●		●	●		●	●	●	
Symphyotrichum boreale (Torr. & A. Gray) A. Löve & D. Löve		●	●	●	●	●						●		●					●	
Symphyotrichum puniceum var. puniceum (L.) Á. Löve & D. Löve						●			●		●	●	●	●	●	●	●	●	●	●
Taraxacum officinale F.H. Wigg.									●		●	●								
Thalictrum venulosum Trel.						●						●		●	●					
Triantha glutinosa (Michx.) Baker																●				
Triantha glutinosa (Michx.) Baker	●		●																	
Trifolium repens L.												●								
Urtica dioica L.			●																	
Utricularia intermedia Hayne							●												●	
Vaccinium vitis-idaea L.												●								
Valeriana dioica L.												●	●				●	●	●	●
Veronica americana Schwein. ex Benth.			●		●															
Vicia americana Muhl. ex Willd. (*4)						●		●			●	●		●	●					
Zizia aptera (A. Gray) Fernald						●						●								

2) Graminoid species

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Agrostis scabra Willd.	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●
Bromus ciliatus L.						●			●			●								
Calamagrostis Adans.												●								
Calamagrostis canadensis (Michx.) P. Beauv.				●							●	●				●			●	
Calamagrostis stricta ssp. *inexpansa* (A. Gray) C.W. Greene		●	●		●	●	●	●	●	●		●	●	●	●	●			●	

95

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Carex aquatilis Wahlenb.	●	●	●	●	●		●	●	●	●	●	●	●			●	●	●	●	●
Carex atherodes Spreng.				●																
Carex aurea Nutt.								●									●		●	●
Carex bebbii Olney ex Fernald									●							●			●	
Carex canescens L.		●						●	●			●	●	●	●		●			
Carex capillaris L. (*1)	●							●	●			●	●	●	●	●			●	●
Carex chordorrhiza Ehrh. ex L. f.											●									
Carex crawfordii Fernald																●			●	
Carex diandra Schrank (*1)	●							●	●							●			●	
Carex dioica L.																●				
Carex disperma Dewey		●									●			●					●	●
Carex L.			●	●		●		●	●		●	●	●	●	●	●				
Carex gynocrates Wormsk. ex Drejer	●		●	●			●	●		●	●	●	●	●	●		●	●	●	●
Carex interior L.H. Bailey	●							●								●				
Carex lacustris Willd.																				●
Carex lasiocarpa Ehrh.							●		●									●		
Carex leptalea Wahlenb.											●		●	●	●		●			
Carex media R. Br.			●										●							
Carex microglochin Wahlenb.	●																			●
Carex pauciflora Lightf.																				●
Carex praegracilis W. Boott			●			●	●	●							●			●	●	●
Carex saxatilis L.	●																			●
Carex siccata Dewey													●							
Carex trisperma Dewey		●												●						
Carex utriculata Boott			●	●		●	●	●	●	●		●	●	●		●			●	●
Carex vaginata Tausch													●	●	●		●			
Eleocharis R. Br.								●											●	
Eleocharis quinqueflora (Hartmann) O. Schwarz	●															●				●

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Elymus trachycaulus (Link) Gould ex Shinners (*4)					●	●		●			●	●	●	●	●		●		●	●
Festuca ovina L.		●																		
Juncus balticus Willd.	●	●	●		●	●	●	●	●		●	●	●	●	●	●	●		●	●
Leymus innovatus (Beal) Pilg.					●	●	●	●	●	●		●		●	●				●	
Luzula multiflora (Ehrh.) Lej.											●	●		●	●					
Phalaris arundinacea L.		●																		
Phleum pratense L.					●	●						●								
Poa palustris L.		●	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●
Rhynchospora alba (L.) Vahl			●																	
Trichophorum cespitosum (L.) Hartm.																●				
Triglochin maritima L.	●							●								●				
Triglochin palustris L.										●									●	

3) Shrub Species

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Betula glandulosa Michx.	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Dasiphora fruticosa (L.) Rydb.	●	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●
Juniperus communis L.	●																			
Juniperus horizontalis Moench												●								
Rosa acicularis Lindl.															●					
Salix alaxensis (Andersson) Coville																			●	●
Salix bebbiana Sarg.	●				●		●			●		●	●	●	●	●	●	●	●	●
Salix candida Flüggé ex Willd.	●		●		●		●	●		●						●	●	●	●	
Salix discolor Muhl.															●					
Salix exigua Nutt.				●	●	●			●											
Salix glauca L.					●							●								
Salix L.											●									
Salix lasiandra Benth.						●														

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Salix maccalliana Rowlee (*4)		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			•	
Salix planifolia Pursh	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

4) Tree species

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Picea A. Dietr.																•				
Picea glauca (Moench) Voss	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Picea mariana (Mill.) Britton, Sterns & Poggenb.	•		•		•		•	•		•			•		•	•				
Pinus banksiana Lamb.				•	•					•			•	•		•	•			
Pinus contorta Douglas ex Loudon		•				•		•		•	•	•	•	•	•	•		•		
Pinus L.													•					•		
Populus tremuloides Michx.											•									

5) Moss species

Latin names and authorities	MN02	MN28	MN21	MN01	MN22	MN25	MN34	MN31	MN32	MN33	SA34	SA25	SA32	SA30	SA31	SA33	SA23	SA20	SA26	SA01
Aulacomnium palustre (Hedw.) Schwaegr.	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Aulacomnium turgidum (Wahlenb.) Schwaegr.													•							
Bryum pseudotriquetrum (Hedw.) Gaertn. et. al.		•	•	•		•	•	•	•	•	•	•		•	•		•	•	•	•
Calliergon giganteum (Schimp.) Kindb.			•	•			•	•		•	•				•					
Calliergon richardsonii (Mitt.) Kindb. in Warnst.				•		•				•						•	•		•	
Campylium stellatum (Hedw.) C. Jens.	•		•	•			•	•		•	•		•	•	•	•	•	•	•	•
Catoscopium nigritum (Hedw.) Brid.																•			•	
Climacium dendroides (Hedw.) Web. & Mohr		•			•	•			•				•	•	•	•			•	•
Drepanocladus aduncus (Hedw.) Warnst.											•		•		•					
Dicranum polysetum Sw.														•		•				
Hamatocaulis vernicosus (Mitt.) Hedenäs	•	•	•		•		•	•		•	•	•	•	•	•	•	•	•		•
Hypnum lindbergii Mitt.		•		•	•	•			•				•	•		•			•	•
Limprichtia revolvens (Sw.) Loeske			•				•	•		•	•			•	•	•	•	•	•	•

|																				
Meesia triquetra (Richt.) Ångstr.							●	●									●	●		●
Paludella squarrosa (Hedw.) Brid.			●						●									●	●		
Plagiomnium ellipticum (Brid.) T. Kop.		●	●	●	●	●	●		●	●	●	●	●	●	●		●	●	●	●
Platydictya jungermannioides (Brid.) Crum	●		●			●									●					
Pleurozium schreberi (Brid.) Mitt.									●											
Pohlia nutans (Hedw.) Lindb.	●		●	●				●		●										
Polytrichum strictum Brid.		●	●		●				●	●	●	●	●				●	●		
Ptilium crista-castrensis (Hedw.) De Not.		●							●	●	●		●	●	●		●			●
Scorpidium scorpioides (Hedw.) Limpr.	●								●								●		●	
Sphagnum angustifolium (C. Jens. ex Russ.) C. Jens. in Tolf		●	●						●	●	●		●	●			●	●		
Sphagnum capillifolium (Ehrh.) Hedw.	●	●	●		●				●	●	●	●	●	●	●		●	●		
Sphagnum fuscum (Schimp.) Klinggr.			●		●	●			●									●		
Sphagnum riparium Ångstr.						●					●									
Sphagnum teres (Schimp.) Ångstr. in Hartm.					●				●											
Sphagnum warnstorfii Russ		●	●		●				●	●	●	●	●				●	●	●	
Thuidium recognitum (Hedw.) Lindb.	●																			
Tomentypnum nitens (Hedw.) Loeske	●	●	●		●	●	●		●	●	●	●	●	●	●	●	●	●	●	●
Warnstorfia fluitans (Hedw.) Loeske				●											●			●		

Appendix C
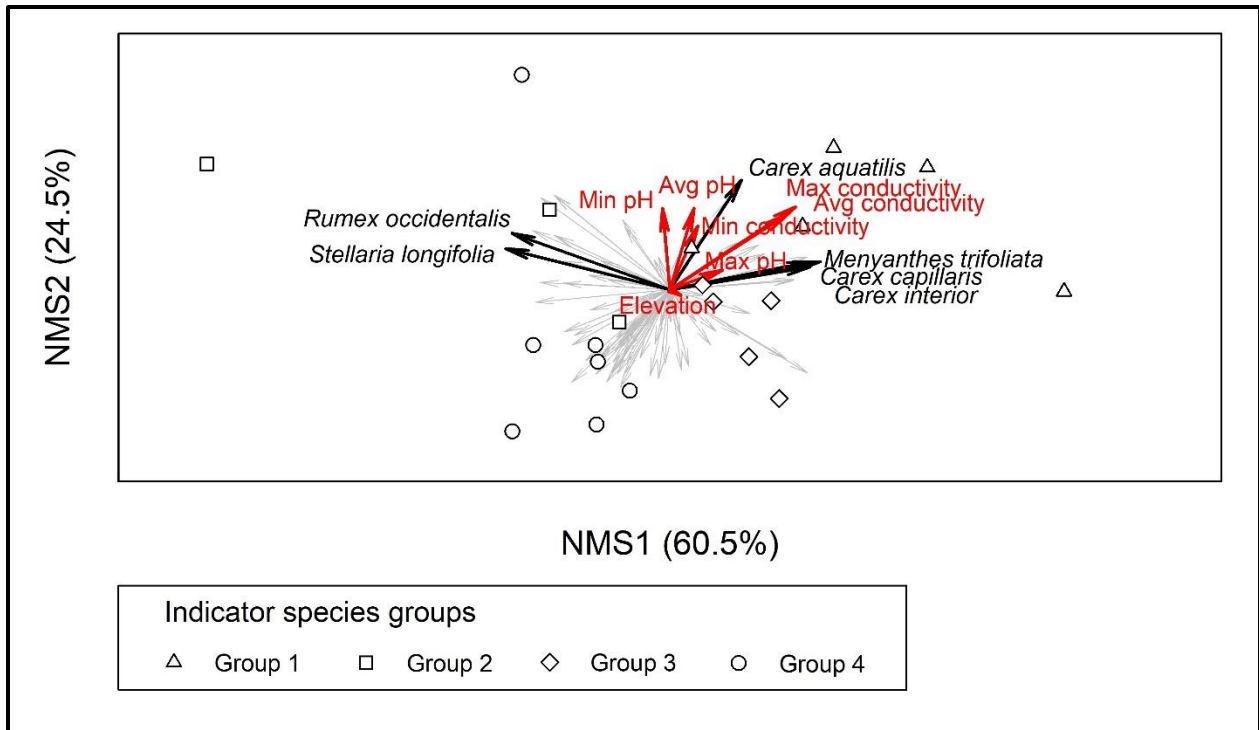
Figure Appendix C1. Two-dimensional solution for non-metric multidimensional scaling (NMS) ordination and vector biplot for maximum cover data of vascular plants. Sites are represented by their group membership to the four distinct assemblages (see Chapter 2 Results) as triangles for Group 1, squares for Group 2, diamonds for Group 3, and circles for Group 4, and ordinated on axes NMS1 and NMS2, with gray vectors representing all cover classes, black vectors representing cover classes with a r^2 cut-off ≥ 0.4, and red vectors representing environmental variables (no cut-off applied).
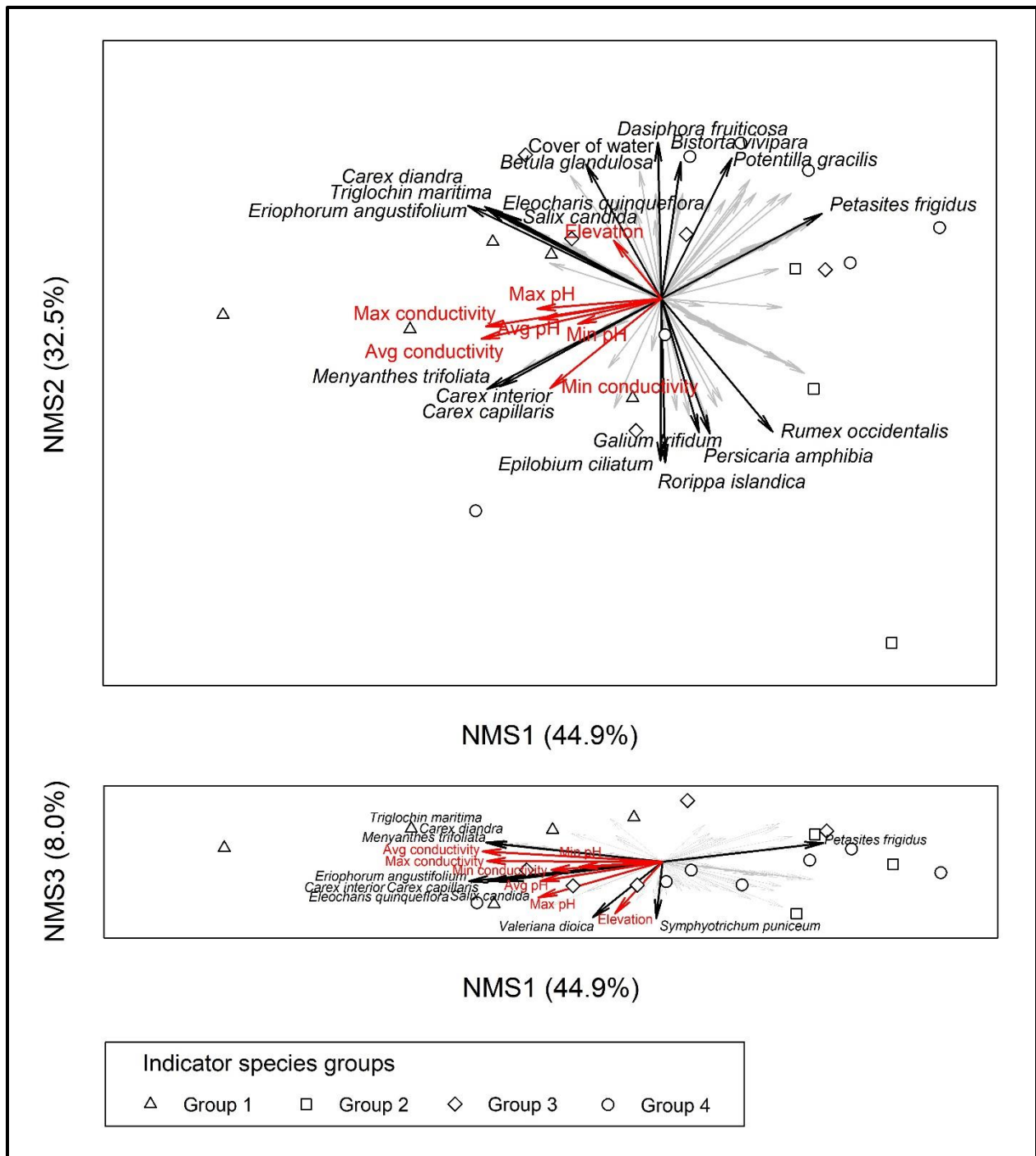
Figure Appendix C2. Three-dimensional solution for non-metric multidimensional scaling (NMS) ordinations and vector biplots for occurrence data of vascular plants and mosses. Sites are represented by their group membership to the four distinct assemblages (see Chapter 2 Results) as triangles for Group 1, squares for Group 2, diamonds for Group 3, and circles for Group 4, ordinated on axes NMS1 and NMS2 (top panel) and on axes NMS1 and NMS3 (bottom panel), with gray vectors representing all cover classes, black vectors representing cover classes with a r^2 cut-off ≥ 0.4, and red vectors representing environmental variables (no cut-off applied).
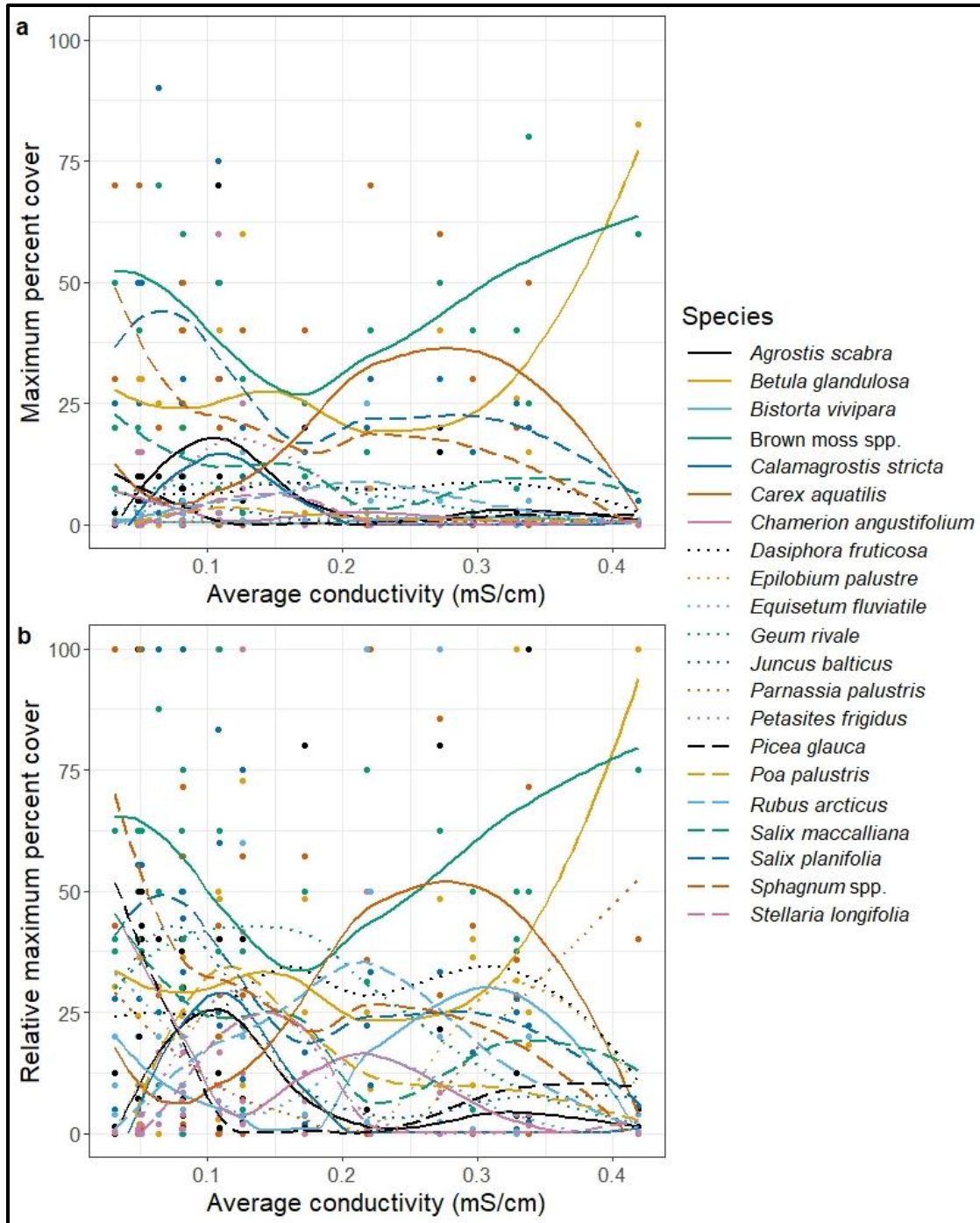
Appendix D

Figure Appendix D1. Species conductivity niche plots for the 21 species present at >50% of sites showing a) their quadrat maximum percent cover values plotted against site average conductivity (mS/cm) smoothed by the LOESS method; and b) showing their quadrat maximum percent cover values relativized by site maximum plotted against site average conductivity (mS/cm) to increase visibility of trendlines of species with low percent cover values, smoothed by the LOESS method.
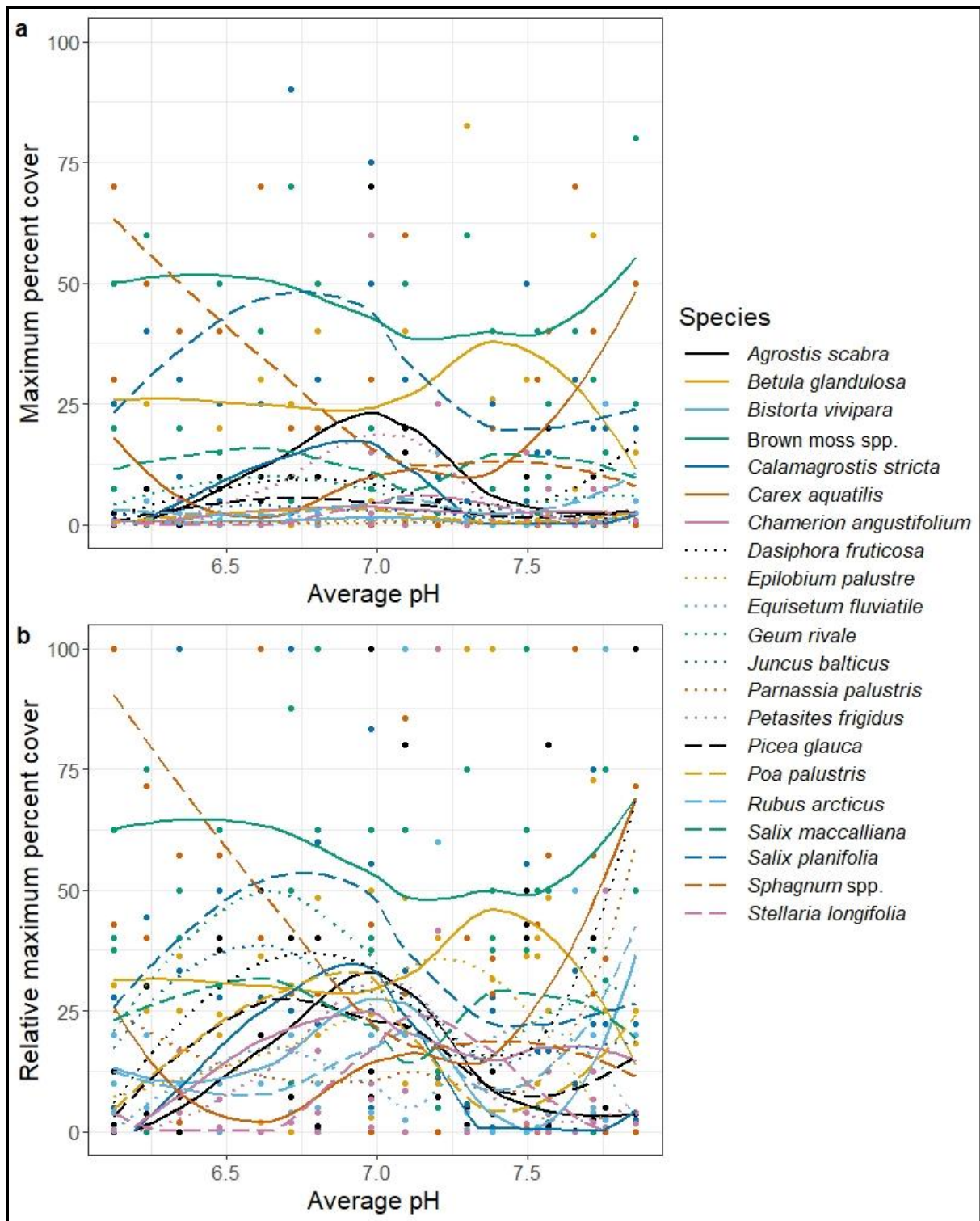
Figure Appendix D2. Species pH niche plots for the 21 species present at >50% of sites showing a) their quadrat maximum percent cover values plotted against site average pH smoothed by the LOESS method; and b) showing their quadrat maximum percent cover values relativized by site maximum plotted against site average pH to increase visibility of trendlines of species with low percent cover values, smoothed by the LOESS method.