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Functional Diversity:
Quantifying Patterns across the Tundra Biome

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Thesis submitted for the degree of Doctor of Philosophy
School of Geosciences, University of Edinburgh

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Declaration

The work presented in this thesis is wholly my own and includes nothing that has been conceived in collaboration with others except when part of a jointly-authored publication, as indicated below. When completed as part of a jointly-authored publication, my contribution and that of the other authors has been explicitly specified. Throughout this thesis, appropriate credit has been given throughout where reference has been made to the work of others. None of the work presented here has been submitted for any other degree or professional qualification at the University of Edinburgh or any other institution.

The three research chapters of this thesis (**Chapters 2-4**) were written as manuscripts for which I was the primary author. Each of the chapters are currently either under review or in the process of being prepared for publication. As these works invariably involved collaboration, I use the pronoun 'we' rather than 'I'. Each chapter is self-contained (excluding supplementary materials which can be found in **Chapter 6: Appendices**) but the sections, figures and figure headings have been renumbered to reflect its place within the wider thesis. The working reference, title and roles of collaborators for each manuscript/chapter is as follows:

Chapter 2 (**Current Status:** In preparation, expected submission October 2024)

Everest, J.J., Elmendorf, S.C., Wauchope, H.S., Myers-Smith, I.H., Zaja, E.V., Jerome, D., Subrt, J., Hoad, C.G., In preparation. Considering geographic proximity improves gap-filling performance in tundra plant traits. *Journal as yet undecided*. [Submitting as Opinion Piece].

Author contributions: JJE, SCE and IHMS conceived the study. JJE collected the field data with help from EVZ, DJ, JS and CGH. JJE performed the statistical analyses with help from SCE and HSW. JJE wrote the manuscript with assistance from the same co-authors.

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Contributing Authors, TTT Contributing Authors, (67 others...), In preparation. Functional diversity of tundra vascular plants across space and time. *Glob. Ecol. Biogeogr.*

Author contributions: JJE and IHMS conceived the study based on an idea from the ArcFunc working group. JJE performed the statistical analyses with input from SCE, IHMS, ADB, MGC and HSW. JJE wrote the manuscript with assistance from the same co-authors, alongside ALB, MV, JL and RGB. All authors provided contributing feedback to the manuscript.

Chapter 4 (**Current Status:** Reject & resubmit August 2023, resubmitted February 2024)

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Author contributions: JJE and SCE conceived the study. JJE performed the statistical analyses with help from SCE, EVC and ALB. All authors provided contributing feedback to the manuscript.

Co-author contributions

In addition to the three first author publications outlined above, I have contributed to a number of other manuscripts as a named author. None of the work of these publications is included in this thesis, but they are listed below for reference.

Björnsdóttir, K., Thomas, H.J.D., Pacheco-Riaño, L.C., **Everest, J.J.**, Elmendorf, S.C., Cornelissen, J.H.C., Schrodt, F., Blok, D., Kattge, J., Hallinger, M., Schaepman-Strub, G., Tape, K. Wilmking, M., sTUNDRA Working Group, International Tundra Experiment, ... Myers-Smith, I.H, Bjorkman, A.D. In preparation. Tundra vegetation change does not alter community litter decomposability. *Journal as yet undecided*.

Scharn, R., Björk, R.G., …, **Everest, J.J.**, …, International Tundra Experiment. In preparation. Plant abundance drives β-diversity changes in the Arctic. *Journal as yet undecided*.

Bjorkman, A.D., …, García Criado, M., **Everest, J.J.**, …, International Tundra Experiment. In preparation. The ITEX+ composition database: Thirty years of experimental warming and monitoring of tundra plant communities. *Arctic Science*.

Abstract

Widespread vegetation change is underway throughout the northern high latitudes in response to pervasive and accelerating Arctic warming. Such changes are becoming increasingly well documented with key aspects such as phenology, species composition and trait make-up known to be shifting across the tundra biome. However, one area that remains underrepresented in tundra vegetation studies is functional diversity, known to be a principal determinant of ecosystem function and consequently, services. Communities comprising higher functional diversity are considered more stable and resistant to global change impacts and as such, any loss of functional diversity under the influence of warming could have cascading impacts on ecosystem services and resultant feedbacks. Tundra functional diversity is hence an overlooked subject area with the potential to strongly influence ecosystems and communities throughout the far north in the coming decades. This thesis tackles this knowledge gap by: characterising its biome-scale biogeographic patterns and potential drivers (Chapter 3); identifying limitations in currently accepted gap-filling methodologies (Chapter 2); and developing new remotely-sensed approaches to better understand patterns in tundra functional diversity (Chapter 4).

In Chapter 2, I used *in situ* trait data collected on individuals of multiple species under near-identical environmental and temporal conditions to determine the influence of explicitly incorporating spatial hierarchies on gap-filling performance in tundra trait matrices. I found that gap-filling across progressively higher spatial and taxonomic hierarchies reduced the accuracy of trait estimates, although such patterns were seen to be both scale and trait-specific. In Chapter 3, I undertook a biome-wide, in situ, cross-site synthesis of over 2,000 plots spanning ~40 years to determine, for what I believe is the first time, biome-scale biogeographic patterns in tundra vascular plant functional diversity across space and time and identify potential drivers of such patterns. I found that spatial patterns in functional diversity conform to those seen in species and functional diversity across latitudes globally and that whilst functional diversity exhibited no net directional change over time, plot-scale changes were strongly related to changes in functional group cover. Finally, in Chapter 4, I used airborne hyperspectral imagery from the Front Range, Colorado, USA to determine whether optical remote sensing can accurately track fine-scale differences in functional diversity throughout alpine tundra ecosystems across both space and time. I found that the method showed promise across space, tracking patterns in functional beta-diversity within years across our sample region, but exhibited limited potential over time, highlighting continued issues with remotely sensed time series in assessments of biodiversity. Overall, I believe this thesis has helped tackle large unknowns surrounding tundra functional diversity and has highlighted key research areas to target in the near future as rapid Arctic warming continues.

Lay Summary

Climate change is perhaps *the* global issue of contemporary times. We will all experience its impacts and nowhere will escape its influence. These effects, however, are not felt equally across the world, with some areas facing disproportionately greater change than others. Defining the area of greatest impact is complex and can be viewed in many ways. For instance, the world's low lying countries will feel the grip of sea level rise first. Northern communities reliant on sea ice formation may most feel the grip of seasonal ice loss. Tropical coastal communities will likely bear the brunt of the increasing frequency and magnitude of cyclone activity. When viewed in terms of rates of temperature increase, however, there are a few clear winners, or perhaps losers, that are warming at rates well above the global average. One such area is tundra, and it is here that this thesis will be focussed.

The tundra refers to areas found globally above the treeline, be that in the Arctic and high latitudes or in the upper reaches of the world's mountains. They are often, albeit not always, cold and harsh environments and typically characterised by short, small plant life such as shrubs, grasses, mosses and small flowering plants. Whilst covered considerably less often in the world's media when considering climate change impacts than other regions, such as tropical rainforests and savannahs, the tundra is an area of considerable importance. For instance, it sits at the boundary between the frozen and living worlds, it encompasses half the world's soil carbon and is home to countless animal and human communities who depend on it to sustain life. Given its fundamental importance, it is essential that we know where, how and why it might change in the coming decades given the rapid warming it is destined to experience. To know how it will change, you have to understand all of its constituent parts, including the plant life, a key component of the tundra.

There remain clear gaps in our current understanding of tundra plant life, however. Certain changes are becoming increasingly well understood. Shrubs are expanding northwards and upwards tracking warmer temperatures, plants are flowering earlier in line with earlier spring warming and the region is becoming greener as warming drives increased photosynthesis. Other areas however, retain much uncertainty. One such area considers how tundra plants perform functions in the environment, functions such as the retaining of water, binding of soil or storage of carbon. To understand how plants function, you need to understand their key physical and

chemical characteristics, or traits. How tall are they? How big are their leaves? How much do they weigh? Each of these traits influences the functions and actions plants perform. The more diverse their traits, the more diverse the functions and the more stable these plant communities are likely to be in the face of changes, such as warming. It therefore follows that any loss of traits likely results in a loss of functions and stability in turn. However, little has currently been done to understand this diversity of traits across the full tundra environment. Moreover, many of the methods currently available to measure such things appear unsuited to the task, often using incomplete data due to the difficulties involved in collecting data in remote tundra environments. This thesis therefore set out to tackle these issues, address these knowledge gaps and shed new light on tundra trait diversity.

I begin by measuring the diversity of plant traits across the full region, using datasets collected over the past 40 years at more than 100 locations throughout the tundra. In doing so, I highlight the locations of tundra trait diversity for the first time, determine why it's found where it is and how it is changing less over time than we would perhaps expect. I follow this up by assessing how confident we can be in such conclusions based on the methods used and the data gaps they encompass. This work highlighted the significance of spatial location when filling in missing trait data, and provided suggestions for how to tackle these issues in the future to increase the accuracy of our analyses. Finally, I explore the potential of new methods that use airborne imagery to track changes in trait diversity across both space and time. We found that whilst such methods provide promise across space, their use over time remains limited.

This thesis hence paints a full picture of trait diversity across the tundra region for the very first time, highlights key issues in our current approach and provides suggestions for how to rectify them in the future. In doing so, it not only allows us to better understand the current picture, but potentially allows us to better predict how trait diversity may change in the coming decades under the influence of continued global warming. Given the rapid rate of warming in the tundra, and the potential scale of change, such predictions may prove invaluable. Finally, the implications of this work stretch beyond the tundra alone. The world is an interconnected system, where changes in one location feed into changes elsewhere, amplifying impacts across the globe. Our work may therefore one day facilitate predictions of change not just within the tundra, but how associated knock-on effects may be felt further afield, potentially impacting us all.

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Time for some thank yous! First and foremost, to my two primary supervisors, Hannah Wauchope and Sarah Elmendorf. To Hannah, I am sure you had absolutely no intention of adopting a stray PhD student on your first day as a lecturer, and for that I can only apologise. Despite my abrupt arrival however, it proved to be an inspired move and working with you this past year has been a true pleasure. You are an excellent supervisor and an even better person and I know Tani, Iona, Cess and Felipe all agree and will benefit from that as I have over the remainder of their projects. To Sarah, I'm sure when you merrily agreed that I could come and visit Boulder for a semester in early 2023, you similarly didn't expect to be stuck meeting with me every week for the following 18 months, but how glad I am that we have. Boulder was a fantastic time, but your support and assistance in the months since have been the real highlight. I couldn't have finished this PhD without your help and this thesis is, in large part, thanks to you!

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Now to the rest, I will keep it brief. My family made me promise that "under no circumstances should I include them in my acknowledgements" as it was unneeded and unwarranted and we can just celebrate at home soon. I don't agree, but will keep to my promise. To the many friends who accompanied me in the field, the office (occasionally), in Boulder and on all my other adventures, what a ride. To name but a few: Edith, Calum, Erica, Jiri, Diana, Elise, Madi, Clara, Zabrina, Kata, Inka, Judith, Zana, Eric, Colin, Sammy, Austin, Miles, Hannah, James, Pedro, Lake, Jorge, Jamie, Zhiqi, Hannah, Alice, Carla, Marrick and Helen… And to the many friends who were in no way linked to my work but kept me entertained over the past four years, mostly

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Two to go. Firstly to Tim Lane, a glaciologist at Liverpool John Moores University. Until the age of 14 or so, being the train nerd I was, I was determined to grow up and become an engineer, mostly so I could build trains (I thought that's what engineers did). Around this time however, Tim came into my school to give an assembly, and spent 20 minutes showing us pictures of his work travelling through Greenland in a boat to do science. I watched this assembly, immediately changed my mind and went home and told my mum that "I want to do science now". Well, roll on almost exactly 10 years and I too spent the summer of 2023, travelling through Greenland in a boat to do science. So, to Tim, my original inspiration.

Then finally, I should thank Scotland. I left Cambridge in 2020 with the misguided view that I should live and work in London, as it seems most 20-something grads seem to do. Indeed, getting an offer from Edinburgh was somewhat inconvenient to my plans. How wrong I was. I told Sam Frengley of my predicament and he in less than polite terms told me to "stop being dumb and move to Scotland, what was I doing?". Well I begrudgingly followed his advice and moved to Scotland, and it may perhaps be the best choice I've ever made. Despite the weather, which I'll be honest does suck a bit, Scotland is a truly wonderful place. I may have finished a PhD, but for me the memories will always be the hiking, biking, climbing, skiing, running and every other plan, wise or unwise, that we've concocted in the highlands and beyond. So to Scotland (and I guess Sam), thanks for a grand four years.

Contents

List of Figures

1

Introduction

1.1 Background

1.1.1 The tundra

The tundra biome sits at the forefront of contemporary climate change. Arctic amplification has driven rates of high-latitude warming to four times those of the global average (England et al., 2021; Manabe and Wetherald, 1975; Rantanen et al., 2022) whilst elevation-dependent warming is raising temperatures throughout the world's mountain environments (Palazzi et al., 2019; Pepin et al., 2015, 2022; Rangwala and Miller, 2012). Such warming has resulted in a tundra system characterised by increasing unpredictability and pervasive change (Miller et al., 2010). Given the rate of warming and the consequently dynamic nature of the tundra biome, it is here that we can see the impacts of rapid, accelerating warming predicted for much of the world playing out in real time (Meredith et al., 2019). Such impacts are widespread, spanning all aspects of the high latitude system (e.g., Corell, 2006; Miller et al., 2010; Yamanouchi and Takata, 2020), including the terrestrial tundra vegetation, where a vegetation regime shift appears to be underway (Elmendorf et al., 2015).

Contemporary changes to tundra vegetation are numerous, with shifts in vegetation composition, traits, phenology and diversity becoming increasingly apparent (Callaghan et al., 2011). Tundra-wide shrub expansion, through increased *in situ* abundance (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2011, 2019a) and shrubline encroachment (García Criado et al., 2020; Myers-Smith and Hik, 2017), is widespread and reflected in a biome-wide spectral 'greening' trend (Berner et al., 2020; Myers-Smith et al., 2020; Myneni et al., 1997). Tundra phenology is shifting (Oberbauer et al., 2013) with advances in spring phenology witnessed throughout the biome (Bjorkman et al., 2020; Gallois et al., 2024; Myers-Smith et al., 2019a; Prevéy et al., 2019). Species turnover is commonplace with gains and losses maximised in the areas of greatest warming (García Criado et al., 2023a). Finally, trait composition is shifting to favour plants of greater height, leaf area and resource acquisition rates (Bjorkman et al., 2018a;

Elmendorf et al., 2012a; Myers-Smith et al., 2019a; Niittynen et al., 2020; Thomas et al., 2020). Shifts in tundra vegetation are hence clear, and progressing at pace throughout the biome.

Such pervasive vegetation change is likely to have significant implications for tundra ecosystem function and regulation, trophic interactions and wider ecosystem feedbacks. For instance, shifts in tundra vegetation and land cover have the potential to drive wholesale changes in tundra nutrient cycling, hydrology and albedo (Bjorkman et al., 2020; Pearson et al., 2013), critical in an environment where permafrost soils contain upwards of half the world's soil carbon (Schuur et al., 2015). The impacts of local and regional scale changes to tundra vegetation risk being magnified, and in doing so, generating climate-based feedbacks operating across local to global scales (Bjorkman et al., 2020; Chapin et al., 2005; Elmendorf et al., 2012a; Euskirchen et al., 2009; Pearson et al., 2013). As such, understanding how tundra vegetation influences, and indeed is influenced by, such feedbacks is of critical importance to better inform projections of future change (Elmendorf et al., 2015). In order to do so, a nuanced and thorough understanding of how tundra vegetation interacts with ecosystem processes and functions must be developed. Tundra vegetation and its associated change must therefore be assessed and viewed through the lens of functional ecology.

1.1.2 The tundra through a functional lens

Plant functional traits are the key structural, physiological and biochemical characteristics that both impact resource uptake and use in plants (Jetz et al., 2016; Kattge et al., 2011), and mediate their responses to and effects on surrounding environments, species and trophic levels (Miedema Brown and Anand, 2022; Perez-Harguindeguy et al., 2016). As such, the functional traits encompassed by a community are intrinsically and mechanistically linked to key ecosystem functions and services, such as soil fertility, water availability and climate feedbacks (Díaz and Cabido, 2001; Hagan et al., 2023; Häger and Avalos, 2017; Lavorel et al., 2007; Miedema Brown and Anand, 2022; Musavi et al., 2015; Ottoy et al., 2017; van der Plas et al., 2020; Wang et al., 2019; Zylstra et al., 2016). It follows that shifts in these functional traits within a community are likely to have cascading impacts on the fundamental ecosystem services on which floral, faunal and human communities rely (Imbert et al., 2021). Functional traits are therefore considered critical to understanding how ecosystems respond and adapt to increased environmental perturbations, such as warming (McMahon et al., 2011; Myers-Smith et al., 2019b; Shan et al., 2012). Changes in the abundance of certain species or traits within a community may thus provide an early indication of impending tipping points in the provision of its ecosystem services (Schweiger and Laliberté, 2022; Villéger et al., 2013, 2008), highlighting the clear importance of functional traits to tundra plant communities.

Acknowledging this fundamental importance, work focussing on tundra functional traits and their associated changes has increased dramatically in recent years and become a mainstay of tundra ecology (e.g. Bjorkman et al., 2018a; Funk et al., 2017; García Criado et al., 2023b; Häger and Avalos, 2017; Ottoy et al., 2017; Reich et al., 1997; Shipley et al., 2016; Thomas et al., 2018, 2020; Villéger et al., 2013). For instance, we know now that plant height is increasing with warming across the tundra, but that other key traits lag far behind expected rates (Bjorkman et al., 2018a). Similarly, it is also known that between-species plant trait relationships seen globally are generalisable to the high latitude tundra and global extremes (Thomas et al., 2020), and that winner and loser species under a warming climate are not differentiable by their constituent trait space (García Criado et al., 2023b). Beyond these findings, new biome-scale trait datasets have been compiled to better inform tundra trait analyses (Bjorkman et al., 2018b) and novel spectral technologies are increasingly employed in an attempt to better characterise tundra traits across space and time (Nelson et al., 2022; Thomson et al., 2021). Whilst all such findings are invaluable to the wider, holistic understanding of tundra plant traits, one essential component of tundra functional ecology has been overlooked in recent years. Namely, functional diversity.

1.1.3 But what of functional diversity?

Specific definitions vary, but here I consider functional diversity to be the range, variability and evenness of plant functional traits within a community (Villéger et al., 2008). Moreover, it is precisely this range, variability and evenness of plant traits in particular that defines the functions, processes and services encompassed by the community (Miedema Brown and Anand, 2022). In this thesis, we consider two key facets of functional diversity: functional richness and evenness. The two metrics work in tandem. Functional richness quantifies the volume of multi-dimensional trait space filled by a community, whilst functional evenness considers the regularity with which abundance is distributed throughout this trait space. Put simply, functional richness considers the variety of different traits within a community whilst functional evenness considers how evenly the present traits are represented (Villéger et al., 2008). Both metrics encompass significant information regarding ecosystem processes, function and stability. More functionally rich communities typically exhibit more efficient and varied resource use (Díaz and Cabido, 2001), whilst the most dominant traits within a community's trait makeup is considered the chief determinant of the functions an ecosystem performs (Díaz et al., 2007). Indeed, the diversity and dominance of certain plant traits have been consistently linked to key ecosystem processes such as primary productivity and nutrient cycling across biomes, ecosystems and plant types (Díaz et al., 2007). Furthermore, communities with higher functional richness are considered more stable and have a higher capacity to resist and be resilient to warming and other global change impacts (**Figure 1.1**; Niittynen et al., 2020). Consequently, those with lower functional diversity typically incorporate a lower range and variability of traits and hence, functions, making them vulnerable to a loss of ecosystem functions and services, in turn threatening their regulation and long-term persistence (Figure 1.1; Callaghan et al., 2011; Imbert et al., 2021). Understanding and quantifying tundra functional diversity is hugely important in determining the stability and future of tundra ecosystems and key services under the influence of a rapidly warming climate.

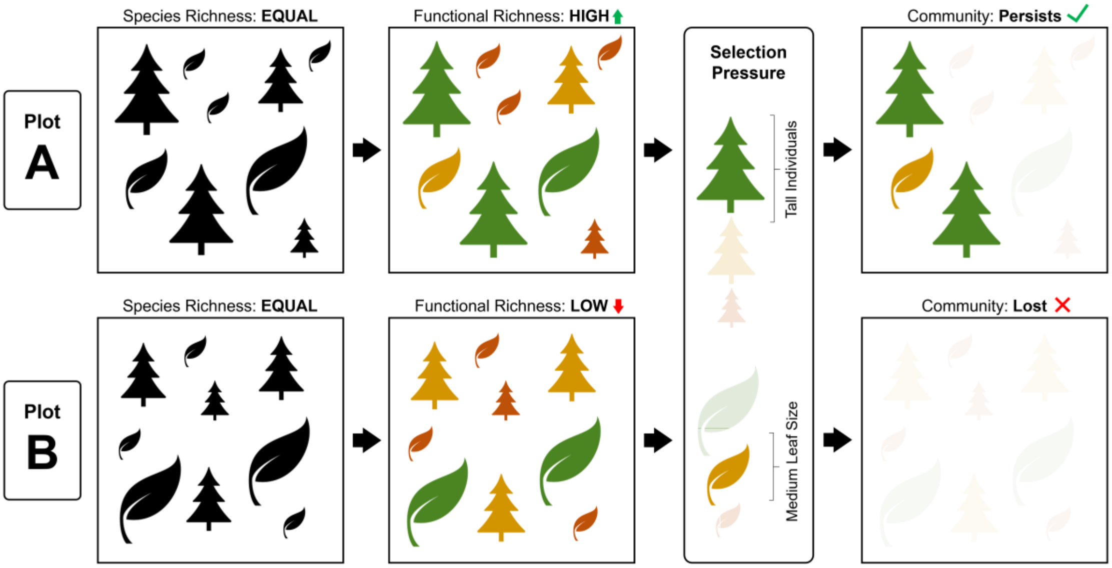


Figure 1.1 | Species richness, functional richness and stability. Whilst Plot A and Plot B comprise the same two species, and hence species richness, their functional richness differs. Individuals in Plot A encompass a greater diversity of plant heights and leaf sizes than those in Plot B, hence Plot A expresses a greater trait variety and consequently functional richness. This higher functional richness increases the likelihood the community contains individuals with traits better suited to a new selection pressure (e.g., climate warming), and hence, is able to persist under the new prevailing environmental conditions. As such, under this simulated scenario, the community in Plot A is able to persist whilst the community in Plot B is likely lost.

Certain timely studies are beginning to meet the challenge of quantifying functional diversity across the tundra. For instance, Rissanen et al.'s (2023) local-scale and Niittynen et al.'s (2020) regional-scale studies provide key insights into the role fluvial factors and snow play in mediating warming impacts on functional diversity in Norway's far north. However, to the best of my knowledge, little has been done to quantify and understand the distribution, drivers and characteristics of functional diversity across the tundra biome at the wider scale. It is not known whether patterns in functional diversity seen globally extend to the far reaches of global trait space (Edie et al., 2018; Schumm et al., 2019; Thomas et al., 2020). Furthermore, studies assessing functional diversity typically rely on incomplete trait records, leading to sparse trait matrices that align poorly with plant composition records across space and time (Joswig et al., 2023; Schrodt et al., 2015). Gap-filling methods are increasingly commonly used to address such data gaps, however, there remains no consensus over optimal methods and the relative inaccuracies current techniques encompass. Finally, whilst new approaches are pioneering the use of spectra to characterise numerous aspects of tundra vegetation, it remains uncertain whether such methods can be applied to investigate tundra functional diversity across space and, critically, time (Féret and Asner, 2014; Laliberté et al., 2020; Rocchini et al., 2018; Schweiger and Laliberté, 2022). Such questions require urgent answers, presenting a tantalising knowledge gap that this thesis sets out to tackle.

1.2 Thesis

1.2.1 Thesis aims

This thesis addresses critical knowledge gaps concerning tundra functional diversity at the biome scale. Broadly speaking, I aim to determine why tundra functional diversity is distributed like it is, how it is changing over time, and what methods can we develop to best characterise such patterns. More specifically, I hope to tackle three main areas, namely: 1) understanding its distribution and drivers across the wider tundra over space and time; 2) determining the performance of currently available gap-filling methods to achieve such aims; and 3) developing novel spectral methodologies to enhance future assessments across spatial and temporal scales (see **Figure 1.2**). Whilst brief details of these three broad aims are outlined below, specific research questions, hypotheses and predicted findings can be found in full within each of the relevant chapters of the thesis (**Sections 2.1**, **7.1**, **4.1**). The three broad aims of this thesis are as follows:

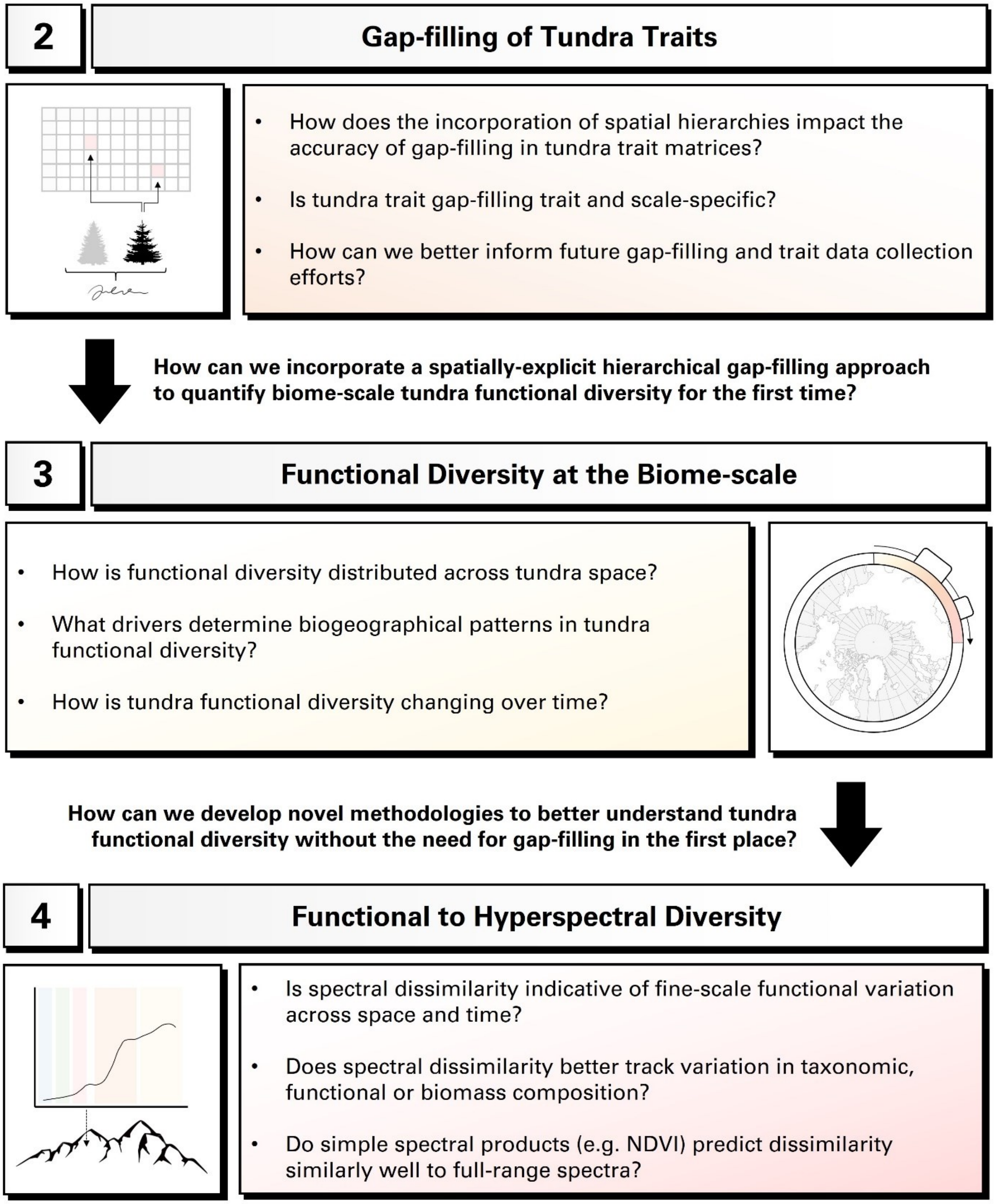
1) **Quantifying biome-scale distributions of tundra functional diversity.** I aim to determine biome-scale spatial patterns in tundra functional diversity for the very first time, elucidate key drivers of such patterns, and quantify their change over time.

2) **Assessing gap-filling performance in tundra trait studies.** I aim to incorporate spatial hierarchies into current gap-filling methods to assess the impacts of gap-filling from non-local measurements on tundra trait studies and better inform future gap-filling efforts.

3) **Investigating functional diversity through spectra.** I aim to assess the potential of hyperspectral data in quantifying local-scale tundra β-diversity to determine the feasibility of using spectra to remotely track tundra functional diversity over space and time.

1.2.2 Thesis structure

This thesis consists of five main chapters. These include this introductory chapter (**Chapter 1**), followed by three research chapters (**Figure 1.2**; **Chapters 2-4**), each of which were written independently as a standalone peer-reviewed manuscript and are either under review or in the final stages of being prepared for publication. For details of their current status, please see the **Declaration**. A synthesis chapter (**Chapter 5**) follows the research chapters, drawing out themes from across the thesis and offering some key conclusions. Supplementary materials for each of the three research chapters are provided in the **Appendices** (**Chapter 6**).



2 **Gap-filling of Tundra Traits**

- How does the incorporation of spatial hierarchies impact the accuracy of gap-filling in tundra trait matrices?
- Is tundra trait gap-filling trait and scale-specific?
- How can we better inform future gap-filling and trait data collection efforts?

How can we incorporate a spatially-explicit hierarchical gap-filling approach to quantify biome-scale tundra functional diversity for the first time?

3 **Functional Diversity at the Biome-scale**

- How is functional diversity distributed across tundra space?
- What drivers determine biogeographical patterns in tundra functional diversity?
- How is tundra functional diversity changing over time?

How can we develop novel methodologies to better understand tundra functional diversity without the need for gap-filling in the first place?

4 **Functional to Hyperspectral Diversity**

- Is spectral dissimilarity indicative of fine-scale functional variation across space and time?
- Does spectral dissimilarity better track variation in taxonomic, functional or biomass composition?
- Do simple spectral products (e.g. NDVI) predict dissimilarity similarly well to full-range spectra?

Figure 1.2 | Structure of the thesis. A conceptual diagram detailing the thesis' three research chapters and the main aims each chapter intends to address.

1.3 References

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2

Considering geographic proximity improves gap-filling performance in tundra plant traits

2.0 Abstract

Recent years have seen a rapid growth in studies seeking to characterise tundra vegetation through the lens of plant traits because of their links to ecosystem function and services. Such studies often rely on inconsistent and incomplete trait records, leading to sparse trait matrices that match poorly with plant composition records across space and time. Gap-filling methods, such as ‘phylogenetic imputation’, are becoming increasingly commonly used to populate such sparse matrices, however there remains no consensus over the best way to do this . Here, we leverage fine-scale *in situ* trait data collected on individuals of multiple species under near-identical environmental and temporal conditions to determine the influence of explicitly incorporating spatial hierarchies on gap-filling performance. We show that inaccuracies between true and estimated trait values typically grow when using trait records from greater spatial and taxonomic distances. We further highlight that such patterns are trait and scale-specific, and that gap-filling from more distant taxonomic levels may enhance gap-filling accuracy under certain spatial constraints and scenarios. Finally, we provide key suggestions for how to better gap-fill in sparse tundra trait matrices, and how to target data collection to minimise the need for gap-filling in the first place. Incorporating spatial hierarchies into existing gap-filling methods may therefore increase the accuracy with which tundra functional ecology can be characterised in the future.

2.1 Introduction

Functional traits – key biochemical, physiological and structural characteristics impacting resource uptake and use in plants (Jetz et al., 2016; Kattge et al., 2011) – are intrinsically linked to ecosystem functions and services (Díaz and Cabido, 2001; Hagan et al., 2023; Häger and Avalos, 2017; Lavorel et al., 2007; Miedema Brown and Anand, 2022; Musavi et al., 2015). As such, functional traits are key parameters in understanding how ecosystems may adapt and respond to increasing environmental perturbation (McMahon et al., 2011; Myers-Smith et al., 2019; Shan et al., 2012). Changes in species and trait composition within communities are likely to have wide-ranging influences on their associated ecosystem services (Callaghan et al., 2011; Imbert et al., 2021) and could provide possible indications of fundamental tipping points in future ecosystem service provision (Schweiger and Laliberté, 2022; Villéger et al., 2013). Reflecting this importance, a rapidly growing body of work has developed in recent years that characterises changes in vegetation composition and diversity through the lens of functional ecology and traits (e.g. Bjorkman et al., 2018a; Funk et al., 2017; García Criado et al., 2023b; Häger and Avalos, 2017; Niittynen et al., 2020; Ottoy et al., 2017; Reich et al., 1997; Shipley et al., 2016; Thomas et al., 2020, 2018; Villéger et al., 2013).

Functional ecology research relies on functional trait databases, such as TRY (Kattge et al., 2020, 2011), which contain measurements of traits of individual plants sampled across species and locations. However, despite the rapid increase in trait-based approaches to vegetation assessment, these databases remain spatially and taxonomically sparse (Jetz et al., 2016; Joswig et al., 2023), limiting analyses and inferences. In an ideal scenario, trait values would be measured on all individuals of each required species at every plot and time point to capture both intra- and interspecific trait variability and accurately characterise the functional composition of a location at any given time (Kattge et al., 2011; Kazakou et al., 2014). In reality however, this kind of targeted sampling across large areas is a hugely time consuming and resource intensive undertaking (Schrodt et al., 2015) and such records rarely exist (e.g., Wheeler et al., 2023). Instead, trait databases are typically collated from individual studies and opportunistic data, which lack any coherent global sampling design or protocol (Joswig et al., 2023). As a result, global-scale trait matrices are characterised by sparsity and unequal representation across taxonomy, space and time (Poyatos et al., 2018; Shan et al., 2012).

Determining the most appropriate way to conduct functional ecology analyses when the underlying trait matrices are incomplete remains a contested topic. One option is to delete plot records which exceed a specified threshold for the proportion of missing data (e.g. Huxley et al., 2023), or even to run ‘complete case analyses’, in which only plots with trait measurements for all constituent species are used (Pakeman, 2014; Poyatos et al., 2018). Whilst ensuring high trait coverage, these approaches dramatically reduce overall sample sizes and can bias results as only plots containing the most commonly sampled species are retained (Johnson et al., 2021; Molina-Venegas et al., 2018; Nakagawa, 2015; Nakagawa and Freckleton, 2008; Sandel et al., 2015). More recently, the use of imputation, or ‘gap-filling’ to fill-in missing values in sparse trait matrices has increasingly been considered the most effective way to overcome many of these limitations (e.g. Johnson et al., 2021; Joswig et al., 2023; Molina-Venegas et al., 2018; Poyatos et al., 2018; Schrodt et al., 2015; Shan et al., 2012). The manner in which to gap-fill however, remains uncertain with no consensus over an optimal method.

In recent years, ‘phylogenetic imputation’ has come to the fore as a primary method through which to gap-fill missing values in plant trait matrices (e.g. Joswig et al., 2023; Molina-Venegas et al., 2018; Schrodt et al., 2015; Shan et al., 2012). In principle, the more closely phylogenetically related two species are, the more closely related their traits will be due to a shared evolutionary history, with individuals of the same species being most closely related of all (Lovette and Hochachka, 2006; Swenson, 2014). Indeed, trait values have often been shown to be consistent within species across spatial scales for many, albeit not all, commonly used plant traits (Kazakou et al., 2014), supporting the assumption that interspecific, rather than intraspecific, differences primarily drive variability in tundra plant traits (Kattge et al., 2011; Poyatos et al., 2018). Phylogenetic imputation leverages these relationships and fills in missing data by modelling trait values from individuals of the same or closely related taxa across larger geographic extents (Schrodt et al., 2015; Shan et al., 2012). In recent years, more sophisticated methods incorporating additional information, such as trait-environment relationships and multi-trait correlations (Schrodt et al., 2015), have developed to better inform the imputation of missing values (Joswig et al., 2023).

Based on the assumption that intraspecific variation in traits is less than interspecific variation (Kattge et al., 2011; Poyatos et al., 2018), missing trait values are typically infilled by calculating average values per trait from all individuals of a species within the studies’ geographical extents (e.g. Fried et al., 2012; Huxley et al., 2023). Should there not be any values from a species for a given trait, averages are then calculated at the genus, family or even growth form level to ensure trait matrix completeness (e.g. Bjorkman et al., 2018a; Niittynen et al., 2020; Rissanen et al., 2023a). A key constraint of this method however, is that it ignores the key role spatial scale has to play in determining trait variation (Cordlandwehr et al., 2013; Jónsdóttir et al., 2023). In particular, within-species plant traits are known to vary significantly across space due to both genotypic variation and phenotypic plasticity in response to local environmental constraints (Cordlandwehr et al., 2013; Garnier et al., 2001; Kattge et al., 2011; Mokany and Ash, 2008). As a result, whilst once considered to be of minor influence when compared to that of interspecific trait variation (Kattge et al., 2011; Poyatos et al., 2018), intraspecific variation is now thought to contribute between 25% (Siefert et al., 2015) and 40% (Kattge et al., 2011) of global plant trait variation, with its relative contribution differing depending on the spatial scale at which it is observed (Thomas et al., 2020). This challenges the assumption of phylogenetic imputation, that the trait values for a single species or other taxonomic unit are consistent across the breadth of a study's geographical extent.

Given how plant traits are now known to vary between populations, locations and environmental conditions (e.g., Bjorkman et al., 2018a; Cordlandwehr et al., 2013), we believe that gap-filling should explicitly consider the influence of spatial variation on within-taxa trait signals. Reflecting this, in a following study we incorporated a hybrid taxonomic and spatial hierarchical gap-filling approach into our analysis of biome-scale tundra functional diversity (Everest et al., In prep.; **Chapter 3**). In this, we built upon the standard phylogenetic imputation approach outlined above (e.g. Bjorkman et al., 2018a; Huxley et al., 2023; Niittynen et al., 2020; Rissanen et al., 2023a) by nesting spatial units within taxonomic units to ensure trait values from more closely-related spatial units were used within each taxonomic unit (e.g. species, genus) as a priority, only progressing to higher spatial units should no trait values be available more locally (**Chapter 3**; **Section 2.2.5**). We expected this method to improve gap-filling performance, hence this study was designed to assess the validity of our chosen two-step hierarchical approach for use in the analyses in **Chapter 3**, and address three main aims:

1) Determine how the use of gap-filling across both spatial and taxonomic hierarchical scales impacts the accuracy of estimates of trait values within tundra communities.

2) Identify whether the impacts of gap-filling are trait and scale-specific.

3) Understand how best to inform future gap-filling and plant trait data collection efforts in future studies of tundra functional ecology.

In order to meet these aims, we undertook a regional-scale field campaign across northwest Canada in summer 2022. Specifically, we implemented a standardised protocol where we collected composition and trait records for a consistent number of individuals per species per plot across a multi-site network. We leveraged the trait data collected on multiple individuals of the same species both under near-identical environmental and temporal conditions, together with trait data collected by others across much broader spatial scales, to understand the impacts of gap-filling from non-local measurements on functional trait studies. These analyses allow us to assess and inform gap-filling performance in studies of tundra functional ecology where intensive, local-scale trait collection is not feasible. We do, however, acknowledge that due to time-consuming and remote nature of the data collection required for this study (**Section 2.2**), our findings are based on a limited quantity of data with a narrow spatial and temporal focus. As such, we believe the value of this study is as a proof-of-concept, a channel through which to challenge issues with gap-filling methodologies and suggest novel thought-provoking approaches supported by empirical data.

2.2 Materials and Methods

2.2.1 Study areas

Our study area comprised three separate locations from across the subarctic tundra of northwest Canada. These locations, henceforth known as 'sites', were: 1) Kluane Plateau in the Kluane Wildlife Sanctuary of the southern Yukon (YT), 2) Goldensides Mountain in Tombstone Territorial Park of the central Yukon, and 3) Samuel Glacier in Tatshenshini- Alsek Provincial Park of northern British Columbia (B.C.; **Figure 2.1**). Within each site, subsite(s) were located in areas of subarctic tundra environments, and were chosen to cover a wide variety of vegetation types. Whereas the Tombstone and Samuel Glacier sites contained just a single subsite, the Kluane site

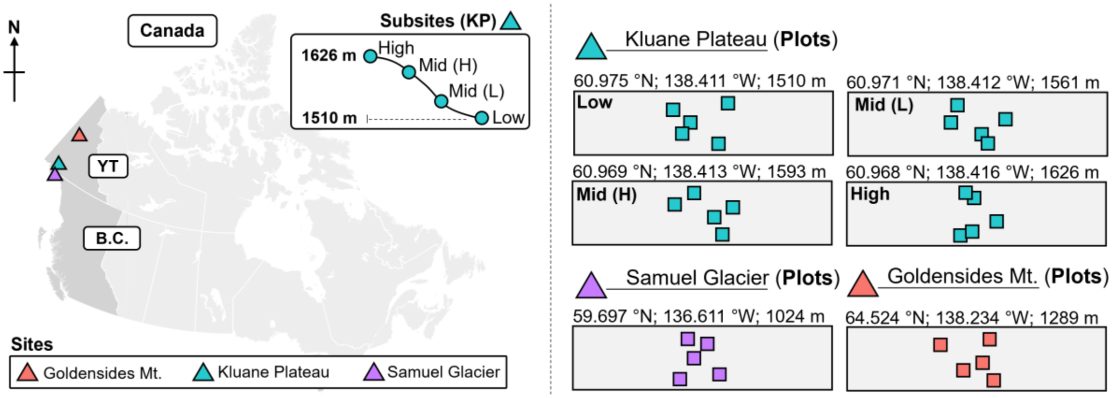


Figure 2.1 | Study locations across northwest Canada. The locations of the plots sites (3), subsites (6) and 1 x 1 m^2 assessed plots (30) sampled across British Columbia and the Yukon in 2022.

contained four subsites spread across an elevational gradient spanning 126 m (1510 – 1626 m; **Figure 2.1**). Each subsite contained five individual 1 x 1 m plots, leading to an overall sample size of 30 plots: 20 in Kluane and a further five each at both Tombstone and Samuel Glacier (**Figure 2.1**). The location of each plot within the subsite was determined by randomly generating a bearing (0 – 360 °) and distance (0 – 30 m) at which to place the plot away from the subsite centroid point. All plots were hence within a 30 m radius of the subsite centre. All three sites comprised entirely alpine tundra vegetation cover, are partially or completely snow covered from September to June and experience relative climatic extremes annually with mean annual temperatures (2000-2020) in Kluane of -3.6 °C, in Tombstone of -6.7 °C and at Samuel Glacier of -0.5 °C (Fan and van den Dool, 2008).

2.2.2 Plant composition data

Vascular plant composition data was collected in the field across the network of 30 1 m^2 plots (**Figure 2.1**). We used a 'top-hits only' point-framing approach with intersections at every 10 cm, recording the first vascular plant species, if any, hit at each of the 100 pin drops. We collected trait data on individuals of the five most common species by cover within each of the 30 sampling plots. When multiple species were equally fifth-most common, the species on which to collect traits was randomly selected. In cases where less than five species occurred in a plot, trait data on all species was taken. Sampling occasionally fell outside the brief tundra flowering period, making the identification of graminoid and horsetail species, particularly *Carex sp.*, problematic. Despite eliciting expert opinion, we had low confidence in the IDs of sampled species, so all graminoid and horsetail species were removed from the analyses, thereby reducing the number of sampled species per plot. Our simplified plots therefore contained all 32 remaining forb and shrub species from which relative cover was calculated (**Table S2.1**). The average number of taxa identified to species per plot was ~ 4.0 which represented on average 70.4 % of the cover of all species in the original plots. Finally, the composition data was taxonomically standardised using The Plant List (TPL, 2023) within the R package 'Taxonstand' (version 2.4; Taxonstand, 2023) to ensure comparability with the global trait data (**Section 2.2.4**).

2.2.3 Field trait data

In this study, we assessed largely the same traits as in **Chapter 3** to ensure comparability between studies. As before, the stipulated traits all: (1) have demonstrated importance to tundra ecosystem functioning (Bjorkman et al., 2018a; Niittynen et al., 2020; Thomas et al., 2018, 2020); (2) contribute strongly to the two main axes in plant trait space – leaf economics and size (Thomas et al., 2020); and (3) are well represented in plant trait databases. The traits selected for analysis included: leaf dry matter content (LDMC; g g^{-1}), leaf area (mm^2), leaf nitrogen concentration (leaf N; mg g^{-1}), leaf phosphorus concentration (leaf P; mg g^{-1}), plant height (hereafter, height; m), and specific leaf area (SLA; mm^2 mg^{-1}). Seed dry mass (SDM) was removed however due to foreseen sampling difficulties. Trait data was collected in the field on specific individuals from within the 30 assessed 1 m^2 composition plots (**Figure 2.1**). For each of the five (or less) selected species per plot (**Section 2.2.2**), traits were measured on five individuals. If there were less than five individuals, traits were measured on as many individuals as possible.

For each individual, we first measured height before collecting five leaves (or as many as possible if the individual had less than five leaves). These leaves were later: (1) scanned and analysed using Fiji ImageJ (Schindelin et al., 2015) to determine their area; (2) weighed for their fresh mass; (3) dried for 72 hours in a drying oven before being weighed for their dry mass. From leaf area, fresh mass and dry mass, it was possible to calculate both SLA and LDMC. LDMC values are missing from the Tombstone site (**Figure 2.1**) as we did not have a balance to measure fresh mass at the site. The leaves from all five individuals of the same species per plot were then ground and mixed for both leaf N and leaf P analysis, carried out by the University of Edinburgh School of Geosciences Chemical Analysis Facility. Samples from the five individuals were mixed to give a single leaf N and P value per species per plot, due to the high quantity of leaf material needed for the chemical analyses. If the leaves of the species in question were insufficiently large, an additional number of leaves from different individuals of the same species within and immediately surrounding the plot were collected to ensure there was sufficient sample material with which to run the analyses. Overall, this trait data collection provided us with height, SLA, LDMC and leaf area values for (up to) five individuals per assessed species per plot, and a single leaf N and leaf P value per assessed species per plot. The height, SLA, LDMC and leaf area values were subsequently averaged to also give a single value per assessed species per plot.

2.2.4 Tundra biome trait data

For our gap-filling analyses, we used largely the same biome-wide trait database described in **Chapter 3,** and methods are near identical. We repeat them here again for ease of understanding. Data for the six continuous traits were extracted from two key global-scale databases of plant traits: the TRY plant trait database (version 5; Kattge et al., 2020) and the Tundra Trait Team (TTT) database (version 1; Bjorkman et al., 2018b). Each contains numerous records for multiple assessed traits (including our specified six) on hundreds of species across the tundra (TTT) and world (TRY). All Northern Hemisphere records from the TTT database were retained as they were sampled from known tundra locations (including alpine plots) whereas in the TRY database only records from above 60° N were retained as we couldn’t be certain records from below 60° N were drawn from tundra environments. Trait values for any species found within these geographic ranges were retained for use in trait gap-filling (**Section 2.2.5**). The majority of final trait values were sourced from the TTT database with a smaller number of trait measurements included from TRY, leading to a combined total of 51,462 unique records across the six continuous traits. The respective proportions of this total contributed by each trait were: height (36.8%; 18,955 records); SLA (19.0%; 9,789 records); leaf area (17.2%; 8,857 records); LDMC (13.3%; 6,857 records); leaf N (10.2%, 5,235 records); and leaf P (3.4%; 1,773 records).

Quality control was undertaken following the methods of Bjorkman et al. (2018a), García Criado et al. (2023a) and **Chapter 3**. Steps included: data cleaning, reorganisation and standardisation of species taxonomy using The Plant List (TPL, 2023) within the R package ‘Taxonstand’ (version 2.4; Taxonstand, 2023a). Both automated and manual error checking was also incorporated during the production of the final dataset to ensure the accuracy of the retained records. Error checking included, but was not limited to, the identification of duplicate records, removal of significant outliers and erroneous data values and standardisation of accepted vegetative and reproductive height records. For full details on the automated and manual error checking, see **Figure S3Tab.1**.

2.2.5 Gap-filling

In order to observe how gap-filling influences multi-trait diversity in tundra vegetation, it was essential we had a value for each trait at every spatial and taxonomic hierarchical level for each species record in all 30 plots. Where possible, we generated these values by taking the average value for a trait from all the data in the combined database for a given spatial and taxonomic hierarchical level. However, in some cases, there was not sufficient data available at all levels, leaving values for some traits at different levels missing. We therefore created a two-step hierarchical gap-filling algorithm to generate the required values (**Figure 2.2a**). The two steps were: (1) primary gap-filling (**Section 2.2.5.1**), which generated mean trait values across spatial and taxonomic hierarchies (as described in **Chapter 3**); then (2) secondary randomisation (**Section 2.2.5.2**), which infilled missing values by estimating within-hierarchy differences from neighbouring groups. For simplicity, the following explanations are for the gap-filling of one trait, per species record per plot. This process was applied for all trait values across all composition records and plots.

2.2.5.1 Primary gap-filling

The gap-filling algorithm's first step works across two different hierarchical scales, with trait means being generated across a spatial (S) hierarchy within each taxonomic (T) hierarchical unit (**Figure 2.2b**). Taxonomically, trait means are generated first at the species level (T1), followed by the genus (T2), family (T3) and functional group levels (T4; shrub and forb; **Figure 2.2b**). At the finer scale, within each taxonomic level, trait means are generated across a progressively widening spatial hierarchy. For each record, calculations occur first within the relevant plot (S1), followed by the relevant subsite (S2) and site (S3), then relevant 0.5 ° x 0.5 ° latitude-longitude grid cell (S4), followed by the region (continent; S5), and finally, globally (S6; **Figure 2.2b**). The progression of hierarchical units from most specific to least specific hence runs: T1:S1 (species:gridcell), T1:S1, ..., T1:S6, T2:S1, …, T2:S6 up to T4:S6 (functional group: global; **Figure 2.2c**).

For instance, *Salix reticulata* was the first species recorded at Kluane's high subsite in plot 3 (KP_H_P3; **Figure 2.1; 7.2a**). At the species:plot (T1:S1) level, trait means are calculated by averaging the values from the five individuals of *Salix reticulata* measured within that plot, KP_H_P3. At the species:subsite (T1:S2) level, means are calculated from all *Salix reticulata* individuals within the whole subsite, rather than the plot alone, whilst at the species:global (T1:S6) level, any *Salix reticulata* values globally are used. The process is the same across the taxonomic progression. For instance, trait values at the genus:plot (T2:S1) are calculated by averaging all

Salix records from within the plot KP_H_P3, values at the family:site (T3:S3) calculated by averaging all *Salicaceae* records from within the wider Kluane site, and so on (**Figure 2.2a,c**).

2.2.5.2 Secondary randomisation procedure

In this study, we were aiming to emulate real-world scenarios where gap-filling is required due to a lack of trait data at the desired taxonomic and spatial hierarchical units. For example, someone may want, but not have, trait data for *Salix reticulata* at the site level. They would therefore need to take averages of data from other *Salix* species within the site, or data from *Salix reticulata* across larger areas. To mirror this, we removed values from the hierarchical levels below the level being estimated when calculating our gap-filled averages. For instance, as seen in **Figure 2.2a**, the first species record at KP_H_P1 was also *Salix reticulata*. To calculate the species:plot (T1:S1) level means, all trait values for *Salix reticulata* within that plot were used. However, to calculate the genus:plot (T2:S1) level trait averages for the same record, *Salix reticulata* records were removed to simulate real-world scenarios where these trait records don't exist and gap-filling is required. Therefore, only trait values from other *Salix* species within the plot could be used. The problem we encountered however, was that in many cases, we did not have data from multiple species of the same genus within a plot (T2:S1), or two or more genera from the same family within the same subsite (T3:S2) and so on. This prevented us from generating gap-filled values as there are no additional values from which to take averages.

To simulate the typical patterns of missing data encountered in real world trait gap filling applications, we used a secondary randomization procedure (**Figure 2.2a**) that estimated, for any given taxonomic:spatial hierarchy, the average amount of variation across all records within the same hierarchical unit, and then randomly allocated this variation to the record in question in order to generate a gap-filled value. More specifically, for each hierarchical unit, the algorithm first (Stage 1; **Figure 2.2a**) calculates the median standard deviation of trait values for all instances when there is at least two or more of the specified taxonomic level within the specified taxonomic unit. For instance, it took the median standard deviation of all instances when two or more species of the same genus (e.g. *Salix*, *Dryas*, *Anemone*) occur within the specified spatial unit (e.g. plot). It then determined the 'baseline' value for each record (Stage 2; **Figure 2.2a**), taken as the mean trait value from the original, now removed trait values for the composition record being assessed. Finally, it estimates the missing trait value (Stage 3; **Figure 2.2a**) by selecting a random number from a normal distribution centred on the 'baseline' value with a standard deviation equal to the calculated median standard deviation described previously. It runs through this random selection 50 times (Stage 4; **Figure 2.2a**), taking a mean of the random selected numbers to minimise the impact of extreme random selections, with this generated value then being used to fill in the missing trait value at the specified gap-fill level. The proportion of missing values and use of the secondary gap-filling method was not significantly correlated with the calculated distance values (*Spearman Rank: p* = 0.16), thereby suggesting it did not notably influence the results (**Figure S2.2**). For full details of the number of records and species used in primary gap-filling, and the number of records missing requiring secondary gap-filling, see **Figure S2.2**.

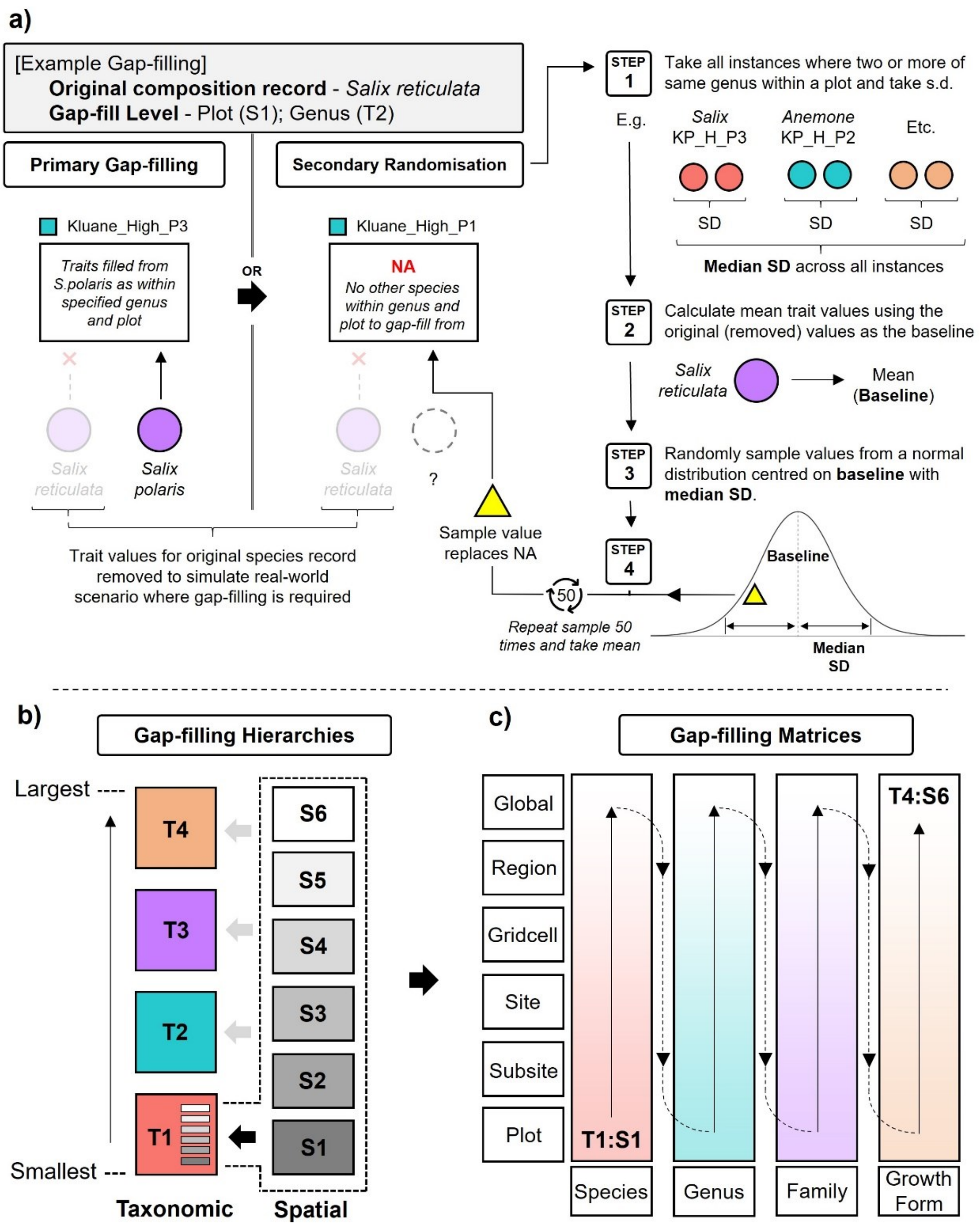


Figure 2.2 | Two-step gap-filling and randomisation procedure. a) The two-step process used to ensure 100% trait coverage across our global trait matrix at all spatial and taxonomic hierarchical levels. Where possible, values were filled using the primary gap-filling method, as detailed in **Section 2.2.5.1** and **Chapter 3**. When this was not possible, values were filled using the 'secondary randomisation' procedure, as detailed in **Section 2.2.5.2**. **b)** The nesting of the spatial hierarchical levels (6) within each of the taxonomic hierarchical units (4). **c)** The order in which values were gap-filled, progressing through each spatial unit within a single taxonomic unit before then moving onto the next.

2.2.6 Single and multi-trait distances

We calculated distance matrices to determine the difference between gap-filled and ‘true’ trait values for both the six traits individually and combined across the plot network. In both cases, we first needed to obtain an overall estimate by plot. The gap-filled trait values were first standardised by subtracting the mean value per trait from the gap-filled value then dividing by the standard deviation. Within each plot, these standardised trait values were then used to calculate a single community-weighted mean (CWM; weighted by relative cover) value per trait at each hierarchical level. To compare the difference in multi-trait composition between hierarchical levels, we used pairwise squared generalised Mahalanobis distance, calculated using the ‘biotools’ package in R (Silva, 2021). Distances were calculated per plot between the ‘true’ CWM values of the six traits, taken as the ‘Species:Plot (T1:S1)’ level trait values, and the trait CWM values at all other levels of gap-filling (e.g. ‘Genus:Plot’ [T2:S1], ‘Family:Subsite’ [T3:S2] etc.). Individual plot values (**Figure S2.1**) were then averaged (mean) across all plots and presented as a matrix.

To compare the differences in single traits between hierarchical levels, percentage differences were calculated between the true CWM values (again ‘Species:Plot’) and CWM values at all other hierarchical levels. These distance and percentage difference values between hierarchical levels were then averaged (mean) across plots and also presented as a matrix.

2.2.7 Variance decomposition

In order to observe where the variance within traits lies, both spatially and taxonomically, we used linear mixed-effect models from the ‘lme4’ package in R (version 1.1-29; Bates et al., 2022). Models were run at two spatial levels: (1) biome-scale, incorporating trait values from both the biome-wide TRY/TTT database and our field data collection in northwest Canada; and (2) local-scale, incorporating values from just the field-collected Kluane dataset. At each spatial scale, we ran an intercept-only mixed-effect model for each of the traits. Each model used logged values for the specified trait as the response variable and incorporated two nested random effects. Trait values were logged to account for the typical log-normal distribution of each trait (Schrodt et al., 2015; Thomas et al., 2020). The first random effect nested the taxonomic hierarchical units of the traits, i.e. (1 | GrowthForm / Family / Genus / Species) whilst the second nested the spatial hierarchical units. At the biome-scale, this ranged from subsite to biome-scale as trait values outside of our field sites were not drawn from specific plots. At the local-scale, the random effect ranged from subsite to site, with the residual variance considered to encompass the variance derived from individuals within the plot. As the leaf N and leaf P data was not collected on individuals and instead only as an averaged value per plot (**Section 2.2.3**), it was not possible to include these traits in the variance decomposition analyses. These analyses were hence run on the four remaining traits: SLA, LDMC, leaf area and height. All analyses were carried out in the R programming language (version 4.2.0; R Core Team, 2022).

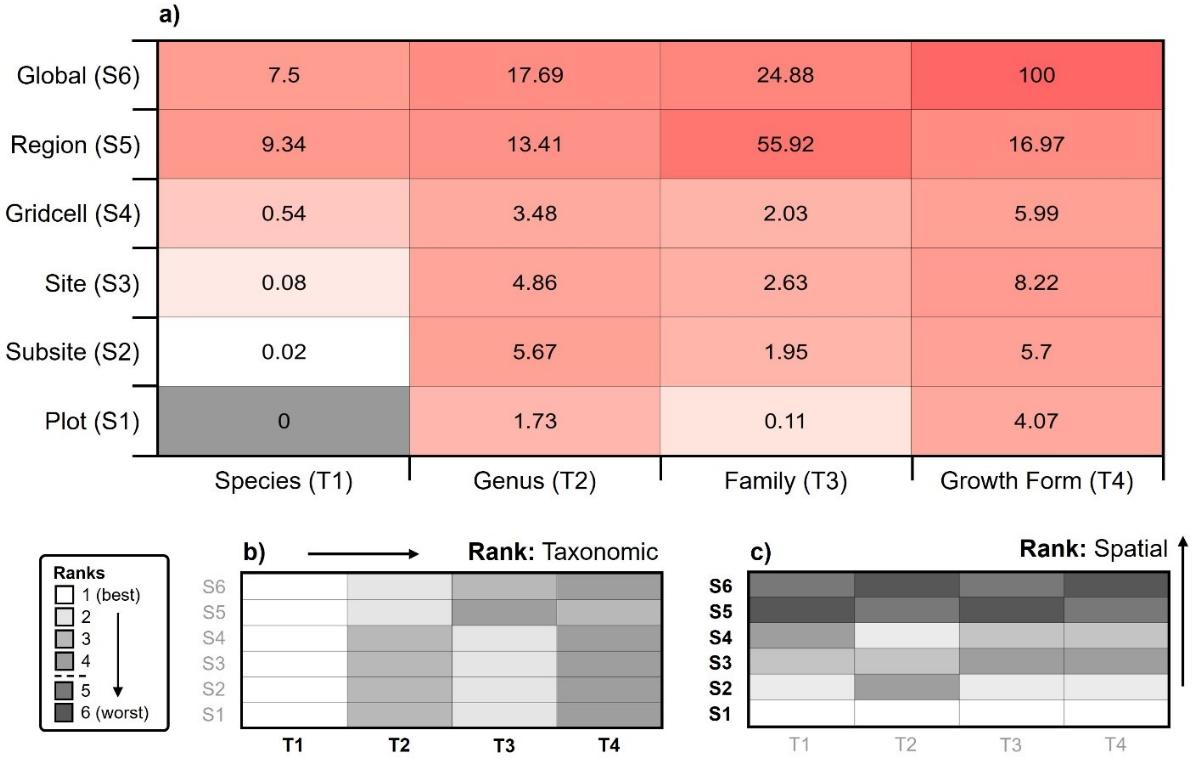
2.3 Results

2.3.1 Gap-filling and multi-trait diversity

Across our network of sampling plots, we found that estimates of CWM multi-trait estimates were different to the ‘true’ value (taken as the species:plot [T1:S1] estimates; **Figure 2.3**) when using every tested combination of spatial and taxonomic hierarchical gap-filling (**Figure 2.3a**). Estimates were typically best in the lower spatial and taxonomic units (lower left) and progressively worse towards the higher hierarchical units (upper right; **Figure 2.3a**). We found variation within these patterns however, and highlight that in certain situations, higher levels actually give trait estimates closer to the known true values (**Figure 2.3a**). This matrix therefore provides potential guidance, within the context of our field locations, regarding the relative accuracy of trait estimates drawn from different hierarchical gap-filling levels.

When viewed taxonomically, multi-trait CWM estimates were shown to be best when using species level gap-filled values, and worst when using growth form level gap-filled values at virtually all spatial hierarchical levels (**Figure 2.3a,c**). When using genus and family level trait gap-filled values, patterns diverged depending on the spatial hierarchical unit used. At more fine spatial levels (plot to gridcell), family level trait values always produced estimates closer to the true value than genus level trait values (**Figure 2.3c**). Conversely, at broader spatial scales (region to global), which rely on trait values sampled globally from TRY and TTT, genus level trait values produced estimates closer to the true value than family level values did (**Figure 2.3c**).

When viewed spatially, estimates became increasingly far from the true value with progression to larger spatial hierarchical units with estimates closest to true at the plot level and furthest at the regional and global levels (**Figure 2.3b**). Patterns across the subsite to gridcell levels displayed notable variability, but most often showed that estimates at the gridcell level were closer to true than those at the subsite and site levels (**Figure 2.3b**). Overall, it appears that the differences stemming from spatial gap-filling are greater than those from taxonomic gap-filling, with a notable step change increase in disparity evident between the gridcell and region hierarchical levels (**Figure 2.3a**). Similarly large differences were also apparent when shifting from species to genus-level values in gap-filling, whilst differences between genus, family and growth form-level gap-filling appeared smaller (**Figure 2.3a**).



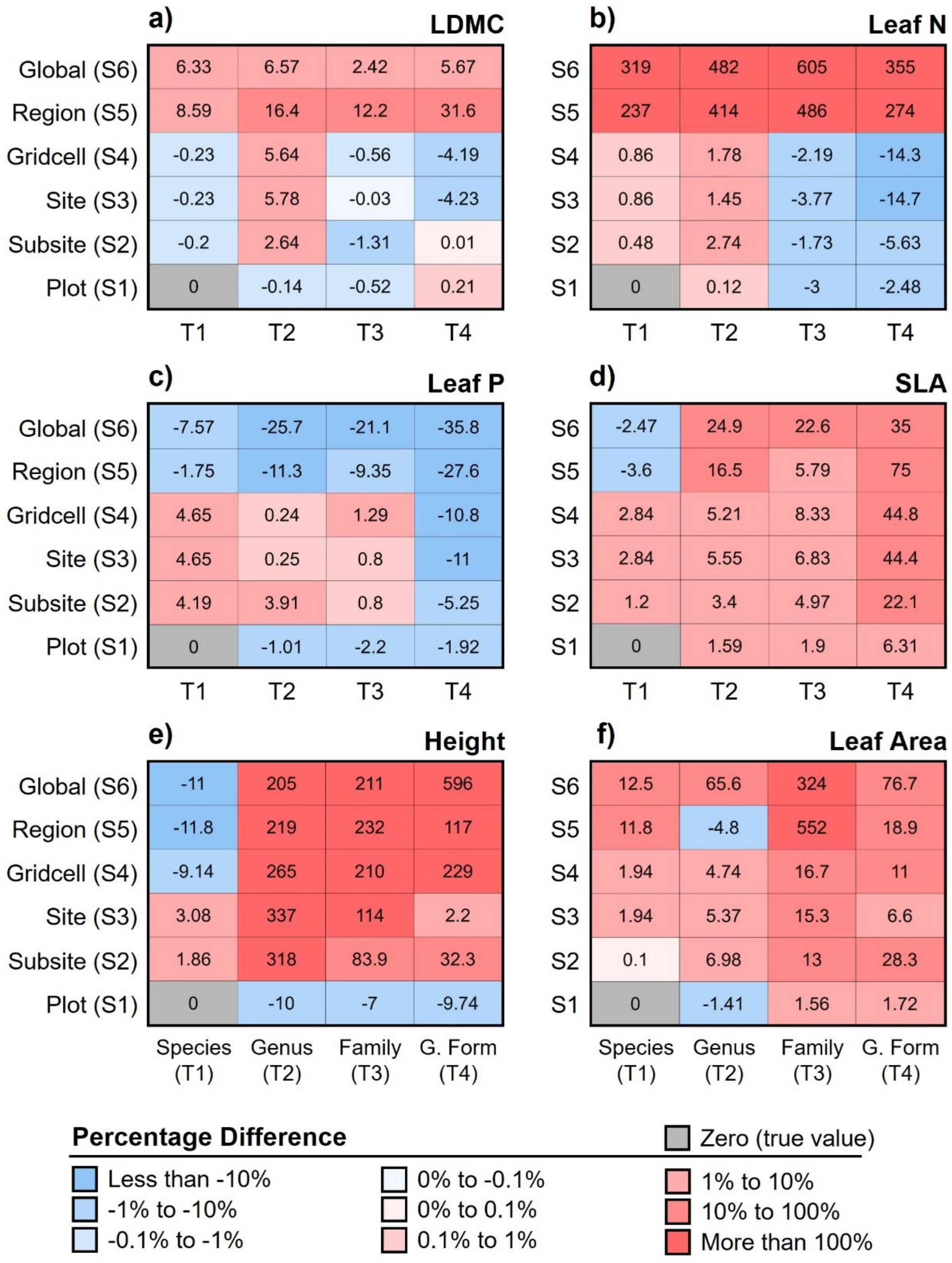
a)

	Species (T1)	Genus (T2)	Family (T3)	Growth Form (T4)
Global (S6)	7.5	17.69	24.88	100
Region (S5)	9.34	13.41	55.92	16.97
Gridcell (S4)	0.54	3.48	2.03	5.99
Site (S3)	0.08	4.86	2.63	8.22
Subsite (S2)	0.02	5.67	1.95	5.7
Plot (S1)	0	1.73	0.11	4.07

Figure 2.3 | Multi-trait distances between true and estimated trait values increase towards the highest levels of gap-filling but show variation within. a) Pairwise squared generalised Mahalanobis distance between true trait values, taken as the 'species:plot' (T1:S1) level, and estimated trait values based on CWM multi-trait values gap-filled at each hierarchical level. This plot represents the averaged distances of the 30 constituent sample plots (**Figure 2.1**). Mahalanobis distances were scaled between 0 and 100 and coloured with a logarithmic scale for ease of interpretation. **b)** Rank of the four taxonomic units, from smallest (best) to largest distance (worst), within each spatial unit; read left to right. **c)** Rank of the six spatial units, from smallest (best) to largest distance (worst), within each taxonomic unit; read bottom to top.

2.3.2 Gap-filling across different traits

We found that the percentage difference between the true and gap-filled estimates of trait values across taxonomic and spatial hierarchies varied strongly in both magnitude and direction between different traits (**Figure 2.4**). Gap-filling predominantly led to an overestimation of true trait values for five of the six assessed traits (**Figure 2.4a,b,d-f**), with the exception of leaf phosphorus concentrations which were largely underestimated at higher gap-filling levels (**Figure 2.4c**). We found considerable variability within these broad trends however, across both taxonomic and spatial hierarchies. For instance, the overestimation of height values increased considerably when moving from the species to genus level (**Figure 2.4e**), whilst the overestimation of SLA experienced the biggest increase when moving from the family to growth form level (**Figure 2.4d**). Conversely, the biggest increase in differences from the true trait values for leaf area (**Figure 2.4f**), LDMC (**Figure 2.4a**) and particularly leaf N (**Figure 2.4b**) all occurred spatially, predominantly when shifting from the gridcell to regional level. The shift from gridcell to regional gap-filling further induced the biggest change in leaf P estimates, shifting from over to underestimation at this spatial hierarchical unit, having also been underestimated at the plot level (**Figure 2.4c**). Shifts from over to underestimation are also evident taxonomically for leaf N, when moving from the genus to family level (**Figure 2.4b**) whilst LDMC exhibited the opposite trend spatially, switching from under to overestimation when moving from subsite to site hierarchical units (**Figure 2.4a**). Whilst all six traits show differing degrees of difference from true trait values across the hierarchical levels, the greatest magnitude of difference was evident in leaf P, and particularly plant height and leaf N where values were being overestimated by up to 600% at the growth form:global and family:global levels respectively (**Figure 2.4b,c,e**). Overall, we found that gap-filling impacts are highly trait dependent and that the magnitude and direction of change across hierarchical units varies strongly between traits.



a) LDMC

	T1	T2	T3	T4
Global (S6)	6.33	6.57	2.42	5.67
Region (S5)	8.59	16.4	12.2	31.6
Gridcell (S4)	-0.23	5.64	-0.56	-4.19
Site (S3)	-0.23	5.78	-0.03	-4.23
Subsite (S2)	-0.2	2.64	-1.31	0.01
Plot (S1)	0	-0.14	-0.52	0.21

b) Leaf N

	T1	T2	T3	T4
S6	319	482	605	355
S5	237	414	486	274
S4	0.86	1.78	-2.19	-14.3
S3	0.86	1.45	-3.77	-14.7
S2	0.48	2.74	-1.73	-5.63
S1	0	0.12	-3	-2.48

c) Leaf P

	T1	T2	T3	T4
Global (S6)	-7.57	-25.7	-21.1	-35.8
Region (S5)	-1.75	-11.3	-9.35	-27.6
Gridcell (S4)	4.65	0.24	1.29	-10.8
Site (S3)	4.65	0.25	0.8	-11
Subsite (S2)	4.19	3.91	0.8	-5.25
Plot (S1)	0	-1.01	-2.2	-1.92

d) SLA

	T1	T2	T3	T4
S6	-2.47	24.9	22.6	35
S5	-3.6	16.5	5.79	75
S4	2.84	5.21	8.33	44.8
S3	2.84	5.55	6.83	44.4
S2	1.2	3.4	4.97	22.1
S1	0	1.59	1.9	6.31

e) Height

	Species (T1)	Genus (T2)	Family (T3)	G. Form (T4)
Global (S6)	-11	205	211	596
Region (S5)	-11.8	219	232	117
Gridcell (S4)	-9.14	265	210	229
Site (S3)	3.08	337	114	2.2
Subsite (S2)	1.86	318	83.9	32.3
Plot (S1)	0	-10	-7	-9.74

f) Leaf Area

	Species (T1)	Genus (T2)	Family (T3)	G. Form (T4)
S6	12.5	65.6	324	76.7
S5	11.8	-4.8	552	18.9
S4	1.94	4.74	16.7	11
S3	1.94	5.37	15.3	6.6
S2	0.1	6.98	13	28.3
S1	0	-1.41	1.56	1.72

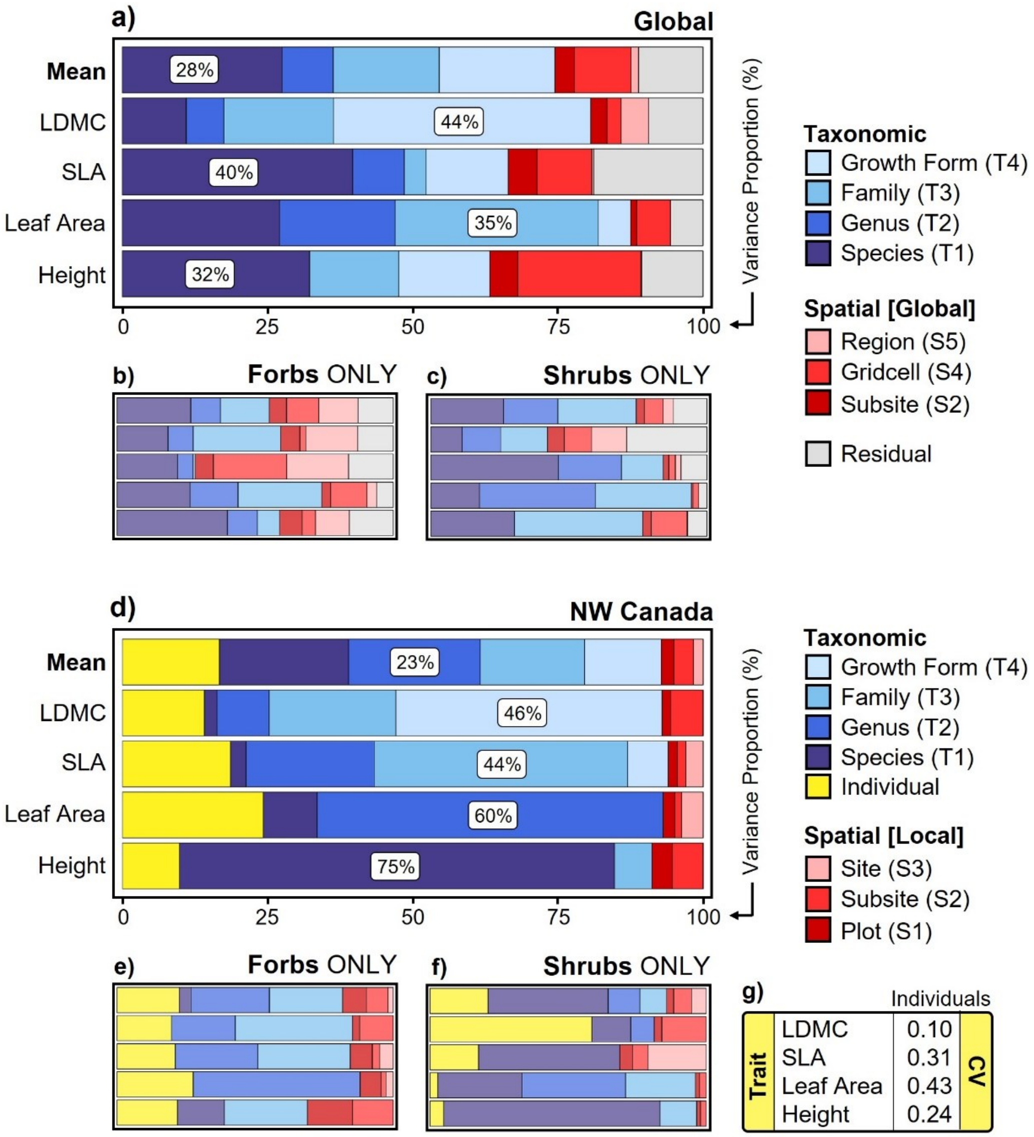
Figure 2.4 | Percentage differences between true and estimated trait values show strong trait and scale-specificity. Percentage difference between true trait values, takes as the 'species:plot' (T1:S1) level, and gap-filled estimated trait values at each level, for each of the six assessed traits, namely: **a)** leaf dry matter content (LDMC); **b)** leaf nitrogen (N); **c)** leaf phosphorus (P); **d)** specific leaf area (SLA); **e)** plant height; and **f)** leaf area. Each plot represents the averaged percentage differences of the 30 constituent sample plots (**Figure 2.1**). Percentage differences were coloured using a logarithmic scale for ease of interpretation.

2.3.3 Variance across scales

When considering trait values sourced from across the full tundra biome, rather than our network of sampling plots alone, we found that the location of the mean variance in trait values is located predominantly but not exclusively within taxonomic rather than spatial units (**Figure 2.5a**). On average, the largest proportion of variance lay within the species (**Figure 2.5a**), however each trait showed quite different distributions of variance. The majority of variance in all four traits occurred taxonomically, within the species for SLA and height, but in the family and growth form for leaf area and LDMC respectively (**Figure 2.5a**). All four traits displayed a notable degree of spatial variation however, most commonly at the gridcell level with the exception of LDMC, with height displaying the greatest variation across space (**Figure 2.5a**).

When using trait values taken solely from our network of sampling plots, we found that virtually all the variation in trait values lay within the taxonomic hierarchy, with little to no variation being found within the smaller, local spatial units, both on average and across each individual trait (**Figure 2.5d**). Taxonomic influences were dominant across all four traits, with the variation in height, leaf area, SLA and LDMC found primarily within the species, genus family and growth form levels respectively (**Figure 2.5d**). Hence, none of the four traits varied notably between locations with the variation lying between different species, genera, families and growth forms. When effects were viewed separately between growth forms, much of the within-trait variation in shrubs tends to be located within taxonomic levels at both the global (**Figure 2.5c**) and local scales (**Figure 2.5f**). This differed from forbs where spatial effects exerted a greater influence on within-trait variation across both global (**Figure 2.5b**) and local scales (**Figure 2.5e**).

Finally, within our field site in NW Canada, we found that a notable proportion of the variation in each trait was contained within the individuals of each species (**Figure 2.5d**). On average, ~20% of the variation of each species was contained within the individuals, peaking for leaf area where up to 25% of the variation could be found (**Figure 2.5d**). Coefficients of variation (CV) ranging from 0.10 for LDMC to 0.43 for leaf area again highlight the notable trait variation present between individuals in our analyses (**Figure 2.5g**). The influence of individuals on within-trait variation was also notable for both forbs and shrubs at the local-scale, although the relative influence differed between traits for the two functional groups (**Figure 2.5e,f**). For instance, almost 25% of the variation in height for forbs could be found in the individual (**Figure 2.5e**). Whilst none of the variation in shrub height was found at the individual level, upwards of 60% of variation in LDMC was instead (**Figure 2.5f**), highlighting the variation in intraspecific influence between traits and functional groups.



Trait	Individuals
LDMC	0.10
SLA	0.31
Leaf Area	0.43
Height	0.24

Figure 2.5 | The relative location of variation between spatial and taxonomic hierarchies differs between local and biome-wide spatial scales.. When using the full trait dataframe spanning the tundra biome, we partitioned the variance between taxonomic and spatial hierarchical levels for **a)** all assessed species, **b)** forb species only, and **c)** shrub species only. We repeated these analyses using just the trait data collected in the field in NW Canada in 2022, and partitioned the variance between taxonomic and spatial hierarchical levels for **d)** all assess species, **e)** forb species only, and **f)** shrub species only. Here, the residual is referred to as 'Individual' (yellow bars) as it captures the intraspecific component but note, we acknowledge that 'Individual' is likely actually 'Individual + Sampling Error', as per the methods of Schrodt et al. (2015) and Thomas et al. (2020). The residual does not represent 'Individual' variation in the global-scale figures as it also encapsulates between-plot differences. **g)** The coefficient of variation (CV) was calculated at the individual level for the four assessed traits. Note, leaf nitrogen and phosphorus could not be included in these assessments as we did not have trait information available at the individual level for either trait (**Section 2.2.3**).

2.4 Discussion

In line with our expectations, we found that gap-filling across not only taxonomic but also spatial hierarchies resulted in discrepancies between true and estimated trait values (**Figure 2.3a**). We found that discrepancies between true trait values and gap-filled estimates grew when traits were inferred from more taxonomically and geographically distant individuals (**Figure 2.3a**). The use of trait values from increasingly broad spatial and taxonomic levels hence, lead to worse gap-filling performance across our study design (**Figures 7.3b,c**). Patterns were not always as expected, and in some cases we found that broader hierarchical levels performed better than lower levels (**Figure 2.3b,c**). We also observed a step-change increase in distances at the region level and above (**Figure 2.3a**). The variation seen across spatial scales hence suggests that gap-filling of tundra traits should incorporate spatial hierarchies in the future. We further found gap-filling performance to be strongly trait specific, with the majority of traits found to be overestimated when using gap-filled trait values (**Figure 2.4**). We also showed that distribution of trait variance between taxonomic and spatial factors was scale-dependent, with the proportion of spatially-derived variance considerably lower at the local-scale than at the biome-scale (**Figure 2.5a,d**). Finally, we highlight the notable degree of trait variability between conspecific individuals growing in close proximity (**Figure 2.5d,g**).

2.4.1 Spatial scale in gap-filling

By collecting standardised trait values on multiple individuals per species per plot under near-identical environmental and time conditions, this study allowed us to directly test the accuracy of gap-filled trait values across hierarchical levels. Our analyses demonstrate clearly that gap-filling leads to discrepancies between true and estimated trait values, a key but rarely tested finding (**Figure 2.3a**; Schrodt et al., 2015). Moreover, these discrepancies grow not just as traits are inferred from those measured on more taxonomically distant individuals, but also when using trait information from plants measured at a greater distance from the target population. (**Figure 2.3b,c**). These results support the use of a hybrid taxonomic-spatial hierarchical gap-filling approach, that we hence employ in **Chapter 3**. Within each taxonomic unit, differences between true and gap-filled values grew with progression to higher spatial units (**Figure 2.3c**), highlighting distance decay in trait signals within species and more generally, the role spatially-derived intraspecific variation plays in determining within-taxon trait variability (Cordlandwehr et al., 2013; Garnier et al., 2001; Kattge et al., 2011; Mokany and Ash, 2008), as seen in in **Figure 2.5d,g**.

Patterns were not monotonic, however. There was an evident step-change in the magnitude of difference when stepping up from the gridcell to the region level (**Figure 2.3a**), likely reflecting a dramatic increase in trait variation over larger spatial units associated with increased genotypic differences and plastic responses to differing environmental conditions (Cordlandwehr et al., 2013; Garnier et al., 2001). This relationship was further reflected in the variance decomposition where spatial variability was notably more influential in determining trait variance at the broader (**Figure 2.5a**) rather than local scales (**Figure 2.5d**), again highlighting the step-change at the region level. Indeed, on average, gap-filled trait values using the broadest taxonomic level (growth form, T4) below the region level were more accurate than using traits from the same species, but collected from areas outside the region (**Figure 2.3a**). Given that the magnitude of difference between true and gap-filled values in the higher spatial levels far exceeded that in the highest taxonomic levels, our results bring into question the widespread practice of using species-level mean traits (e.g., Bjorkman et al., 2018a; Niittynen et al., 2020; Rissanen et al., 2023a) – without regard to location at which traits were collected – as a primary means to infer local trait values.

2.4.2 Practical gap-filling applications

Based on the findings presented above, our analyses can begin to provide practical suggestions on how to better inform gap-filling decisions in assessments of tundra functional ecology. That said, we recognise that all of the results presented, with the exception of the full tundra-wide variance decomposition (**Figure 2.5a-c**), are specific to our individual field setting in northwest Canada (**Figure 2.1**). Therefore, whilst we believe our findings are relevant across tundra sites, the use of exact values and patterns, particularly by trait (**Figure 2.4**) must be treated with caution.

In general our results suggest that when gap-filling one should typically use values at lower spatial or taxonomic levels (**Figure 2.3**). More specifically however, we recommend a two-step approach that explicitly incorporates spatial hierarchies. On average (**Figure 2.3a**), virtually all gap-filled trait values below the region level, even those at the highest taxonomic units (e.g. growth form) are closer to the true trait values than those gap-filled at the region level or higher, even when using species values. In **Chapter 3** (*tundra functional diversity over space and time*), over 64.4% of the values were gap-filled at the region level or higher (**Figure 2.2c**), thus these findings highlight a potential degree of uncertainty in those results. Our findings here therefore suggest that when gap-filling, values should first be selected across all taxonomic and spatial hierarchies below the region level, before then selecting values from the region and global level if needed (**Figure 2.6**).

Furthermore, at all spatial levels below the region threshold, family level gap-filled values provided more accurate estimates than those at the genus level (**Figure 2.3a,b**), despite being a higher taxonomic unit and sharing a more distant phylogenetic relationship and shared evolutionary history (Swenson, 2014). This finding supports that of Schrodt et al. (2015) who similarly found "genus means produced the least reliable results". In this study, we find that values gap-filled at the family level typically often incorporated fewer records and species than those at the genus level (**Figure S2.2**), likely a result of the relatively fewer genera per family than species per genus in tundra trait datasets. Concurrently, we also found significant positive correlations between the number of records or species used in calculating the gap-filled estimate (**Figure S2.2**) and the gap-filling inaccuracy (**Figure 2.3**). That is, the more values incorporated in the gap-filling estimate, the worse it was, likely through the inclusion of increasingly disparate and unrepresentative data. Hence, the fewer values used at the family level may be a contributing factor to the relatively better gap-filling performance witnessed at the family rather than genus level (**Figure 2.3**). Whatever the reason however, these results suggest that below the region

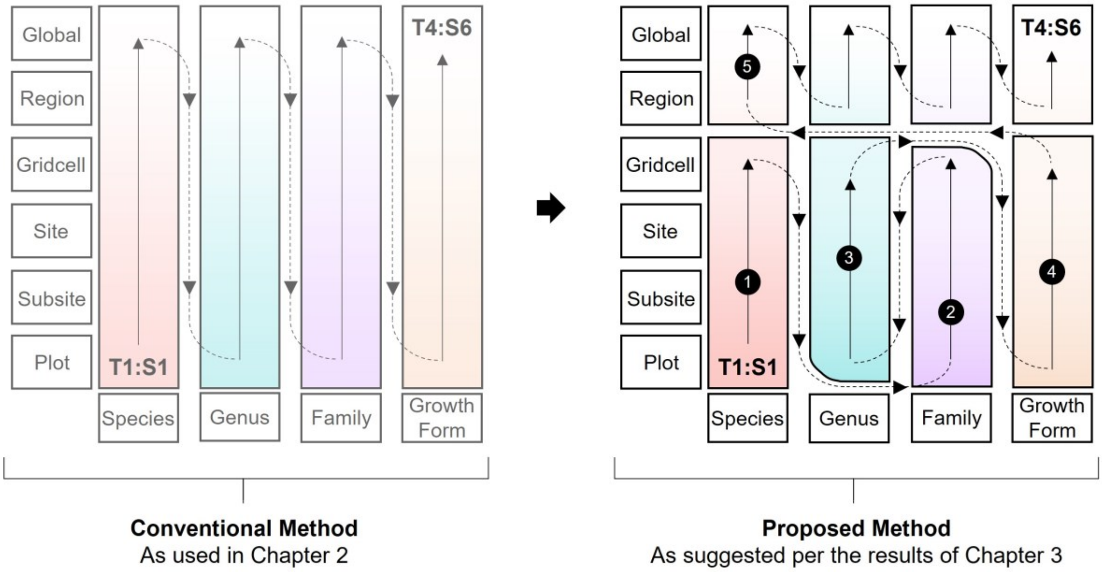


Figure 2.6 | Suggested two-step method for future gap-filling. Based on the findings of these analyses, we suggest a gap-filling approach that first incorporates values across all taxonomic levels (species [1] > family [2] > genus [3] > growth form[4]) below the region level, before progressing above the region level and following the linear progression across taxonomic hierarchies [5] (species > genus > family > growth form).

level in the priority spatial units, it makes sense to use family level values before genus level values when gap-filling tundra trait values (**Figure 2.6**).

Furthermore, whilst the above suggestions consider an averaged approach across all traits, we found the distribution of variance across taxonomic and spatial hierarchies (**Figure 2.5a,d**), and resulting gap-filling performance (**Figure 2.4**), to be strongly trait specific. This supports past studies that have found that the accuracy of estimated trait values varies between traits depending on their plasticity, and the environment and scale of aggregation from which values were sourced (Cordlandwehr et al., 2013). A trait-specific approach could hence be adopted when gap-filling in the tundra to achieve the best possible accuracy overall. For instance, leaf nitrogen and plant height are known to exhibit considerable variation across the tundra biome (Bjorkman et al., 2018a), a finding supported here where we found (over-) estimations of leaf nitrogen and plant height to be extreme at the highest hierarchical levels (up to 600%; **Figure 2.4b,e**). Different gap-filling approaches may however be better suited to best estimate missing values for each of these traits. For instance, gap-filling performance in leaf nitrogen dramatically worsens at the region level (**Figure 2.4b**), suggesting that it should be gap-filled across taxonomic hierarchies within narrower spatial units as a matter of priority (in line with **Figure 2.6**). Meanwhile, gap-filling performance in plant height, experiences a considerable increase in discrepancies when moving from the species to genus level (**Figure 2.4e**). As such, species values across all spatial levels should be used before moving onto genus level values, suggesting that using the original, more conventional gap-filling approach used in **Chapter 3** (**Figure 2.2c**; **Figure 2.6**) performs better for plant height.

A final, counter-suggestion to that proposed in **Figure 2.6**, would be to gap-fill via the calculation of weighted means to facilitate the use of relevant trait data from across all hierarchical levels. By weighting each trait value by the relative performance of its spatial and taxonomic hierarchical level, as determined in this study (**Figure 2.3a**; **7.4**), you maximise the quantity of data incorporated into the gap-filling process whilst also maximising the influence of the data we now know to be most accurate. Whilst these exact numbers and findings are again caveated by the fact they are site-specific (**Figure 2.1**), we believe the patterns and suggestions are generalisable across many tundra sites. Furthermore, it would be possible to apply the protocols and methods developed in this study to calculate site-specific gap-filling performances at other sites to better guide gap-filling performance at all locations throughout the tundra.

2.4.3 Suggestions for trait data collection

Whilst these analyses provide tangible, practical advice on how to enhance gap-filling performance in studies of tundra functional ecology, we recognise that in an ideal world gap-filling would not be necessary at all. In reality, most studies are constrained by the hugely time consuming and labour intensive nature of collecting tundra trait data in often extreme locations (Jetz et al., 2016; Schrodt et al., 2015). This limits the ability of any one field campaign to collect sufficient data to avoid needing to use gap-filling to some extent. In light of this, we believe that our work could give guidance not just on how to improve gap-filling performance, but how to better target trait data collection to reduce the need for gap-filling in the first place. In doing so, it has the potential to increase the accuracy of studies into tundra functional ecology.

For instance, taking the trait-specific example above (**Section 2.4.2**), our results highlight how the accuracy of leaf nitrogen values decreased considerably at the region level (**Figure 2.4b**), suggesting considerable variation in leaf nitrogen across tundra space (Bjorkman et al., 2018a). Therefore, when targeting collection of leaf nitrogen data, we believe it is better to collect data from across a broader swath of the tundra, and to focus less on taxonomic representation given the relatively lower variation between taxonomic levels compared to spatial levels. Contrastingly, plant height values were shown to be largely consistent within species but hugely variable between species at the genus level and higher (**Figure 2.4e**; **Figure 2.5a,d**; Bjorkman et al., 2018a). Hence, when collecting height values, it would be worthwhile to maximise collection across different taxa at the expense of spatial coverage, given the within-species consistency between spatial hierarchies (**Figure 2.4e**).

Whilst we understand focussing on data collection across large areas may not always be possible given the constraints of logistics, funding and fieldsite accessibility, such goals may be facilitated by collaborations and coherent sampling protocols between PIs and groups. Finally, when collecting data within specific field sites, we raise two key suggestions. Firstly, data should be collected on multiple individuals from the same species per plot, thereby incorporating the nearly 20% of overall trait variation found intraspecifically within our sites (**Figure 2.5d**). Secondly, we suggest that trait data should be collected robustly across nested spatial units, leveraging the subsites and if possible, plots that typically exist within tundra field sites. In doing so, this would allow for the matching of composition and trait records, essential in functional ecological studies, to occur at lower spatial hierarchies, which we have shown to markedly increase gap-filling performance (**Figure 2.3a**).

2.4.4 Additional methods

Whilst this work provides a number of suggestions for how we believe tundra gap-filling and trait data collection could be improved, we understand that ours is not the only method for how to better improve gap-filling. For instance, many gap-filling approaches now leverage known correlations between traits and commonly measured environmental variables to better inform the imputation of trait values in specific environmental contexts (Bruelheide et al., 2018; Joswig et al., 2023; Poyatos et al., 2018; Schrodt et al., 2015). Whilst we were able to incorporate rudimentary trait-environment relationships into our gap-filling in **Chapter 4** (e.g. vegetation class), given the lack of environmental data associated with the TRY and TTT trait databases (**Section 2.2.4**), it was not possible to leverage such relationships in this study. However, we do not believe that this method is antagonistic to our own, but rather complementary, and that future functional ecological studies could benefit from incorporating both trait-environment relationships and explicit spatial hierarchies in the future.

Another concept increasingly being assimilated into trait gap-filling efforts in recent years is that of multi-trait relationships, which make use of known correlations between key plant traits to better inform the imputation of gap-filled values (Poyatos et al., 2018; Schrodt et al., 2015). These methods have been shown to perform well in comparison to common gap-filling methods, particularly in large, sparse datasets, such as TRY (Johnson et al., 2021; Joswig et al., 2023; Kattge et al., 2020; Schrodt et al., 2015), and have been shown to estimate trait values comparable to true observed values in case studies (Díaz et al., 2016; Joswig et al., 2023; Schrodt et al., 2015). Nevertheless, elements of their performance remain poorly understood and there is some concern that the very trait-trait and trait-environment correlations used to better impute trait values may actually introduce bias that causes trait values to systematically deviate away from true estimates in some cases (Joswig et al., 2023). More work is needed to fully assess these potential implications (Joswig et al., 2023). As trait datasets grow, methods that incorporate spatial distance, taxonomic distance, environmental distance and multi-trait correlations will become more feasible. In joining together these four approaches – trait-environment relationships, trait-trait correlations and the nesting of explicit spatial hierarchies within taxonomic hierarchies – we believe you could create a more holistic approach to gap-filling that captures the nuance required to more accurately estimate trait values across the tundra.

2.4.5 Future research

Whilst this study advances tundra gap-filling performance and offers tangible solutions through which it may be improved, some areas fall beyond its scope. For instance, as in **Chapter 3**, given the need for pre-existing biome-scale tundra trait datasets, our analyses were limited to using only the common traits and reliably sampled vascular taxa typically found in such databases. Despite their likely importance to tundra functional ecology, there is considerably lower availability of below-ground and non-vascular plant trait data when compared to the vascular, above-ground data used in this study. The increasing availability of both below-ground (Klimešová et al., 2017, 2012) and nonvascular (Lett et al., 2021; Lewis et al., 2017) data however, should facilitate their inclusion in trait databases and assessments of tundra functional ecology in the near future. Similarly, whilst a product of the timing of and prevailing weather conditions experienced during our field campaign, we appreciate that the lack of graminoids in this study partially limits the conclusions we can draw. It is not uncommon for graminoid records to be identified above the species level, indeed almost 7% of graminoids in the ITEX+ database used in **Chapter 3** were only identified at the genus level or higher. They do however, comprise a significant portion of the tundra vegetation and should be incorporated into future studies to determine their respective influence on tundra gap-filling performance across spatial scales.

Furthermore, given the ad hoc manner in which tundra traits are typically sampled, there are very few sites where tundra traits are consistently measured in standardised locations and spatial units over time. Given this lack of coherent time series data, it is near-impossible to accurately match composition records to trait records from the same time period, instead matching temporally averaged trait data to time-specific composition records. Not only does this introduce additional variability into gap-filled trait datasets, it also precludes accurate functional ecological assessments over time by removing any temporal intraspecific trait variation, shown to be significant in one of the few case studies investigating such phenomena (Wheeler et al., 2023). Repeat sampling of traits across standardised spatial units and time periods that match those of composition records is a pressing need to facilitate accurate functional ecological assessments over time. Given the labour intensive manner in which tundra plant traits are measured, it raises important questions regarding the use of wholly alternative methods, such as spectral reflectance (see **Chapter 4**) to better target tundra functional ecology over time.

In line with expectations, we found that tundra traits varied strongly across not just taxonomic, but also spatial hierarchies, highlighting the influence of spatially-derived intraspecific variation in determining tundra traits. Gap-filled trait values were typically shown to be increasingly inaccurate with progression towards higher spatial hierarchies, although patterns were not entirely monotonic. Our results highlight a step change in trait variation and strong reduction in gap-filling performance at the region level, above which gap-filled trait values differed strongly from known values. Below this threshold, we find that family-level mean trait values offer more accurate trait estimates than those at the genus level, reflecting key trait-based differences that exist between species within genera. Patterns across hierarchies, however, were highly trait specific with the relative influence of taxonomic and spatial levels differing markedly between traits. Our results provide a number of key suggestions for how the incorporation of spatial hierarchies can enhance gap-filling performance and the accuracy of assessments in tundra functional ecology. Furthermore, they also offer tangible advice for how to minimise the need for gap-filling by targeting trait data collection where it is most needed. Finally, we considered the complementary nature of this method to other key advancements in plant trait gap-filling. In doing so, we highlight how the assimilation of trait-trait and trait-environment relationships with our spatially explicit hierarchical approach could more holistically capture variation within plant traits and facilitate a more nuanced approach to the imputation of gap-filled plant trait data in tundra settings and beyond.

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3

Functional diversity of tundra vascular plants across space and time

3.0 Abstract

Widespread changes to vascular plant communities are underway throughout the high-latitude tundra in response to rapid and accelerating warming. Yet, while some aspects of plant community shifts are well documented, such as increases in shrub cover, we have yet to quantify changes in tundra functional diversity, a key component of ecosystem functioning. Here, we quantify tundra-wide spatial and temporal patterns in the functional diversity of tundra vegetation through a biome-scale synthesis of *in situ* vegetation surveys and resurveys from 2,087 plots, 352 vascular plant species and 45 sites. We found that indices of functional diversity correlated strongly with species richness and decreased towards more northern latitudes following global gradients. Both temperature and the cover of all investigated functional groups correlated with spatial variation in tundra functional diversity, with higher forb cover related to higher functional richness whilst high cover of any one functional group was associated with low functional evenness. Temporal decreases in functional richness and evenness at the plot scale were linked to increases in certain functional groups, particularly shrubs, over time. Yet, functional diversity exhibited no net directional change across the near 40 year study period. With expected increases in shrub cover over the coming decades, a future decline in functional diversity could occur, potentially altering ecosystem functions and services across the tundra biome with accelerating warming.

3.1 Introduction

Changes to vascular plant communities are widespread throughout the northern latitudes in response to rapid climatic warming (Elmendorf et al., 2012b; Masson-Delmotte et al., 2021; Rantanen et al., 2022). These include shifts in the dominance and distribution of certain species and functional traits within tundra communities (Bjorkman et al., 2018a; Elmendorf et al., 2012b, 2015; García Criado et al., 2020, 2023a; Myers-Smith et al., 2019; Myers-Smith and Hik, 2017; Niittynen et al., 2020; Thomas et al., 2020). The range, variability and evenness of such traits, termed ‘functional diversity’ (Villéger et al., 2008), can alter key ecosystem functions and services (Díaz and Cabido, 2001; Hagan et al., 2023; Häger and Avalos, 2017; Lavorel et al., 2007; Miedema Brown and Anand, 2022; Niittynen et al., 2020; Ottoy et al., 2017; van der Plas et al., 2020; Zylstra et al., 2016). Communities with higher functional diversity are more stable and have higher capacity to resist and be resilient in response to global change impacts (Niittynen et al., 2020). Consequently, a loss of tundra functional diversity may have cascading effects on ecosystem functioning and the provision of ecosystem services, threatening their regulation and long-term persistence (Callaghan et al., 2011; Imbert et al., 2021). Despite the importance of functional diversity, it has yet to be quantified across the tundra biome, preventing explicit characterisation of its spatial distribution and change over time. We addressed this gap through a biome-wide, plot-scale, *in situ*, multi-site synthesis across spatial and temporal scales. Understanding spatial and temporal patterns in functional diversity will allow us to better understand potential implications of climate-induced biodiversity change for tundra ecosystem functions.

Macroecological theory established across other biomes globally, may provide a basis through which to understand spatial patterns in tundra functional diversity. The latitudinal diversity gradient in species richness has been recognised for upwards of a century (Lamanna et al., 2014; Oliveira et al., 2016; Pianka, 1966). Contemporary species richness declines monotonically from the tropics to the tundra (Edie et al., 2018; Mannion et al., 2014). However, the relationship of functional diversity to latitude remains unclear. In the tropical and temperate biomes, biogeographic patterns in functional diversity closely follow those of species richness. Functional richness (the volume of trait space filled by species; Mouchet et al., 2010; Villéger et al., 2008) declines with latitude due to a progressive loss of species and corresponding traits. The remaining species found at higher latitudes are typically more generalist in ecological function due to the demands of more extreme environmental conditions which prevent niche specialisation (Edie et al., 2018; Lamanna et al., 2014). In contrast, more environmentally benign conditions at lower latitudes facilitate higher species richness, with many species performing similar functions, i.e., functional redundancy, and occupying the same regions of trait space (Edie et al., 2018; Pastore et al., 2021). These communities tend to have low functional evenness (how evenly abundance is distributed across trait space; Mouchet et al., 2010; Villéger et al., 2008) whilst functional redundancy (the degree to which multiple species occupy the same or similar positions in trait space) tends to be high (Halpern and Floeter, 2008; Oliveira et al., 2016). With the loss of species towards higher and colder latitudes, species and hence, traits are disproportionately lost from these oversaturated areas of trait space, reducing redundancy and increasing functional rarity and evenness (Edie et al., 2018; Schumm et al., 2019; Violle et al., 2017). García Criado et al. (2023) found that the latitudinal gradient in taxonomic diversity persists throughout the tundra biome, but it is not yet clear whether spatial patterns in functional diversity are similarly consistent.

Spatial patterns of functional diversity in tundra ecosystems likely result from a suite of interacting abiotic and biotic factors (Speed et al., 2019). Given the latitudinal patterns in functional diversity from tropical to temperate biomes, temperature is likely a dominant determinant of biome-scale distributions of tundra functional diversity (Edie et al., 2018; Schumm et al., 2019). The influence of precipitation (Swenson and Weiser, 2010) and moisture (Bjorkman et al., 2018a) on the characteristics and distribution of particular plant traits (e.g., height) is well documented, thus they could also play a role in determining multi-trait diversity at the biome scale. Similarly, the functional group (e.g., shrub, graminoid, forb) composition within a community could play a significant role in dictating its trait composition (Chapin et al., 1996; Lavorel and Garnier, 2002; McGill et al., 2006). Whilst recent analyses suggest only weak relationships between functional group and trait composition (e.g., Bret-Harte et al., 2008; Cornelissen et al., 2004; Hollister et al., 2005; Hudson et al., 2011; Little et al., 2015; Shaver et al., 2001; Thomas et al., 2018), the relationship between functional group and multi-trait diversity is not yet clear. Thus, the relationships between both abiotic and biotic factors and biogeographic patterns in tundra functional diversity must be quantified to complete our understanding of functional diversity across latitudes and among the world's biomes.

As tundra plant composition changes in response to anthropogenic climate change, functional diversity across the tundra should shift. Shrub expansion, increases in vegetation productivity and cover as well as a spectral greening trend observed by satellites are widespread signals of functional shifts throughout the tundra biome (Berner et al., 2020; García Criado et al., 2020; Myers-Smith et al., 2020; Myers-Smith and Hik, 2017). Community-weighted traits are shifting, favouring taller plants with larger leaves and faster resource acquisition strategies (Bjorkman et al., 2018a; Niittynen et al., 2020; Thomas et al., 2020). García Criado et al. (2023a) have also reported that species turnover was common throughout the tundra, yet with no net directional change in species richness across sites, mirroring trends in richness observed at global scales (Blowes et al., 2019; Dornelas et al., 2014). However, change in biodiversity often lags behind warming in the tundra (Stewart et al., 2016), such that directional diversity changes and accompanying functional shifts are expected in the future, even if the global trend of climate warming would be halted. A biome-wide functional diversity shift would likely influence the stability and resilience of communities, potentially modifying global-scale feedbacks between vegetation and climate (Bjorkman et al., 2018a, 2020; Callaghan et al., 2011; Niittynen et al., 2020; Pearson et al., 2013). Thus, understanding changes in tundra functional diversity over time will facilitate the detection of climate feedbacks in a rapidly warming tundra biome.

In order to address the questions and uncertainties outlined above, we investigated three main research questions (RQs), outlined below. To do so, we undertook a biome-scale synthesis of *in situ* vegetation surveys and resurveys spanning 45 sites and 38 years, allowing us to quantify biome-wide spatial and temporal patterns in tundra functional diversity for what we believe to be the first time. Our study builds upon that of García Criado et al. (2023a), which investigated contemporary change in tundra species richness and composition over both space and time at the biome-scale. Their work addressed key questions concerning tundra biodiversity, but in doing so, raised further questions regarding how such species-focussed diversity patterns relate to wider tundra functions, processed and stability. Our analyses therefore follow a complementary methodological framework and modelling approach to García Criado et al. (2023a), thereby ensuring comparability between studies, but approach questions of biodiversity through a functional lens to tackle such unknowns. The questions we ask are as follows:

RQ1: Does functional diversity reflect species richness across the tundra biome?

We expect functional richness to increase with species richness at the plot level (α-diversity) (**H1a**), with a saturating trend at high levels of species richness due to increasing functional redundancy, as seen in other biomes (Edie et al., 2018). We also predict that with increasing latitude, functional richness will decrease alongside species richness whilst functional evenness will increase (**H1b**), as in tropical and temperate biomes (Edie et al., 2018; Halpern and Floeter, 2008; Lamanna et al., 2014; Oliveira et al., 2016; Schumm et al., 2019). However, we do not expect to see any difference in functional richness or evenness between biogeographic regions of the Arctic (**H1c; Figure 3.1**) due to the similar species pool observed across the tundra biome (PAF, 2018).

RQ2: What are the potential drivers of biogeographical patterns in tundra functional diversity?

Given the expected relationship between latitude, species richness and functional diversity throughout the tundra, we hypothesise increased functional richness and decreased functional evenness with warmer temperatures across the tundra biome (**H2a**; Edie et al., 2018; Schumm et al., 2019). Furthermore, based on studies of the influence of precipitation (Swenson and Weiser, 2010) and moisture (Bjorkman et al., 2018a) on tundra plant trait distributions and change, we predict higher functional richness and evenness in wetter and more moist locations (**H2b**; Currie et al., 2004; Grace et al., 2011; Spasojevic et al., 2014; Whittaker, 1960).

Despite the assumed similarity in ecological function between species belonging to the same functional group (e.g., Lavorel and Garnier, 2002; McGill et al., 2006), evidence suggests that plants are highly individualistic and that traditional functional groups explain only limited variation in tundra plant trait composition (e.g., Bret-Harte et al., 2008; Cornelissen et al., 2004; Hollister et al., 2005; Hudson et al., 2011; Little et al., 2015; Shaver et al., 2001; Thomas et al., 2018). Therefore, we do not expect the dominance of functional groups to relate strongly to biogeographical patterns in functional diversity (**H2c**).

RQ3: Is tundra functional diversity changing over time and if so, what factors are associated with its change over time?

While plant height is increasing in a warming tundra (e.g. Elmendorf et al., 2015, 2012; Myers-Smith et al., 2019; Niittynen et al., 2020; Thomas et al., 2020), changes in other traits and aspects of diversity lag behind expected rates (Bjorkman et al., 2018a; Duveneck and Scheller, 2015; Stewart et al., 2016). Furthermore, given the large magnitude of species turnover but overall lack of net, directional change in species richness (García Criado et al., 2023a), we expect similar patterns in functional diversity, with some changes (positive or negative) at the plot-level but no directional change in functional diversity averaged across the biome (**H3a**). Finally, we do not expect changes in functional group cover over time to be reflected in changes in functional diversity (**H3b**).

3.2 Materials & Methods

3.2.1 Plant composition data

Plant composition and abundance data were sourced from the International Tundra Experiment (ITEX+) dataset (Bjorkman et al., In prep.; Henry et al., 2022), an *in situ*, plot-based dataset of plant composition records spanning the tundra biome. The dataset has an inherent spatial hierarchy, with ‘plots’ representing the smallest spatial unit within this setup. Multiple plots are nested within ‘subsites’, typically a cluster of plots grouped by spatial or habitat commonalities within a wider ‘site’, which represents the largest spatial unit within the hierarchical structure. Sites generally contain multiple subsites and span areas ranging from several hundred square metres to tens of square kilometres (García Criado et al., 2023a; Prevéy et al., 2022). The mean number of plots per subsite and site were 14 and 46, respectively (**Figure 3.1a**). Plots were also grouped into larger biogeographic regions defined by both continent and glacial history for the purposes of gap filling in the trait data (**Figure 3.1a**; Abbott and Brochmann, 2003; Ray and Adams, 2001; Zhang et al., 2023). Western North America contained the highest proportion of plots at 35.6%, with Greenland-Iceland comprising 32.0%, Eurasia 26.4% and Eastern North America 9.0%.

We filtered the ITEX+ dataset, predominantly following the workflow of García Criado et al. (2023a), to suit the needs of this study. Plots were retained based on both geographical and methodological criteria. Geographically, only Arctic and subarctic plots above 60° N latitude were retained. Northern hemisphere alpine plots below 60° N (non-Oroarctic plots) were removed due to the different scales and distances over which ecological change occurs in alpine settings. While experiments were implemented at some ITEX+ sites, we retained only non-manipulated, ambient control plots in this study. Furthermore, only plots with consistent size of 1 m^2 or less (mean plot size: 0.59 m^2, range: 0.048 – 1 m^2) were retained between years. This is due to the known increase in plant species richness with plot size as per the species-area relationship (Zhang et al., 2023). While we acknowledge that nonvascular plants can make substantial contributions to ecosystem function, they were not consistently identified to the species level, and were not included in this analysis. Additionally, we removed plots where vascular taxa were not all identified to the genus or species level. We included only plots where abundance was quantified as percent cover or a metric that could be converted to percent cover (e.g. Braun-Blanquet cover classes, point-framing). To homogenise data from disparate sampling methods, the abundance of each

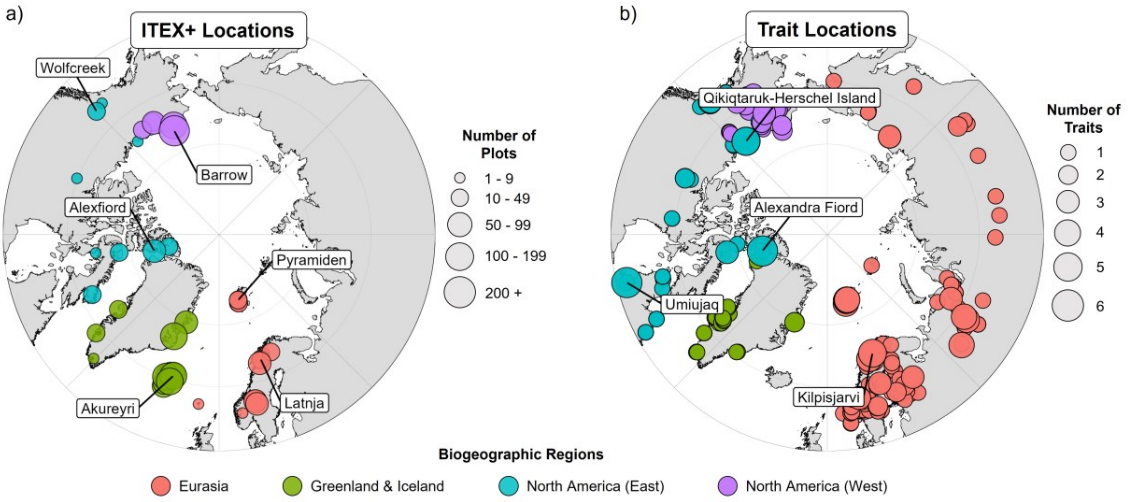

Figure 3.1 | Geographical distribution of our plot-survey data. a) Distribution of the 45 sites from which composition data from the ITEX+ dataset was incorporated. Sites are coloured by biogeographic region and circle size indicates the number of ITEX+ plots analysed from within that site (ranging from one plot in Kluane, YT, Canada to 302 in Barrow, AK, USA). Selected sites with labels are typically those with the largest number of sampled plots in that region. The 45 sites spanned a latitudinal gradient of 20.78°. **b)** Distribution of the 133 locations from which Tundra Trait Team (TTT) (108 locations) and TRY (25 locations) trait data were drawn. Circle size indicates the number of traits sampled at that location (ranging from just one trait at 72 locations, to six traits at two locations, out of a maximum of seven). Sites containing the highest number of sampled traits were labelled. Both maps have a polar projection with a southern latitudinal limit of 55° N.

vascular species in each plot was converted to relative cover (0 – 100%) of vascular plant material per plot. The relative cover per plot of each functional group (shrubs, graminoids and forbs) was calculated by summing the relative cover values of all the species in each functional group within each plot (totalling 100%). We considered plots with ≥ 50% cover of a single functional group to be dominated by that group (i.e., shrub-dominated).

Our final dataset comprised 45,217 plant composition records of 352 identified vascular plant species within 143 genera and 42 families. Quality control was undertaken following the methods of Bjorkman et al. (2018a) and García Criado et al. (2023a). Steps included: data cleaning, reorganisation and standardisation of species taxonomy using The Plant List (TPL, 2023) within the R package ‘Taxonstand’ (version 2.4; Taxonstand, 2023). This dataset was used to assess patterns in functional diversity across both space (**RQ1,2**) and time (**RQ3**). For spatial analyses, we used the latest vegetation survey of each plot only. This resulted in a dataset comprising 2,087 plots across 154 subsites and 45 sites throughout the Arctic and subarctic tundra (above 60 °N latitude) and spanning a period of 34 years (1988 – 2022). For temporal analyses (**RQ3**), we retained only plots that had been surveyed at least twice over a period of at least five years, since diversity trends can be difficult to detect over short time scales (Valdez et al., 2023). This filtering yielded a final dataset of 1,777 plots encompassing 86 subsites and 22 sites for the temporal analysis. The temporal dataset spanned a period of 38 years (1984 – 2022) with a mean monitoring duration of ~14 years (range: 5 to 28 yrs) and a mean of 3.8 time points per plot (range: 2 to 9 surveys per plot).

3.2.2 Climate data

Climate data was sourced for the period 1979 to 2013 from CHELSA (version 1.2.1; Karger et al., 2017), given its fine spatial resolution (1 km × 1 km) and demonstrated accuracy, particularly for precipitation (Datta et al., 2020; Karger et al., 2017; Maria and Udo, 2017). Climatological variables were extracted from the long-term climatologies for each subsite within the ITEX+ dataset. We extracted mean and maximum warmest quarter temperature (WQT), mean and minimum coldest quarter temperature (CQT), and mean annual precipitation (hereafter, precipitation). The four temperature variables were all highly correlated. As such, following García Criado et al. (2023a), we proceeded with mean WQT (hereafter just “temperature”) as our sole temperature variable due to well-documented impacts of summer warming on tundra vegetation (Rayback and Henry, 2005; Van Der Wal and Stien, 2014; Weijers et al., 2010). A categorical soil moisture variable -- dry, moist, or wet – was also extracted from the ITEX+ database for each plot (hereafter just “moisture”).

3.2.3 Trait data

For our functional diversity analyses, we selected traits that: (1) have demonstrated importance to tundra ecosystem functioning (Bjorkman et al., 2018a; Niittynen et al., 2020; Thomas et al., 2020, 2018); (2) contribute strongly to one of the two main axes in plant trait space – the leaf economic spectrum (LES) and size (Thomas et al., 2020); and (3) were relatively well-represented in plant trait databases (see below). Seven continuous, above-ground plant functional traits were selected: leaf dry matter content (LDMC; g g^{-1}); leaf area (mm^2); leaf nitrogen concentration (leaf N; mg g^{-1}); leaf phosphorus concentration (leaf P; mg g^{-1}); plant height (hereafter, height; m); seed dry mass (SDM; mg); and specific leaf area (SLA; $mm^2 mg^{-1}$). Two binary traits, evergreenness and woodiness (yes = 1 and no = 0 in both cases), as derived from the functional group classification of each species (forb, graminoid and deciduous or evergreen shrub), were also included. For more information on the selection of the nine functional traits and their considered relevance to tundra ecosystem function, see **Table S3.1**.

Data for the seven continuous traits were extracted from two global databases of plant traits: the TRY plant trait database (version 5; Kattge et al., 2020) and the Tundra Trait Team (TTT) database (version 1; Bjorkman et al., 2018b). All Northern Hemisphere records from the TTT database were retained as they were sampled from known tundra locations (including alpine plots) whereas in the TRY database only records from above 60° N were retained to align with the criteria used for the inclusion of plant composition data. In addition to extracting trait measurements for species identified in our sample plots, we also extracted trait measurements for any species that was collected within the target geographic range for use in trait gap-filling (**Section 3.2.4**). The majority of final trait values were sourced from the TTT database (47,499 individual records) with a smaller number of trait measurements included from TRY (5,035 records), leading to a combined total of 52,534 unique records across the seven continuous traits. The respective proportions of this total contributed by each trait were: height (36.1%; 18,955 records); SLA (18.6%; 9,789 records); leaf area (16.9%; 8,857 records); LDMC (13.1%; 6,857 records); leaf N (10.0%, 5,235 records); leaf P (3.4%; 1,773 records); and SDM (2.0%, 1,068 records).

Quality control was undertaken following the methods of Bjorkman et al. (2018a), García Criado et al. (2023a) and the ITEX+ dataset. Steps included: data cleaning, reorganisation and standardisation of species taxonomy using The Plant List (TPL, 2023) within the R package ‘Taxonstand’ (version 2.4; Taxonstand, 2023). Records were also sorted into biogeographic regions based on continent and glacial history for gap-filling (**Figure 3.1b**). Both automated and manual error checking was also incorporated during the production of the final dataset to ensure the accuracy of the retained records. Error checking included, but was not limited to, the identification of duplicate records, removal of significant outliers and erroneous data values and standardisation of accepted vegetative and reproductive height records. For full details on the automated and manual error checking, see **Figure S3.1**.

3.2.4 Gap-filling

A prerequisite to calculation of functional diversity indices per plot is to have trait data for all traits for every species occurring in each vegetation plot. However, traits were rarely measured in the exact same sites as vegetation surveys for all co-occurring species and some species-trait combinations were missing altogether (see **Chapter 2**). We therefore created a two-step hierarchical gap-filling algorithm that for each trait per species per plot: (1) generates median trait values across spatial and taxonomic hierarchies, then (2) identifies the median trait value at the lowest hierarchical level that meets data quality requirements and assigns that value to the specified species record.

The gap-filling algorithm's first step works across two different hierarchical scales, with trait medians being generated across a spatial (S) hierarchy within each taxonomic (T) hierarchical unit (**Figure 3.2a**), thereby retaining as much as possible of the raw information on intraspecific trait variation (see **Chapter 2**). The taxonomic hierarchies across which trait medians are generated, from narrowest to broadest, were: species level (T1), followed by the genus (T2), family (T3) and functional group levels (T4; shrub, forb and graminoid). Within each taxonomic level, trait medians are generated across a progressively widening spatial hierarchy. For each record, calculations occur first within the relevant 0.5 ° × 0.5 ° latitude-longitude grid cell (S1), followed by the 5 ° latitudinal band of the source within the biogeographic region (S2), over 60 °N within the biogeographic region of the source (S3), the wider biogeographic region (S4), the wider continent of the source (S5; e.g., Eastern and Western North America become simply North America, Greenland-Iceland remains as Greenland-Iceland) and finally, global (S6). The progression of hierarchical units from most specific to least specific hence runs: T1:S1 (species:gridcell), T1:S2, [...], T2:S1, T2:S2, […] up to T4:S6 (functional group:global; **Figure 3.2b**).

For the second step, median trait values were always selected at the lowest hierarchical level possible (**Figure 3.2b**). In order to ensure the accuracy and representativeness of the median trait value, a threshold based on the number of trait records within the given hierarchical unit (numR) and Z-score had to be met for a median to be selected. If that threshold was not met, the algorithm moves on to the next hierarchical unit and so on until the thresholds are met and a median trait value is selected. If for a given trait record $Z < 2.25$ and $4 \leq \text{numR} < 10$, it was retained. Moving upwards, individual trait records were also retained when $2.25 \leq Z < 2.75$ and

$10 \leq numR < 20$, when $2.75 \leq Z < 3.25$ and $20 \leq numR < 30$ and when $Z < 4$ and $numR \geq 30$. Any record with $Z \geq 4$ was removed. From the remaining dataset, for each composition record and trait, the median trait value from the narrowest hierarchical unit with at least four records remaining was used. This results in a dataset with a single value for each of the seven continuous traits ascribed to each composition record. On average, 64.1% of trait values were drawn from species-level trait values (T1:S1-6), with height (84.1%) and SDM (39.9%) incorporating the highest and lowest proportion of species data respectively (**Figure 3.2c**). Categorical values for 'evergreenness' and 'woodiness' (e.g. 0 or 1) were then added for each composition record but as these traits were calculated from functional group classifications (evergreen shrubs = evergreen, others not; all shrubs = woody, other not), gap-filling was not required (Bjorkman et al., 2018a).

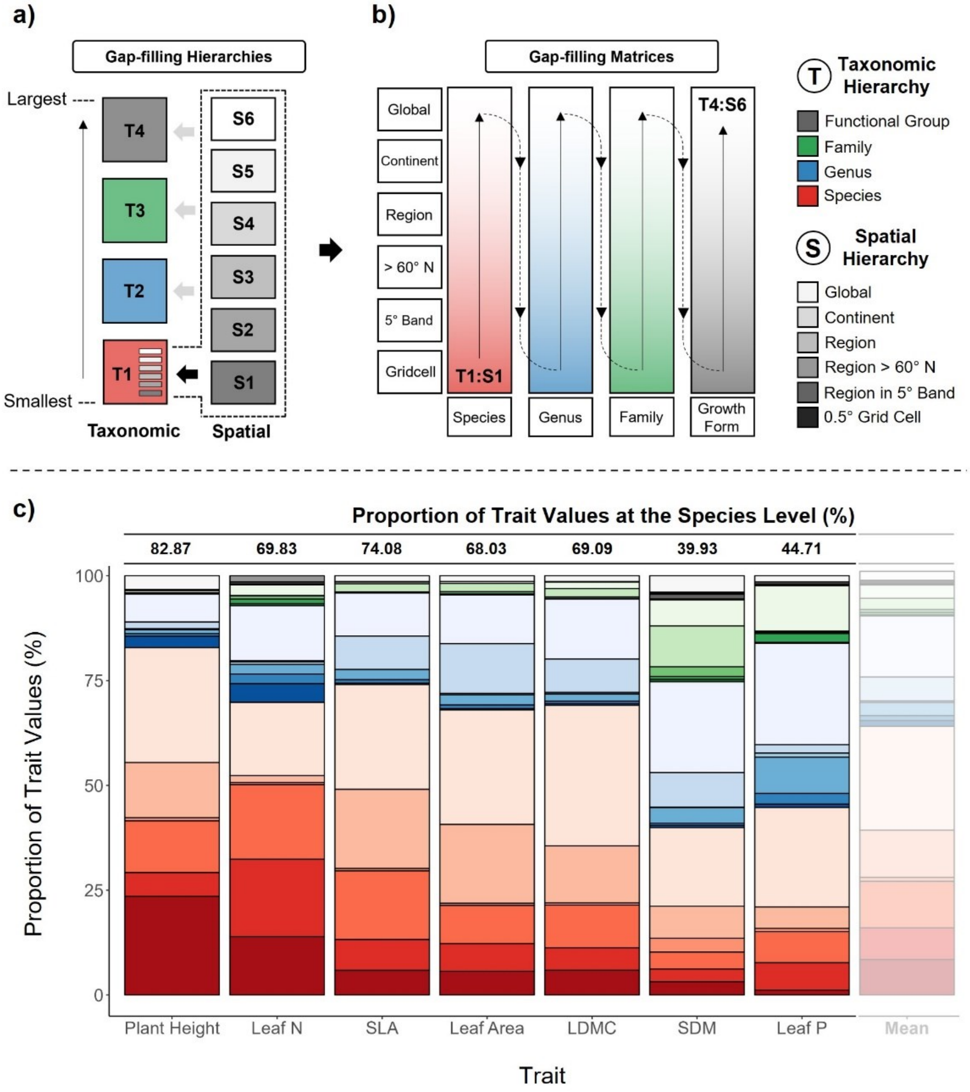

Figure 3.2 | Proportion of trait medians per continuous trait drawn from each hierarchical gap-filling level. a) The nesting of the spatial hierarchical levels (6) within each of the taxonomic hierarchical units (4). **b)** The order in which values were gap-filled, progressing through each spatial unit within a single taxonomic unit before then moving onto the next taxonomic unit. **c)** As per the methods above, each composition record was assigned a median trait value for each of the seven continuous traits at the lowest taxonomic and spatial hierarchical unit possible whilst satisfying criteria concerning the number of records and Z-score associated with its calculation. Woodiness and evergreenness were not included in this plot as they were derived from functional group classifications. This plot highlights the proportion of records per trait that were sampled from each spatial hierarchical unit within each taxonomic hierarchical unit. The overall proportion of trait medians sampled from across all six species units per trait (red bars) are highlighted at the top, ranging from a maximum of 82.87% for plant height to just 39.93% for SDM, with a mean proportion of 64.08% (right-hand bar). Trait abbreviations in the x-axis labels are: Leaf N (leaf nitrogen), SLA (specific leaf area), LDMC (leaf dry-matter content), SDM (seed dry mass) and Leaf P (leaf phosphorus).

3.2.5 Functional Diversity Metrics

Numerous methods exist for the characterisation and quantification of functional diversity. We approached the calculation of functional diversity using the tripartite method first suggested by Mason et al. (2005) and built upon by Villéger et al. (2008) and Laliberté and Legendre (2010). This approach recognizes three dimensions of functional diversity: (1) functional richness, which quantifies the volume of multi-dimensional trait space filled as well as functional (2) evenness and (3) divergence, which concern the regularity and divergence of the distribution of this abundance within the trait space, respectively (Villéger et al., 2008). Each index quantifies different potential dimensions of functional diversity change (Cornwell et al., 2006; Mason et al., 2008, 2007; Villéger et al., 2008) and combinations of these indices are widely used in studies of functional diversity (e.g. Hejda and Bello, 2013; Laughlin et al., 2017; Lozanovska et al., 2020; Niittynen et al., 2020; Yang et al., 2017). Here, we selected two of these indices, functional richness and evenness, a measure of both the quantity and regularity of the functional space filled, for use in this study. The indices were both calculated using the 'FD' package in R (version 1,0-12.3; Laliberté et al., 2023). This package employs a distance-based framework and is highly flexible, accepting any number or type of traits whilst also weighting individual traits by the relative abundance of the constituent species (Laliberté and Legendre, 2010). Using the 'dbFD' function, we calculated functional richness (lower bound at 0 with no upper limit), functional evenness (bound between 0 and 1) and species richness. The convex-hull volume approach used by this function requires at least four species, hence plots with species richness ≤ 3 were assigned NA for both functional richness and evenness computation.

The calculation of functional diversity indices using dbFD involves an initial step of reducing the dimensionality of the trait data for which a number of effective traits (calculated from the original nine traits) must be specified. The number of effective traits used can impact the value obtained when functional diversity measures are calculated (Carvalho and Cardoso, 2020; Laughlin, 2014; Legras et al., 2020; Mammola et al., 2021; Zihao et al., 2021). The exact number of traits used must therefore be carefully considered. In plant communities, the addition of more traits, up to a point, is considered to lead to a better ability to predict functional composition (Laughlin, 2014). The addition of too many traits however, reduces the reliability of calculated functional diversity indices, i.e., the 'curse of dimensionality' (Bellman, 1966; Mammola et al., 2021). The dbFD function employs a two-step method to select the number of effective traits used in functional diversity calculations. It first runs automatic dimension reduction on each plot occurrence through

PCoA on the nine studied raw traits (seven continues; two binary; **Section 3.2.3**) in the input matrix, thereby reducing the impact of collinearity between traits (Carvalho and Cardoso, 2020). The number of effective traits (i.e., PCoA components, or numT) is then selected. The number of species (numS) must always exceed numT in functional diversity calculations (Keyel and Wiegand, 2016; Villéger et al., 2008). We selected numT using the more conservative threshold of $\text{numS} \geq 2^{\text{numT}}$ (option 'min' in the FD package; Laliberté et al., 2023), rather than the threshold numS > numT (option 'max' in the FD package; Laliberté et al., 2023). The option 'min' was chosen to reduce dimensionality and to ensure a more consistent number of 'traits' between plots. Functional richness could be calculated when $4 \leq \text{numS} \leq 23$ (i.e., the maximum species richness observed in our study), hence numT under the 'min' criterion was 2 to 4 compared with 3 to 22 under 'max'. Using this parameterisation, functional richness is defined for all plots with four or more species (87.3% and 92.5% of plots in the spatial and temporal datasets respectively). We also created 12 simplified artificial plots to illustrate how changes in species richness, and hence, numT, alongside other key variables influence the calculation of functional richness and evenness through the dbFD function. Details of the plots and the patterns they illustrate can be found in **Figure S3.2**.

3.2.6 Statistical analyses

Two main groups of statistical models were used in this study: (1) one group based on spatial comparisons (**Section 3.2.6.1**) and (2) the other group based on temporal comparisons (**Section 3.2.6.2**). Where possible, we aligned our statistical methods with those of García Criado et al. (2023a) in order to directly compare changes in functional diversity to changes in taxonomic diversity across the same region. For full details of model structures, see **Table S3.2**.

3.2.6.1 Spatial comparisons

To test whether functional diversity relates to species richness in the tundra (**RQ1**), we fitted two Bayesian generalised multivariate models with: (1) functional richness and (2) functional evenness as the response variables and species richness as the predictor variable in the fixed effects. Functional richness displayed a log-normal distribution (near-zero inflated positive values), hence the functional richness model was fitted using a log-normal response distribution with an identity link function. Functional evenness however was normally distributed so the functional evenness model was run using a Gaussian response distribution with an identity link function. We observed a saturating relationship between species richness and functional richness when species richness was $\gtrsim 14$. We therefore included a quadratic term for species richness in the fixed effects formula of the model of functional richness versus species richness. Both functional richness and evenness models incorporated a nested random intercept term of subsite within biogeographic region to account for the non-independence of both plots within subsites and subsites within regions.

To assess the strength of the relationship linking functional richness, functional evenness or species richness against latitude and between regions (**RQ1**), we fitted further linear models with: (1) functional richness, (2) functional evenness, and (3) species richness as response variables. We used latitude (a continuous variable) and biogeographic region (a categorical variable) as predictor variables in separate models, and included the natural log-transformation of plot size to account for the influence of the species area relationship in both (Drakare et al., 2006; Rosenzweig, 1995). As described above, it is not possible to calculate functional richness for plots with three species or fewer (12.7% of our spatial plots). In order to include these species-poor plots in our functional richness analyses, we assumed that with species richness < 4, functional richness was less than the median observed functional richness of plots with four species, and then ran censored models with this assumption. Whilst functional richness displayed a lognormal response distribution, our models did not converge using this distribution within a censored model structure. Instead, we natural log-transformed the functional richness response variable and ran the model using a Gaussian distribution with an identity link function and back-transformed the output to aid in interpretation. For our functional evenness models, we again used a Gaussian response distribution whilst our species richness models used a negative binomial response distribution with a log link function (used for count data where the variance is greater than the mean). These models used the same random structure as the models of functional richness versus species richness (above).

To identify relationships between functional diversity and potential abiotic and biotic factors across the tundra biome (**RQ2**), we tested the relationship linking: (1) functional richness, (2) functional evenness, or (3) species richness (response variables) against mean temperature, precipitation and shrub/forb/graminoid cover (all continuous) and soil moisture and dominant functional group (both categorical), all in separate models (**Table S3.2**). As we expected functional evenness to be greatest where no functional group dominated the composition, the model testing the relationship between functional evenness and functional group cover included both a linear and quadratic functional group cover term, rather than linear alone. The mixed-effects model structure otherwise followed that used in the analysis of latitude and biogeographic region, above.

3.2.6.2 Temporal comparisons

To assess tundra functional diversity change over time (**RQ3**), we employed a two-step modelling approach, first to determine whether functional diversity and functional group cover were changing over time, and second to identify potential drivers. Using the collection of 1177 temporal plots that had been sampled at least twice over a five year period, we first calculated change over time by fitting linear models (one per plot) with: (1) functional richness, (2) functional evenness, (3) species richness, (4) shrub cover, (5) forb cover, and (6) graminoid cover as response variables and sampling year as the only explanatory variable in the fixed effects. From these linear models, we then extracted the slopes of change over time per plot (yr^{-1}), hereafter simply termed ‘change’ (e.g. functional richness change). The slope values of change in diversity metrics (one per variable per plot) were then used as the response variable in subsequent models. To determine relationships between functional diversity change and possible drivers (**RQ3**), further Bayesian hierarchical models were fitted with: (1) functional richness change, (2) functional evenness change, and (3) species richness change as response variables and latitude, mean temperature, shrub cover change, forb cover change and graminoid cover change as explanatory variables in separate models. As per the spatial analyses, all models included natural log-transformed plot size as a fixed effect and random effects of subsite nested within biogeographic region. All temporal change models were run using a Gaussian response distribution with an identity link function.

All statistical analyses were run in the R programming language (version 4.2.0; R Core Team, 2022). Models were run in a Bayesian framework within ‘brms’ (Bürkner et al., 2023), an R package with a ‘Stan’ backend (Stan Development Team, 2024). Models were run for as many iterations as necessary in order to achieve convergence (minimum 2000 iterations, 500 warm-up), as assessed by trace plots and corresponding R_{hat} scores. In rare instances, the explanatory variable was centred (and outputs back-transformed) to aid convergence.

3.3 Results

3.3.1 Spatial Patterns in Tundra Functional Diversity

Across the tundra biome, we found that plots with higher species richness tended to exhibit higher functional richness (**Figure 3.3a**), but we also found evidence of saturating functional richness in the most species rich plots. In contrast, higher species richness plots exhibited marginally lower functional evenness (**Figure S3.3**), although the CIs overlapped zero. We also found that both functional (**Figure 3.3c**) and species richness (**Figure 3.3d**) declined in tandem with increasing latitude. Functional evenness again showed a contrast with functional richness and species richness and marginally increased at higher latitudes (**Figure 3.3b**), although the CIs for this relationship again overlapped zero. Finally, we found that neither functional richness nor species richness exhibited any significant differences between biogeographic regions, but functional evenness was higher across both North American regions when compared to Eurasia (**Figure S3.4**).

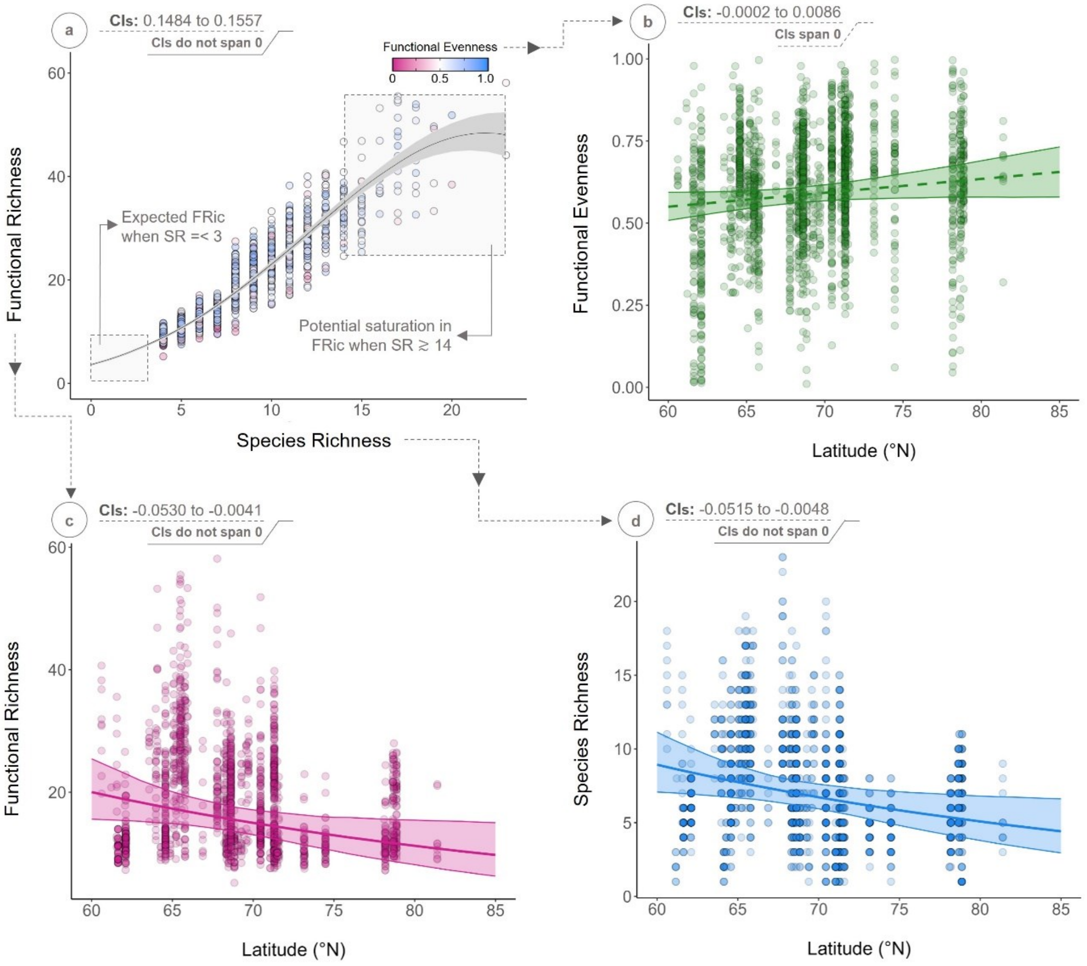

Figure 3.3 | Spatial patterns in functional diversity followed patterns in species richness and latitude throughout the tundra biome. a) Functional richness strongly followed patterns in species richness, showing a strong linear relationship up until species richness equalled ~ 14, beyond which highlighted saturation in functional richness became evident. The detailed 95% confidence intervals (CIs) refers to the slope estimate of the first order model term. Note that the 95% CIs on the quadratic term also does not span zero (-0.0057 to -0.0047). The expected range of functional richness when species richness was less than four is also highlighted to support our censored model framework for the majority of our functional richness models. Points are coloured by functional evenness. **b)** Functional evenness illustrated a small increasing trend with latitude, although the 95% CIs around the slope estimate of latitude overlapped zero. The line and ribbon are drawn from the model outputs in **Table S3.2**. Points represent the functional evenness values of individual plots from within our ‘spatial’ dataset of 2,087 plots (plots with species richness below four cannot have calculated values of functional evenness and functional richness and were not incorporated, hence *n* = 1,950). The lines, ribbons, CIs and points in (c-d) all follow the same approach. **c)** Functional richness exhibited a notable decreasing trend with increasing latitude (*n* = 1,822). **d)** Species richness also exhibited a notable decreasing trend with increasing latitude (*n* = 2,087), as documented in García Criado et al. (2023a).

3.3.2 Potential Drivers of Tundra Functional Diversity

We found that throughout the tundra, functional richness (**Figure 3.4a**) and species richness (**Figure 3.4c**) both showed a positive relationship with temperature whilst functional evenness (**Figure 3.4b**) showed a negative relationship. Relationships between functional richness, functional evenness, species richness and temperature, whilst stronger, mirror patterns with latitude (**Figure 3.3b,c,d**). Both functional richness and species richness showed marginal positive relationships with precipitation (**Figure S3.5**), although functional evenness and precipitation exhibited no notable relationship (**Figure S3.5**). Furthermore, none of functional richness, functional evenness or species richness appeared to be related to soil moisture across the tundra biome (**Figure S3.6**). Relative cover of specific functional groups was also related to functional richness, functional evenness and species richness across the study region. Higher forb cover was associated with both higher functional richness (**Figure 3.4d**) and species richness (**Figure 3.4f**) whilst higher cover of graminoids and, more marginally, shrubs was associated with lower functional richness (**Figure 3.4d**) and species richness (**Figure 3.4f**). When assessed categorically, we found that plots dominated by forbs (> 50% relative cover) also exhibited notably higher functional richness and species richness than plots dominated by shrubs and graminoids (**Figure S3.7**). Finally, we found that all three functional groups displayed the same relationship between relative cover and functional evenness (**Figure 3.4e**). Any functional group comprising a relative cover towards either extreme (i.e. 0% or 100%) resulted in low functional evenness whilst relative cover values distributed more evenly across the three groups resulted in higher functional evenness (**Figure 3.4e**).

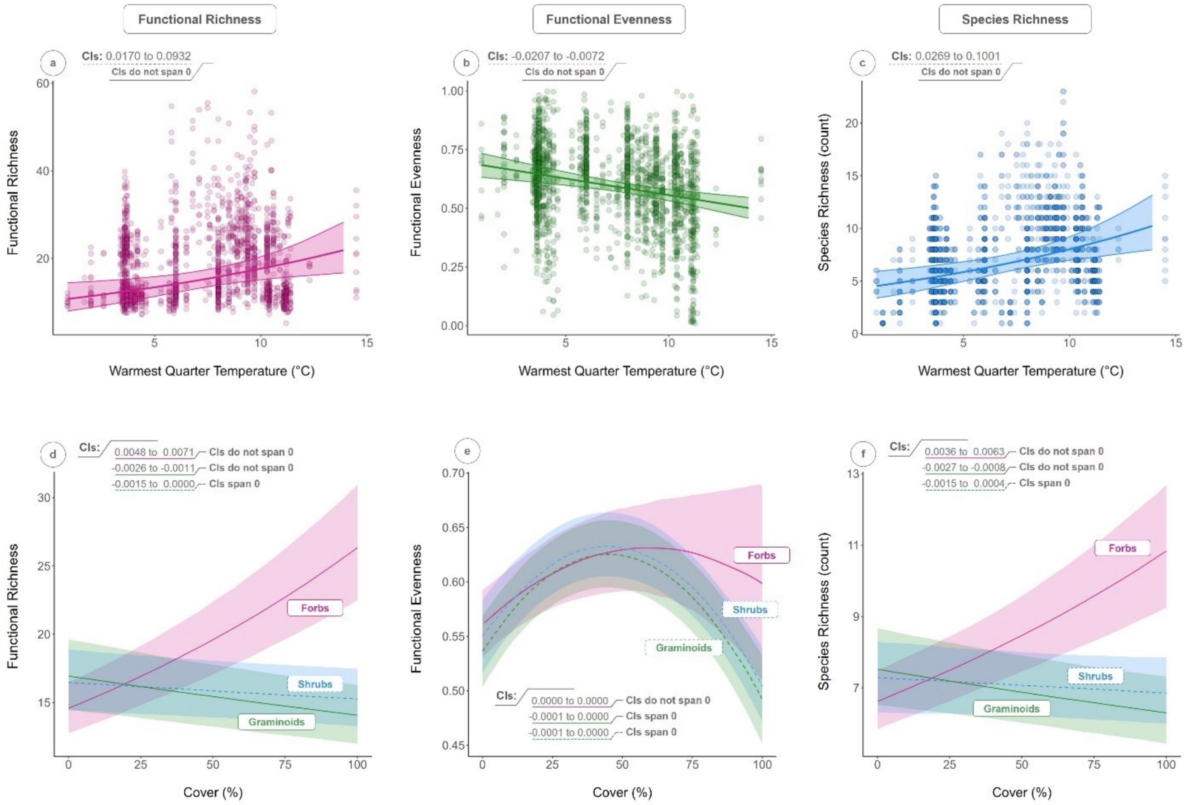

Figure 3.4 | Warmer temperatures and higher forb cover and lower graminoid and shrub cover corresponded with higher functional and species richness, whilst functional evenness was highest in cooler sites and when representation of functional groups was more equal. a) Functional richness was positively correlated with temperature. The line, ribbon and 95% confidence intervals (CIs) are drawn from the model outputs in **Table S3.2**. The points represent the functional richness values of individual plots from within our 'spatial' dataset of 2,087 plots (as in Figure 3.3, *n* = 1,822). The lines, ribbons, points and CIs in (b-c) all follow the same approach. **b)** Functional evenness was notably higher in cooler tundra plots (*n* = 1,950). **c)** Species richness mirrored patterns in functional richness and was highest in warmer tundra plots (*n* = 2,087), as documented in García Criado et al. (2023a). **d)** Higher forb cover led to notably higher values of functional richness whilst higher cover of graminoids, and to a lesser degree shrubs, led to correspondingly lower values of functional richness (*n* = 1,822). Lines, ribbons and CIs are as with (a-c). Individual values per plot are not represented as points as each point would need to be replicated three times, once per cover type. **e)** Functional evenness was highest when cover was more equally represented between functional groups and declined when functional groups became dominant or absent from the plot (*n* = 1,950). Lines, ribbons and points are as with (d). CIs represent the quadratic term of the Bayesian model outputs in **Table S3.2**. **f)** Species richness mirrored patterns in functional richness, with higher forb cover leading to higher species richness whilst higher cover of graminoids, and to a lesser extent shrubs, lead to lower species richness values (*n* = 2,087). This pattern again conformed to the findings of García Criado et al. (2023a). Lines, ribbons, CIs and points are as with (d).

3.3.3 Temporal Change in Tundra Functional Diversity

We did not find a net directional change in functional richness, functional evenness or species richness over time (**Figure 3.5a,b,c**). Many individual plots showed increases or decreases in functional richness, functional evenness and species richness, but the mean change was centred on zero, with an approximately even balance of both increases and decreases across plots within our dataset (**Figure 3.5a,b,c**). Across all plots, we also found no net directional change in forb, graminoid or shrub cover over time (**Figure S3.8**; García Criado et al., 2023). However, the cover change and change in dominance of the forb, shrub and graminoid functional groups was associated with changes in functional richness, functional evenness and species richness (**Figure 3.5d,e,f**) and the direction of associations across time were generally consistent with those across space (**Figure 3.4d,e,f**). Specifically, we found that increases over time in forb cover were associated with greater increases in functional richness (**Figure 3.5d**), functional evenness (**Figure 3.5e**) and species richness (**Figure 3.5f**), whilst increases in shrub and graminoid cover over time tended to decrease functional richness (**Figure 3.5d**), functional evenness (**Figure 3.5e**) and species richness (**Figure 3.5f**). Changes in functional richness, functional evenness and species richness over time were unrelated to either latitude or temperature (**Figure S3.9, S2.10**), with the exception of functional evenness increasing marginally more at higher versus lower latitudes (**Figure S3.9**).

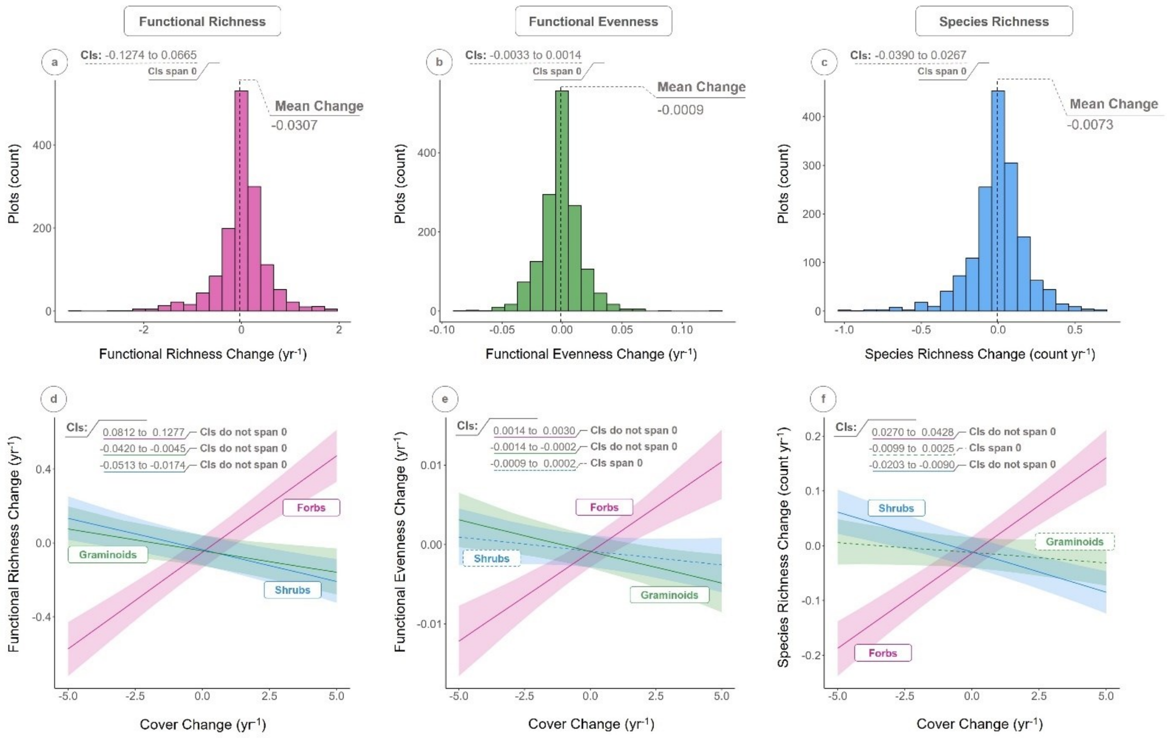

Figure 3.5 | There was no net directional change in functional diversity across the tundra biome, although changes in functional group cover were associated with changing functional diversity with increasing functional richness and evenness corresponding to increasing forb and decreasing graminoid and shrub cover. a), **b)** and **c)** None of functional richness (*n* = 1,433), functional evenness (*n* = 1,526) or species richness (*n* = 1,575) exhibited a net directional change over time in plots surveyed at least twice over a period of at least five years. Change in all three indices was calculated as the slope of the diversity metric per year per plot with 95% confidence intervals (CIs) drawn from the model outputs in **Table S3.2**. The result in (c) matched the results of García Criado et al. (2023a). **d)** Increased forb cover over time drove notable increases in functional richness with increased shrub and graminoid cover leading to concurrent declines in functional richness. Lines, slopes and CIs are drawn from the model outputs in **Table S3.2**. Individual values of functional richness change per plot (*n* = 1,433) are not represented as points as each point would need to be replicated three times, once per cover type. **e)** Increasing forb cover drove increasing functional evenness over time, whilst increasing graminoid, and to a lesser extent shrub, cover generated decreased functional evenness over time (*n* = 1,526). Lines, ribbons, CI and points are as in (d). **f)** Increased forb cover over time resulted in higher species richness, with increasing shrub, and to a lesser extent graminoid, cover drove declines in species richness (*n* = 1,575). Lines, ribbons, CI and points are as in (d). The species richness change results (f) are consistent with the analyses of García Criado et al. (2023a).

3.4 Discussion

We found that throughout the tundra biome, vascular plant functional richness increased with increasing species richness, as it does in other biomes globally (**Figure 3.3a**; Edie et al., 2018). Over space, functional richness was higher in warmer, lower latitude locations whilst functional evenness was maximised in cooler, more northerly tundra regions (**Figure 3.3b,c**; **Figure 3.4a,b**; Lamanna et al., 2014). We found some evidence of saturation in functional richness in the most species rich plots, which implies some level of functional redundancy at high levels of species richness (Oliveira et al., 2016; Schumm et al., 2019). We found that among-plot differences in functional richness and functional evenness were closely related to temperature (**Figure 3.4a,b**) and functional group cover (**Figure 3.4d,e**) across space. Furthermore, whilst we found no net directional change in functional richness or functional evenness over time (**Figure 3.5a,b**), changes in functional diversity were correlated with changes in functional group cover over time, with both functional diversity indices increasing with increased forb cover, and decreasing with increasing graminoid or shrub cover (**Figure 3.5d,e**). Our results suggest that changes in the dominance of shrubs and graminoids associated with climate warming over tundra regions (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2011; Myers-Smith and Hik, 2017) could therefore be accompanied by losses in functional richness and evenness, with potential cascading effects on tundra ecosystem functions in the future.

3.4.1 Global patterns remain consistent throughout the tundra

As predicted (**H1a**), we found a positive relationship between species richness and functional richness at the plot-level across the tundra biome (**Figure 3.3a**). Also consistent with our prediction (**H1b**), we found decreases in functional richness and increases in functional evenness towards higher latitudes in this study (**Figure 3.3b,c**). We found support for our predictions of higher functional richness with warmer temperatures and higher functional evenness with colder temperatures across the tundra biome (**H2a, Figure 3.4a,b**). Our results also offered moderate support for our prediction (**H2b**) that functional richness increases with increased precipitation (**Figure S3.5**), but did not support similar predicted increases in functional richness with increased soil moisture (**Figure S3.6**). We found that functional diversity and evenness had a stronger relationship with temperature than with latitude (**Figure 3.3b,c**; **2.4a,b**). Finally, as predicted (**H1c**), we found no difference in functional richness or evenness between biogeographic regions

(**Figure S3.4**), likely due to the broadly consistent species pools observed across all regions of the tundra biome (PAF, 2018). Our results closely follow patterns in both tundra species richness (**Figure 3.3d**; **2.4c**; García Criado et al., 2023a) and functional diversity from tropical and temperate biomes (Edie et al., 2018; Oliveira et al., 2016; Schumm et al., 2019).

While functional richness increased linearly with species richness in species-poor plots, a result of the increased trait variability that additional species provide (**Figure S3.2**; Halpern and Floeter, 2008; Oliveira et al., 2016), beyond a species richness of ~14, we found that tundra functional richness begins to plateau (**Figure 3.3a**). This finding suggests that the addition of further species into the community contributes little in terms of new trait variation, instead amplifying redundancy (Oliveira et al., 2016; Schumm et al., 2019). A study of marine bivalves noted that communities with low species richness often consist of generalists, such that much of the trait variability found in higher-species richness communities can still be found in lower-species richness communities (Edie et al., 2018). Many of the additional species found only in higher-species richness communities occupy the same 'hyperdiverse' regions of functional space and have somewhat redundant functions (Halpern and Floeter, 2008). Hence in less species rich plots lacking these species, trait space is more evenly occupied and redundancy is reduced, driving an overall increase in functional evenness in high latitude, species-poor locations (Edie et al., 2018; Schumm et al., 2019). At the global-scale, biogeographic patterns in functional diversity are known to closely follow temperature-driven, latitudinal gradients in species richness (Edie et al., 2018; Lamanna et al., 2014) and our results show that these global relationships remain consistent throughout the tundra to the northern latitudinal extremes.

3.4.2 Biotic and abiotic factors influence functional diversity

Contrary to our prediction that functional group composition would be decoupled from biogeographical patterns in functional diversity (**H2c**), we found that functional group composition, alongside temperature, strongly influenced tundra functional diversity. We found that functional richness was higher in plots with higher forb cover and lower shrub and graminoid cover (**Figure 3.4d**). Past tundra vegetation analyses suggest only weak relationships between functional group composition and trait composition (Körner et al., 2016; Little et al., 2015; Thomas et al., 2018), potentially due to high functional convergence in the northern high latitudes. For species to survive in harsh Arctic climes they must possess similar strategies and traits, regardless of their functional group, leading to homogenisation of traits and growth forms across traditional groups (Thomas et al., 2018). However, our results here emphasise that growth forms do vary in important ways in terms of the variability in functions performed in extant communities. Indeed, forb species in this study were shown to occupy a largely distinct region of the functional trait space to that of graminoid and shrub species, which conversely exhibited predominantly overlapping distributions within multivariate trait space (**Figure S3.11**). Potential reasons for this variation and the decreased functional richness in shrub and graminoid dominated plots include the trait space these functional groups occupy as well as their competitive dominance.

Shrub and graminoid groups incorporate less trait variation than forbs which increases their functional homogeneity and thus may reduce their functional richness (Thomas et al., 2018). Shrubs can dominate plots, displacing sub-canopy and less competitive species (Boscutti et al., 2018; Pajunen et al., 2012, 2011; Scharnagl et al., 2019; Walker et al., 2006; Wallace and Baltzer, 2020), whilst graminoids, being good competitors, typically exclude species-rich forb groups due to greater height and enhanced nutrient uptake from deeper-reaching roots (Bråthen et al., 2021; Klanderud et al., 2015; Liu HuiYing et al., 2018; Myers-Smith et al., 2019). When a single dominant or few co-dominant species with similar traits are able to outcompete diverse forb species, both species and – more importantly – functional richness will be reduced. Furthermore, we found that a dominance, or near absence, of any functional group resulted in decreased functional evenness (**Figure 3.4e**). When all functional groups are represented, trait space is more evenly occupied and functional evenness reaches a maximum (**Figure 3.4e**). Put together, these results suggest that biogeographic patterns in tundra functional diversity are a result of a complex suite of interacting abiotic (e.g., temperature) and biotic (e.g., functional group composition) variables across the northern high latitudes.

3.4.3 Functional change lags behind warming

In line with results for species richness (García Criado et al., 2023a), and consistent with our prediction (**H3a**), we found no net directional change in functional richness or evenness over time during a period of rapid warming at high latitudes (**Figure 3.5a,b**). We suggest three potential explanations for this lack of change: slow species turnover, mean trait shifts in the absence of changing trait diversity, and turnover amongst functionally similar species. Firstly, plant immigration and establishment are slow processes, particularly in cold ecosystems dominated by long-lived perennial species (Alexander et al., 2018; Duveneck and Scheller, 2015). As such, changes may not manifest for decades, limiting the influx of new species, and hence traits into tundra communities (Bjorkman et al., 2020). Furthermore, in a study of tropical forests, changes in mean trait values occurred in the absence of shifts in trait variability (Carreño-Rocabado et al., 2012). Hence, whilst the region of functional space occupied by a community shifted over time, the net volume, and thus functional richness, remained consistent over time. Such changes may also be being observed across the tundra biome, where plant height is increasing as compositional turnover increasingly favours taller species with larger leaves and faster resource acquisition (Bjorkman et al., 2018a; Niittynen et al., 2020; Thomas et al., 2020). However, these increases in mean trait values appear not to be accompanied by increased trait diversity. A similar phenomenon may be being observed in our analyses. Finally, not all changes in species composition result in changes in functional diversity. For instance, García Criado et al. (2023b) found that both ‘winner’ and ‘loser’ shrub species in the tundra typically occupied similar trait spaces, thereby highlighting that turnover does not always introduce new trait variability to an ecosystem. A combination of these reasons likely drive the overall lack of net directional functional diversity change seen in our study and highlight why, despite rapid warming, tundra communities are not yet exhibiting the shifts in functional diversity we may expect.

3.4.4 Functional groups influence functional diversity change

Despite a lack of net change in functional diversity, numerous individual plots exhibited both increases and decreases over time (**Figure 3.5a,b**), similar to results for trends in taxonomic diversity (García Criado et al., 2023a) and global biodiversity patterns of winners and losers amongst a backdrop of ‘no net change’ (Dornelas et al., 2019). Furthermore, contrary to our prediction (**H3b**), we found that changes in functional group cover corresponded with changes in functional diversity over time (**Figure 3.5d,e**), as they did across space. Increasing forb cover was associated with increased species richness and in turn, functional richness, whilst increasing cover of graminoids and shrubs corresponded with decreases in species and functional richness, both across space and time (**Figure 3.4d,f**; **2.5d,f**). Relationships between functional group cover and functional richness were hence consistent across space and time throughout the tundra. Furthermore, over time, increased cover of forbs corresponded to increased functional evenness, whilst increased shrub and graminoid cover was associated with reduced functional evenness (**Figure 3.5e**). These opposing relationships could be due to shrub and graminoid species dominating plots whereas forbs are often less dominant, leading to unequal occupation of trait space (Klanderud et al., 2015; Liu HuiYing et al., 2018; Pajunen et al., 2012, 2011; Wallace and Baltzer, 2020).

We did not find evidence for increased shrub cover over time in this dataset (**Figure S3.8**; García Criado et al., 2023, 2020) despite warming-induced shrub expansion having been seen in studies from across the northern high latitudes (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2011; Myers-Smith and Hik, 2017). The ITEX+ dataset includes ecological monitoring of plant community composition over time at plot-scales, potentially not capturing vegetation change occurring at landscape scales in particular environmental contexts (García Criado et al., 2023a). We have shown that shrub increase is related to declines in tundra functional richness and functional evenness, hence any future shrub expansion, as is expected, could lead to biome-wide declines in both indices (**Figure 3.5d,e**). Less diverse and functionally rich and even communities perform fewer functions and are less stable and resistant to sudden landscape-scale changes (Cui et al., 2024; Niittynen et al., 2020). Therefore, if tundra shrub expansion is widespread in the future, this could alter ecosystem functions and services across the biome, and the wildlife and people that rely on those services (Callaghan et al., 2011; Imbert et al., 2021).

3.4.5 Future research

Our objectives were to investigate biome-scale patterns in tundra functional diversity across both space and time. A trade-off of this approach is that our investigations were limited to including only commonly measured traits and reliably censused taxa. The contributions of root traits and nonvascular species to ecosystem function is potentially substantial, yet their current taxonomic and geographic coverage remains lower than that of above-ground vascular traits. There is an increasing availability of below-ground (Klimešová et al., 2017, 2012) and nonvascular (Lett et al., 2021; Lewis et al., 2017) plant data and we anticipate that as these data sets grow, they may be able to be incorporated in future syntheses of tundra functional diversity. Plant composition data are also becoming increasingly available from underrepresented areas of the tundra, such as Russia (**Figure 3.1a**; Zemlianskii et al., 2023). More comprehensive trait datasets with sampling undertaken across a greater number of years and sites better aligned with those of the composition records would also permit more ecologically meaningful characterisation of temporal and spatial variation in functional diversity. Finally, the continued development of tools beyond plot-based *in situ* surveys, such as hyperspectral imaging, may facilitate higher spatial and temporal resolution assessments of large-scale patterns in tundra functional diversity in the future (see **Chapter 4**; e.g. Beccari et al., 2023; Schneider et al., 2017; Schweiger et al., 2018).

We show that biome-scale spatial and temporal patterns in tundra functional diversity are driven by both abiotic and biotic drivers. The biogeographic patterns that we found in tundra functional diversity extend known global latitudinal gradients in functional diversity (Edie et al., 2018; Halpern and Floeter, 2008; Oliveira et al., 2016; Schumm et al., 2019) to the far northern reaches of our planet. While we did not find a net directional shift in tundra functional diversity, against expectations, we did find opposing roles of change in the cover and dominance of forb versus graminoid and shrub functional groups on tundra functional diversity over time. Increasing forbs and decreasing graminoids and shrubs lead to increasing functional richness, with similar results for functional evenness, although surprisingly shrubs were not as strong a driver of changes in functional evenness as forbs and graminoids (**Figure 3.5e**). However, expected widespread increases in tundra shrub cover (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2011; Myers-Smith and Hik, 2017) are likely to drive declines in functional richness and evenness across the biome, leading to a declining resistance of tundra ecosystem function with warming and resulting vegetation change over time. While functional redundancy in lower-latitude tundra ecosystems may provide a buffer to the loss of certain key functions, enhanced shrub expansion would likely outweigh such moderating influences due to the highlighted declines in functional evenness that accompany the domination of any one functional group (**Figure 3.4e**), particularly shrubs (**Figure 3.5e**). If in future there are losses in tundra functional diversity, this could influence ecosystem functions, processes and consequently services across the biome.

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4

Evaluating the utility of hyperspectral data to monitor local-scale β-diversity across space and time

4.0 Abstract

Plant functional traits are key drivers of ecosystem processes. However, plot-based monitoring of functional composition across both large spatial and temporal extents is a time-consuming and expensive undertaking. Airborne and satellite remote sensing platforms collect data across large spatial expanses, often at regular temporal intervals, raising the tantalising prospect of spatially and temporally consistent detection of biodiversity change through remotely sensed methods. Here, we test the degree to which *in situ* measurements of taxonomic and functional β-diversity, defined as pairwise dissimilarity either between sites, or between years within individual sites, is detectable in airborne hyperspectral imagery across both space and time in an alpine vascular plant community in the Front Range, Colorado, USA. Functional and taxonomic dissimilarity were significantly related to spectral dissimilarity across space, but lacked robust relationships with spectral dissimilarity over time. Biomass showed stronger relationships with spectral dissimilarity than either taxonomic or functional dissimilarity over space, but exhibited no significant associations with spectral dissimilarity over time. Comparative analyses using NDVI revealed that NDVI alone explains much of the variation explained by the full-range spectra. Our results support the use of hyperspectral data to detect fine-scale changes in vascular plant β-diversity over space, but suggest that methodological limitations still preclude the use of this technology for long-term monitoring and change detection.

4.1 Introduction

Plant functional traits are a primary determinant of ecosystem services ranging from soil fertility levels to water availability and climate feedbacks (Díaz and Cabido, 2001; Häger and Avalos, 2017; Lavorel et al., 2007; Miedema Brown and Anand, 2022; Ottoy et al., 2017; Wang et al., 2019; Zylstra et al., 2016). Shifts in the functional traits – the suite of biochemical, physiological and structural characteristics that affect the uptake and use of resources (Jetz et al., 2016) – of plant communities are therefore likely to have cascading effects on fundamental ecosystem services on which communities – floral, faunal, human or otherwise – rely (Imbert et al., 2021). Changes in the abundances of species with particular traits may provide an early indicator of future tipping points in ecosystem service provisioning (Schweiger and Laliberté, 2022; Villéger et al., 2013). As such, detecting changes in plant community functional composition is a critical component of biodiversity monitoring.

One method for detecting important changes in ecosystem services is by tracking β-diversity, a suite of metrics that quantify the dissimilarity in species and more recently functions across communities over space and time (Anderson et al., 2011; Bishop et al., 2015). β-diversity (change in community structure) can be quantified as simply variation among sites or along pre-defined environmental gradients; here we employ the former definition. A recent synthesis of biodiversity change emphasized that species replacement – not change in species richness – is the dominant form of global biodiversity change seen in long-term monitoring studies (Blowes et al., 2019). However, given the time-consuming and costly nature of the on-the-ground sampling needed for longitudinal monitoring of taxonomic β-diversity, the geographic extent of rapid changes in community composition remains unknown. Assessing whether widespread changes in functional β-diversity are also occurring is similarly challenging due to the costs associated with in-situ sampling of traits over spatial domains beyond the local-scale and/or extended time periods (Serbin and Townsend, 2020).

Remote sensing offers the possibility of enhanced characterisation of vegetation diversity by providing repeat, consistent measurements across large, often under sampled spatial extents (Anderson, 2018; Wang et al., 2022). This application requires spatially extensive time series of imagery with sufficient spectral resolution and range to detect change on the ground (Wang and Gamon, 2019). There is a trade-off between the spatial, temporal and spectral resolution of most remote sensing datasets currently available (Gamon et al., 2019; Turner, 2014), but newly launched programs seek to fill this gap. For example, the EnMAP hyperspectral satellite (EnMAP, 2023) is now providing global-scale hyperspectral imagery at requested intervals, whilst NASA’s ABoVE and NEON’s AOP missions have provided high resolution airborne hyperspectral imagery with typically annual repeats over large areas (Miller et al., 2019; NEON, 2023a). Both the continued collection of spatially and temporally consistent hyperspectral data and its assessment against *in situ* field data are required to determine the feasibility of using remotely sensed hyperspectral data in global biodiversity assessment and monitoring. A coupled approach that leverages field data to provide context and real-world validation for remotely sensed data may prove to be the most effective method to monitor biodiversity at global scales (Baldeck and Asner, 2013; Gholizadeh et al., 2019; Gillespie et al., 2008; Turner et al., 2003).

Spectra have been used to characterize multiple aspects of terrestrial vegetation diversity, including taxonomic, phylogenetic and functional diversity (Schweiger et al., 2018; Stasinski et al., 2021; Wang et al., 2022, 2018). Plots with high spectral diversity typically exhibit high species richness (taxonomic α-diversity) (Carlson et al., 2007; Gholizadeh et al., 2019; Kishore et al., 2023; Marzialetti et al., 2021; Rocchini, 2007; Van Cleemput et al., 2023; Wang et al., 2018). However, it is ultimately not taxonomy per se, but rather variation in physiological and structural traits that determine a plant's optical properties (Gholizadeh et al., 2019; Serbin and Townsend, 2020; Ustin and Gamon, 2010; Wang et al., 2022, 2018). Imaging spectroscopy has long been known to accurately characterise physical and biochemical properties of key ecological processes (Gamon et al., 2023; Haboudane et al., 2004; Tagliabue et al., 2019; Ustin et al., 2004; Zarco-Tejada et al., 2001). As a result, spectral signatures typically reflect the particular ecosystem functions plants provide (hereafter plant functional traits) (Dahlin et al., 2013; Homolová et al., 2013; Meng et al., 2019; Schneider et al., 2017; Suding et al., 2008; Thomson et al., 2021; Wang et al., 2019) and likely track functional composition more strongly than taxonomic composition (Serbin and Townsend, 2020).

A growing corpus of research has investigated the relationship between spectral diversity and plant functional diversity (Beccari et al., 2023; Schneider et al., 2017; Schweiger et al., 2018). Most studies to date have focused on the local scale (α-diversity) component of functional diversity, with very few assessing plant functional β-diversity components (Asner et al., 2017). In contrast there are numerous examples of tracking taxonomic β-diversity (changes in species composition) across space with hyperspectral data (Baldeck and Asner, 2013; Féret and Asner, 2014; Féret and De Boissieu, 2020; Laliberté et al., 2020; Rocchini et al., 2018). It has been argued that tracking changes in plant functional traits *through time* on globally relevant scales can be achieved only through hyperspectral time series due to the cost-prohibitive nature of field campaigns (Jetz et al., 2016). The strong connections between optical properties and plant functional traits also suggest that detecting functional turnover over time may in fact be easier than detecting species turnover.

Despite this strong theoretical grounding, we are not currently aware of any studies investigating the value of hyperspectral imagery in detecting functional β-diversity over time. One reason for the absence of such studies is likely limitations in the availability of comparable spectral time series data (Gamon et al., 2019). Other technical issues may also make the application of hyperspectral remote sensing data to detect functional β-diversity over time challenging. Plant traits, and hence optical properties, evolve asynchronistically throughout and between growing seasons (Gamon et al., 2020; Gholizadeh et al., 2020, 2019; Rossi et al., 2022; Serbin and Townsend, 2020; Wang et al., 2022; Yang et al., 2016). As a result, disentangling long-term change in vegetation function from intra-annual variability may prove difficult. Multi-site airborne campaigns generally face a host of scheduling issues related to unpredictable weather and transit times in between sites, which can lead to inconsistency in revisit periods (Musinsky et al., 2022). This inconsistency in timing can reduce the comparability of multi-year hyperspectral time series and prove challenging for detection of functional diversity over time (Rocchini et al., 2018).

Whilst spectral studies of the vegetation diversity have been carried out in numerous settings, alpine tundra ecosystems typically remain less well represented in hyperspectral studies compared to other key biomes (Gholizadeh et al., 2019; Van Cleemput et al., 2023). This is likely due to the fine-scale compositional and functional heterogeneity that typically characterises tundra communities (Nelson et al., 2022; Rossi et al., 2022; Yang et al., 2020). It is also likely a result of the inherent issues of inaccessibility, cloud cover and extreme weather that working in such environments as the tundra encompass.

Here, we evaluate the capacity of airborne hyperspectral imagery to monitor fine-scale vascular plant functional β-diversity, in alpine tundra vegetation, over both space and time, specifically inter-annually. We define β-diversity as pairwise dissimilarity between sites, or between years for individual sites, in either taxonomic, functional, or spectral dimensions (Anderson et al., 2011; Bishop et al., 2015). We will ask three main questions: 1) is spectral dissimilarity indicative of fine-scale functional variation across space and/or time; 2) does spectral dissimilarity most closely track *in situ* dissimilarity in functional composition, taxonomic composition, or biomass (an exemplar ecosystem function frequently targeted in remote sensing campaigns); and 3) do simpler, derived spectral products, namely the normalised difference vegetation index (NDVI), predict such dissimilarity similarly well to full-range spectra?

4.2 Materials and methods

4.2.1 Study area

The study area, henceforth termed the ‘Saddle’, is located in a depression between two knolls on Niwot Ridge, in the Indian Peaks Wilderness of the Colorado Front Range, USA (**Figure 4.1**). It comprises a grid of 88 1 m^2 long-term monitoring plots, each grouped into one of eight vegetation classes (**Figure 4.1**) (Spasojevic et al., 2013). The site is monitored as part of the Niwot Ridge Long-term Ecological Research Program (Niwot Ridge LTER, 2023). The plots are located within an area ~ 550 x 450 m in size (40.06 °N, -105.59 °E) and range in elevation from 3510 ~ 3570 m a.s.l. (**Figure 4.1**) (NEON, 2023b). The area comprises entirely alpine tundra and experiences relative climatic extremes annually. The site is predominantly snow covered between the months of December and May and experienced mean summer temperatures of 8.6 ~ 9.8 °C between 2017 and 2020 (White et al., 2023).

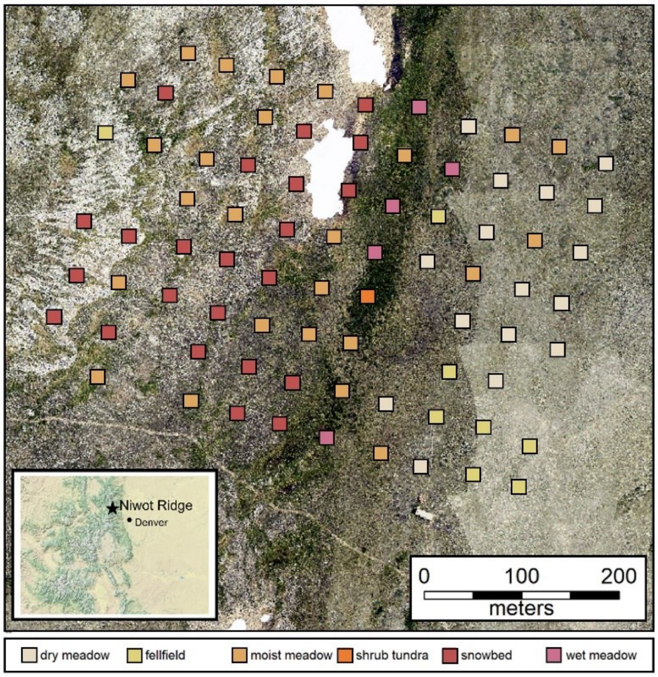

Figure 4.1 | Study locations on Niwot Ridge. The location of the 78 1 x 1 m^2 assessed plots distributed across the Saddle grid between the East and West Knolls of Niwot Ridge, their corresponding vegetation classes (see legend) and the location of the Niwot Ridge LTER within the Colorado Front Range (see inset). Background imagery is sourced from NEON’s high-resolution orthorectified camera imagery mosaic (RGB, 0.1 x 0.1 m resolution) (NEON, 2023c) whilst the inset map is sourced from ESRI © 2014 National Geographic Society, i-cubed.

4.2.2 Field measurements

Three long-term, *in situ* monitoring datasets were utilised in this study: 1) plant species composition, 2) above-ground biomass harvests, and 3) plant functional traits. Both composition and biomass data were collected from the 88 Saddle grid plots (**Figure 4.1**). Composition data has been collected throughout the Saddle since 1989, with annual measurements taken since 2010 (Walker et al., 2022a). All occurrences of both living and non-living plant and non-plant material were recorded using 100 pin drops and an 'all-hits' method within the 88 point framing plots. Tundra plant communities typically comprise both canopy and sub-canopy species (Ma et al., 2020) and in order to accurately elucidate community-level dissimilarity, both canopy and sub-canopy species must be accounted for (Ustin and Gamon, 2010). As such, we used an 'all hits' approach. However, whilst field measurements sample both canopy and sub-canopy species, the limited penetration ability of optical remote sensing often prevents the sampling of much of the sub-canopy, particularly in shrub-dominated plots, leading to underrepresentation of sub-canopy individuals and their respective traits within the spectral profile (Ma et al., 2020). As such, we also ran our analyses using a 'top hits' only approach to determine the impact this limited optical penetration had on our ability to characterise community diversity; see **Figure S2.1**.

Species were taxonomically standardised to the World Flora Online (WFO) Plant List (The Plant List, 2013). Relative cover was then calculated as the percentage of the total hits per plot ascribed to each vascular plant species recorded; non-vascular species were removed due to insufficient ID at the species level. This resulted in a final plot count of 78 (**Figure 4.1**); seven 'barren' plots containing no vascular plant hits were removed, as were two manipulated 'snow fence' plots and one incorrectly geolocated plot. Living vascular plant material comprised 84.9 % of top hits within the retained plots, whilst non-vascular plant material comprised 2.64%. Plot-level biomass data has been collected since 1992 (Walker et al., 2022b). In each sampling year, a single net primary productivity (NPP) value was measured from a representative area adjacent to each long-term monitoring plot using a combination of clipped biomass and allometry; the latter to prevent damage to sensitive cushion plants. Both datasets were trimmed to the years 2017 ~ 2020 to match the hyperspectral imagery availability (**Section 4.2.3**). The resulting datasets therefore consisted of 78 plots in each of the four years (316 total), comprising 85 species overall.

Trait records were obtained from samples collected in unmanipulated areas distributed more widely across the Saddle and surrounding tundra at Niwot Ridge during the years 2008 ~ 2009, 2017 ~ 2018 and 2021 (Spasojevic et al., 2022). Traits were sampled predominantly in July and some in August. Whilst our trait data are not temporally aligned with the sampled composition and spectral data, this study benefits from trait measurements being sampled from within the near vicinity of the composition plots at a similar time of year (**Figure 4.1**). In contrast, many trait studies rely on values aggregated across larger spatial and taxonomic scales (**Chapter 2**; Bjorkman et al., 2018; Maitner et al., 2023). Trait values from all measured years were included to maximise the overall size and taxonomic coverage of the dataset. Eight traits – plant height (cm), leaf dry matter content (LDMC; mg g^{-1}), specific leaf area (SLA; cm^2 g^{-1}), δ15N (‰), δ13C (‰), and leaf chlorophyll (µmol m^2), N (%) and C (%) concentrations – were measured following standard protocols (Perez-Harguindeguy et al., 2016). Each trait relates to the two main axes in plant trait variation - resource acquisition and plant structure (Thomas et al., 2020), is deemed significant to tundra functions and is widely used in tundra trait studies (Bjorkman et al., 2018). Species names were also standardised to the WFO Plant List to allow for the joining of trait values to individual species in the composition records. In total our trait dataset contained 10,303 trait measurements. Trait values were ascribed to individual species via a gap-filling algorithm that generates median trait values – both within vegetation classes and overall – at the species, genus, family and functional group (shrub, forb and graminoid) levels (**Figure S4.2**). Trait medians were first calculated for each trait within a single species and vegetation class (**Figure 4.1**), then by species alone, then by genus within each vegetation class and so on up to the functional group level, with each species composition record assigned a value for each trait at the lowest taxonomic hierarchy possible. An average of 87.9 % of records were assigned at the species level or lower (**Figure S4.2**). Plant species together with their traits facilitated the calculation of functional dissimilarity across the Saddle (**Section 4.2.4**).

4.2.3 Hyperspectral imagery

Airborne hyperspectral imagery was sourced from the National Ecological Observatory Network (NEON) ‘spectrometer orthorectified surface directional reflectance mosaic’ (DP3.30006.001; (NEON, 2023a). The level-three processed, 1 x 1 m spatial resolution, 426 band imagery is spectrally calibrated, atmospherically corrected, orthorectified and output onto a uniform 1 x 1 km spatial grid. The spectra encompass a spectral resolution of 5 nm and range from 380 nm to 2500 nm (NEON, 2023a). Imagery is available across the full study site and is provided as a single mosaic collected between July and August annually from 2017 ~ 2020 (NEON, 2023a). NEON aims to collect data around the point of peak greenness each year, with data typically collected from flights on three or four days each season. The Saddle (**Figure 4.1**) was typically covered by multiple flightlines on multiple days each season, so reflectance values for individual pixels are selected by NEON from the flightlines with the highest quality cloud conditions and at the closest proximity to nadir (NEON, 2023a). In 2017, 2018 and 2020, all pixels covering the Saddle were selected from the same flightlines during mosaicking, whilst in 2019 pixels were selected from flightlines captured on consecutive days (14th August – 72 plots, 15th August – 6 plots; **Figure 4.2**).

Spectra were extracted from this imagery at the coordinate of each of the 78 retained plots using a circular buffer of 1 m radius; mean spectral reflectances were calculated from all the cells encompassed by each buffer. A 1 m buffer was selected over a 0 m or 3 m buffer to correct for potential geolocation issues in the data (0 m) whilst minimising the risk of inadvertently capturing different vegetation types to that comprising the plot (3 m) (Inamdar et al., 2020); pairwise spectral differences between plots were largely indistinguishable regardless of the buffer selected (R^2: ~0.978 – 0.988; **Figure S4.3**). Spectral bands both at the spectral extremes (< 400 nm and > 2400 nm) and those that capture atmospheric water (1340 ~ 1445 nm and 1790 ~ 1995 nm) were

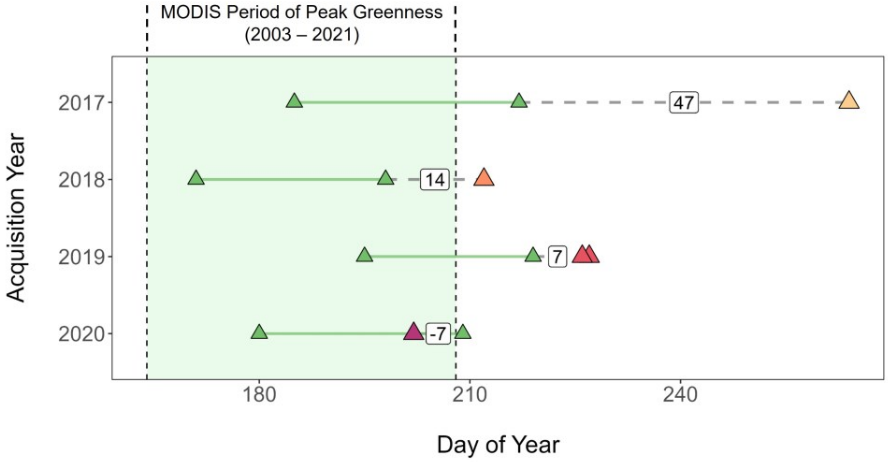

Figure 4.2 | Timing of hyperspectral data acquisition was generally delayed relative to peak greenness. The coloured triangles represent the day(s) on which the NEON hyperspectral imagery was sampled, the green triangles and lines represent the measured period of peak greenness as measured by NEON's tundra phenocams on Niwot Ridge, with the labelled numbers representing the offset (days delayed) between the end of peak greenness and the date of NEON data acquisition. The green rectangle illustrates the targeted hyperspectral sampling window: mean period of peak greenness between 2003 ~ 2021, as measured from MODIS satellite imagery (Musinsky et al., 2022).

then removed (Schweiger and Laliberté, 2022). Broad-band NDVI was calculated from the extracted spectra using wavelengths corresponding to those utilised in the Sentinel-2 10 m bands (band 4: 633 ~ 695 nm; band 8: 726 ~ 938 nm) (European Space Agency, 2023a). NDVI is an index known to saturate at high biomass levels (Goswami et al., 2015), however due to the relatively low biomass values in this high elevation tundra environment, few plots exceeded the threshold at which NDVI saturation is known to become problematic. To avoid potential artefacts due to shading or exposed soil, specific plots in individual years were removed from analyses based on the plot's respective degree of shading and photosynthetically-active vegetation. A near-infrared (NIR) mask (NIR > 0.2; 752 ~ 1048 nm) was employed to remove shaded plots (Rüfenacht et al., 2014; Schweiger and Laliberté, 2022), whilst a NDVI mask (NDVI > 0.2; 667 and 827 nm) was utilised to remove plots with limited vegetation cover (Schweiger and Laliberté, 2022).

Further processing steps frequently applied to hyperspectral data include brightness normalisation, spectral smoothing and dimensionality reduction. Following the calculation of NDVI and NIR, we brightness normalised our spectra (calculated as the square root of the sum of the reflectances squared) (Feilhauer et al., 2010), but chose not to carry out smoothing or dimensionality reduction. Differences in illumination are known to cause large variations in 'brightness' of plant spectra, which may in turn obscure the spectral signals of certain leaf traits (Wang et al., 2022). Based on both this and the known influence of illumination differences on both intra-annual and inter-annual hyperspectral data collection, we proceeded with brightness normalisation; results both with and without brightness normalisation were near identical (**Figure S4.4**). Smoothing of the resulting spectra, a commonly used method in spectral studies of biodiversity (Van Cleemput et al., 2023), was also considered to remove random noise (Park et al., 2018), however we declined to undertake this step as it was likely to remove fine-scale, discriminatory features in the spectra. Similarly, dimensionality reduction via principal component analysis (PCA) was also considered, as is standard in many hyperspectral studies given the high-dimensionality of hyperspectral data (Féret and Asner, 2014). We again declined to undertake this step due to the loss of fine-scale variation and spectral information that occurs in the discarded principle components (Asner et al., 2012). For an example of the resulting spectra in one year, see **Figure S4.5**.

4.2.4 β-diversity calculations

Pairwise dissimilarity measures between plot-pairs were calculated for each of the four following metrics – taxonomic composition, functional composition, biomass and spectral composition, (Schweiger and Laliberté, 2022), in order to characterise β-diversity across the Saddle. Methods to calculate β-diversity from remote sensing imagery typically rely on distance-based measures (Rocchini et al., 2018). Different dissimilarity measures were utilised for each variable to ensure the method used was appropriate to the data type. Taxonomic dissimilarity was calculated as abundance-weighted Bray-Curtis dissimilarity, the most commonly used distance metric for species abundance data (Bray and Curtis, 1957; Ricotta and Pavoine, 2022). Functional dissimilarity was calculated as 'functional dissimilarity', or 'FDis' (Ricotta and Pavoine, 2022), a generalised version of their parametric measure aimed at unifying the Euclidean distance and the Bray-Curtis dissimilarity in a manner suitable for use with community composition data. We calculated FDis using median trait values incorporating all years for all eight measured traits as we lacked location or year-specific values for species traits. As a result, interannual variability in FDis reflects only compositional change and does not incorporate trait plasticity or intraspecific trait variability. Biomass dissimilarity was characterised as the absolute value of the difference between each plot-pair.

Euclidean distance was the selected measure of β-diversity for NDVI and spectral reflectance (**Section 4.2.3**). Numerous methods have been used in recent studies to determine 'spectral dissimilarity'. We therefore investigated three separate metrics – 1) Euclidean distance (Chauhan and Krishna Mohan, 2014; Schweiger et al., 2018; Schweiger and Laliberté, 2022), 2) Manhattan distance (Van Cleemput et al., 2019), and 3) Spectral Angle Metric (SAM) (Chauhan and Krishna Mohan, 2014; Van Cleemput et al., 2019) – to determine their respective utility in characterising spectral distance across the Saddle. Upon investigation, it was clear that all of Euclidean distance, Manhattan distance and SAM conformed very closely to one another (**Figure S4.6**). Euclidean distance between outputted spectra was selected for reasons of both simplicity and consistency.

Pairwise dissimilarity measures were calculated across both space and time. Spatially, dissimilarities were calculated between pairs of plots within individual years (e.g. all plot-pairs in 2017 only), generating 3081 unique plot combinations per year (**Figure S4.7**). Temporally, distances were calculated for individual plots (e.g. plot 27 only) and between all the pairwise year combinations, generating 6 unique year combinations per plot (**Figure S4.8**). In doing so, it was possible to facilitate comparisons of dissimilarity in all four assessed variables across the saddle over both space and time. After applying the NDVI & NIR masks (**Section 4.2.3**), 11,367 (from a possible 12,324) plot-pair and 453 (from a possible 474) plot-year combinations were retained from the spatial and temporal spectral dissimilarity datasets respectively.

4.2.5 β-diversity comparisons

In order to determine whether increased spectral dissimilarity is indicative of increased functional dissimilarity, matrices for both functional and spectral dissimilarity were statistically compared using Mantel tests (He and Zhang, 2009; He et al., 2009; Mantel, 1967); spectral matrices were also modelled against taxonomic and biomass distance matrices. Mantel tests were run using the ‘Pearson’ correlation parameter with 9999 permutations. This method allows for the significance of correlations between pairwise dissimilarity matrices to be assessed whilst accounting for the fact that each plot is included in multiple comparisons (Mantel, 1967). Mantel tests were run between plots within single years for spatial comparisons, and between years for a single plot for temporal comparisons, permuting over all year pair combinations (n = 6; **Figure S4.7**; **S4.8**). Both R and *p*-values were obtained from the Mantel tests to determine both the effect size and significance of any given relationship. Given the small number of paired year combinations per plot in the temporal analyses, the statistical power was insufficient to generate meaningful *p*-values; the calculated R remained sufficient to facilitate between-plot comparisons however. To summarise general patterns in the temporal analyses, mean R values were calculated using the individual R values from the temporal Mantel tests run on each of the 78 plots. Spatial and temporal Mantel tests were also run between NDVI distance matrices and functional, taxonomic and biomass dissimilarity matrices.

4.3 Results

4.3.1 Functional ~ hyperspectral relationships

Throughout our study area, functional dissimilarity was positively associated with spectral dissimilarity over space (**Figure 4.3a**) but not time (**Figure 4.3b**). Spatially, the Mantel tests

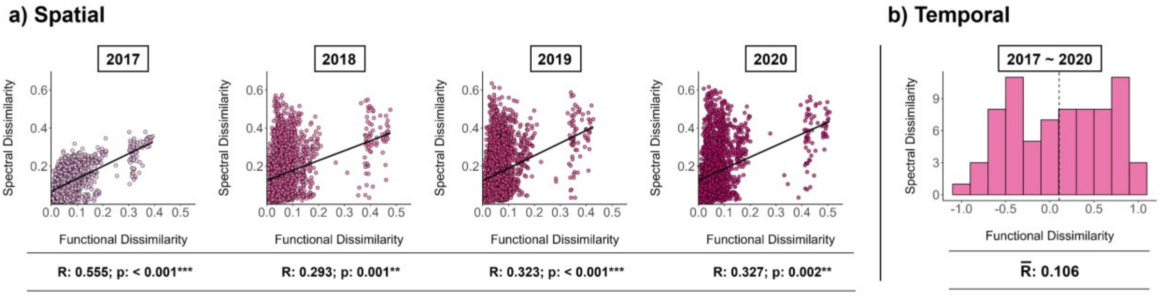

Figure 4.3 | Pairwise spectral dissimilarity among plots is greater for more functionally dissimilar plots across space but not time. The relationships between functional and spectral dissimilarity: (a) between all plot pairs within each studied year, and (b) for each plot between each pair of study years (e.g. 2017 – 2018, 2017 – 2019 and 2017 – 2020; the dotted line represents the mean dissimilarity). Mantel R and *p* statistics for each year (spatial comparisons only) and averaged over all years (R bar; temporal comparisons only) are provided below the relevant panels (**Section 4.2.5**). Linear regression lines are provided as a visual fit of the data.

exhibited significant relationships (*p*: < 0.001 ~ 0.002) between functional and spectral dissimilarity within each year, typically with moderate R statistics (R: 0.293 ~ 0.555). However, there is little evidence to suggest that plots with substantial functional dissimilarity over time exhibit a greater degree of spectral dissimilarity across the same time period (mean R: 0.106). While we had relatively less power to detect significant relationships across time, with only 4 years of data as compared to 79 plots within each year, the lower R values suggest spectral dissimilarity over time is less strongly related to functional dissimilarity over time than space. A cluster of more functionally dissimilar plot-pairs was evident in all years that reflect strong differences in traits between the one shrub-dominated plot in our study area (plot 37) and the remaining, herbaceous-dominated plots (**Figure 4.3a**). Analyses were re-run without plot 37 (**Figure S4.9**) to ensure that results were robust even without the inclusion of this plot. The direction and significance of all results remained the same between spectral and functional, taxonomic and biomass dissimilarity (**Figure 4.4a,c**), with only a small reduction in R values (**Figure S4.9**). Hence, ‘shrubby’ plot 37 does exhibit a substantial shift in functions compared to the non-shrub dominated plots, but was not the primary determinant of the results.

4.3.2 Taxonomic and biomass ~ hyperspectral relationships

Relationships between taxonomic and spectral dissimilarity were broadly similar to those between functional and spectral dissimilarity (**Section 4.3.1**). Over space, when considering taxonomic

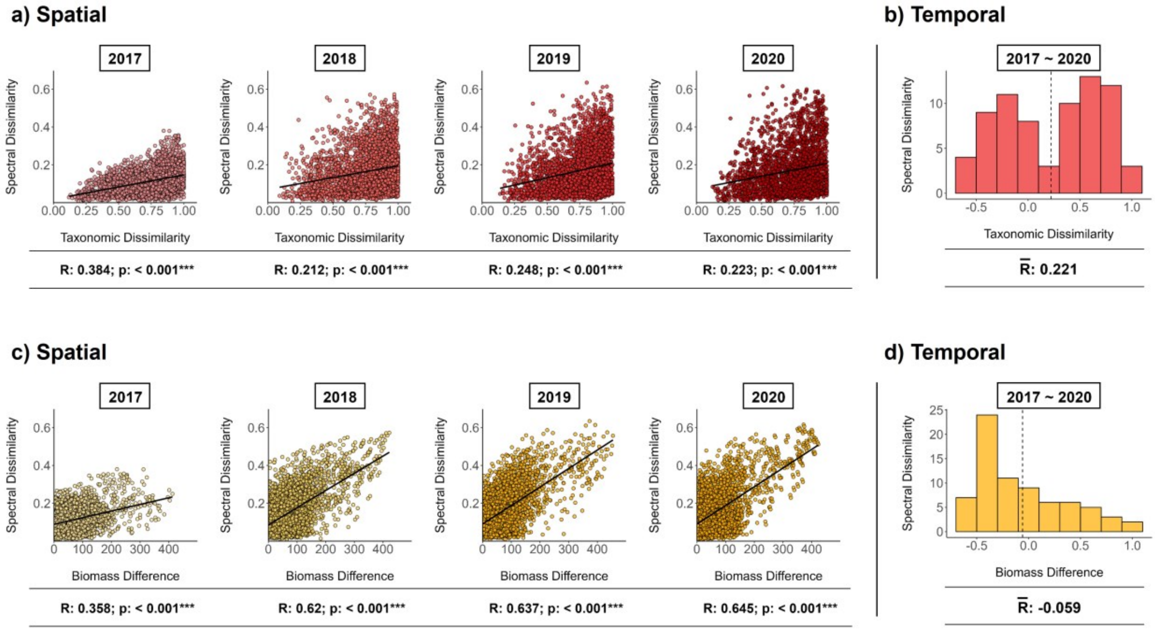

Figure 4.4 | Pairwise spectral dissimilarity among plots is greater for more taxonomically dissimilar plots and those with greater differences in biomass across space but not time. The relationships between spectral and both taxonomic and biomass dissimilarity: (a, c) between all plot pairs within each studied year, and (b, d) for each plot between each pair of study years (e.g. 2017 – 2018, 2017 – 2019 and 2017 – 2020; the dotted line represents the mean dissimilarity). Mantel R and *p* statistics for each year (spatial comparisons only) and averaged over all years (R bar; temporal comparisons only) are provided below the relevant panels (**Section 4.2.5**). Linear regression lines are provided as a visual fit of the data.

dissimilarity, the mantel tests again exhibited significant relationships with spectral dissimilarity (*p*: < 0.001). The strength of the spatial relationships was moderate (R: 0.212 ~ 0.384), and tended to be slightly less than the strength of the relationships between functional dissimilarity and spectra (**Figure 4.4a**). Unlike the functional results however, the relationships between taxonomy and spectra over time were similarly strong (mean R: 0.221) to those across space. Whilst the spatial relationships were robust to dropping bottom hits, the temporal results largely disappeared when using top hits only (**Figure S4.1**; mean R: 0.037). As such, we have low confidence in this result. Change in biomass over space was more strongly associated with spectral dissimilarity than either functional or taxonomic dissimilarity. Spatially, biomass is significantly (*p*: < 0.001) and strongly (R: 0.358 ~ 0.648) related to spectral dissimilarity across all years (**Figure 4.4c**), more strongly than either functional or taxonomic dissimilarity (**Figure 4.3a**; **4.4a**). Biomass however conversely exhibited no meaningful relationship over time between *in situ* and spectral data and displayed the lowest temporal values (mean R: -0.059; **Figure 4.4d**).

4.3.3 Functional, taxonomic & biomass ~ NDVI relationships

Using NDVI to explain taxonomic, functional and biomass dissimilarity yielded results that were largely similar to those using full spectra (**Figure 4.5**). Mantel tests exhibited significant yet moderate relationships between NDVI and both functional (*p*: < 0.001 – 0.002; R: 0.244 ~ 0.315) and taxonomic dissimilarity (*p*: < 0.001; R: 0.215 ~ 0.325) across space (**Figure 4.5a,c**), with similar patterns also displayed between both metrics and spectral dissimilarity (**Figure 4.3a**; **4.4a**).

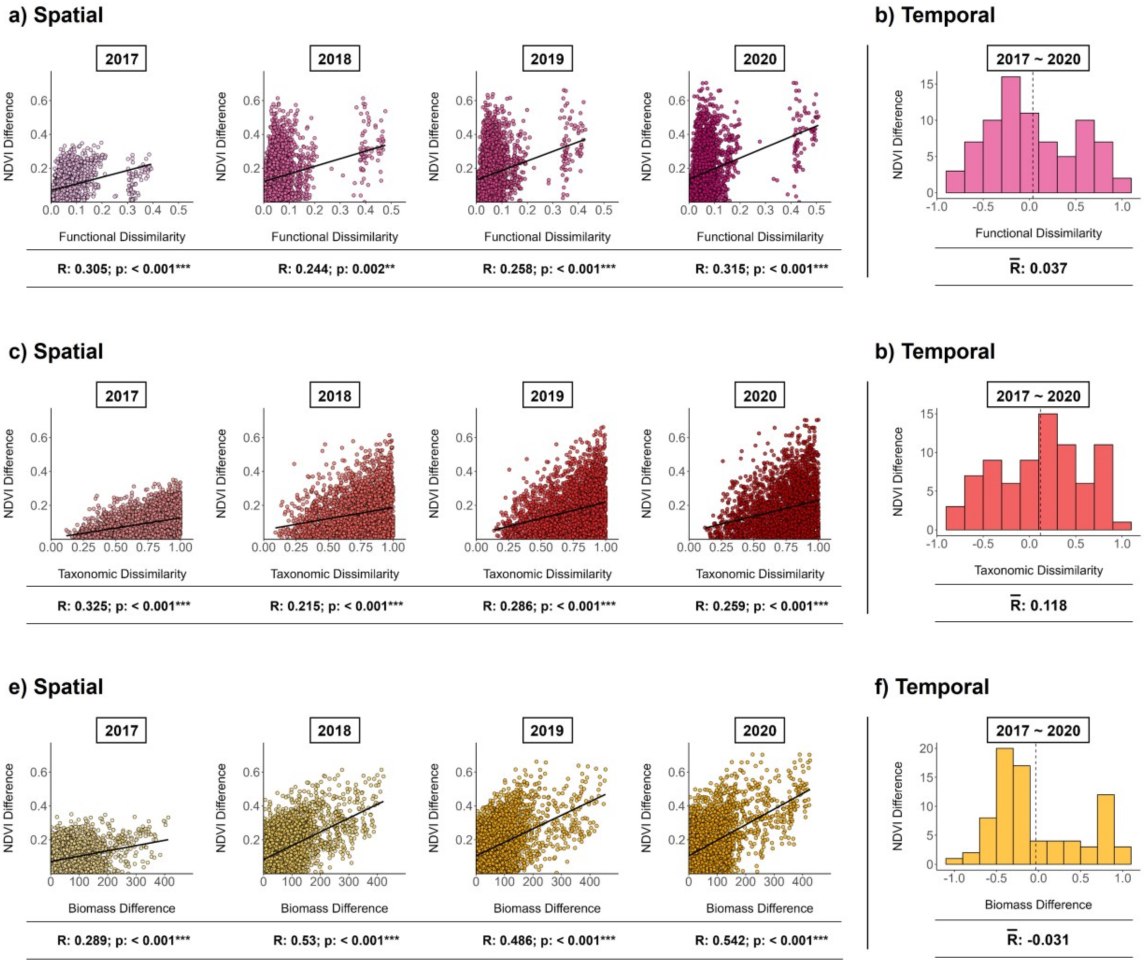

Figure 4.5 | Functional, taxonomic and biomass dissimilarity among plots track differences in NDVI across space but generally not time. The relationships between NDVI dissimilarity and each of functional (a, b), taxonomic (c, d) and biomass dissimilarity (e, f). Spatial dissimilarity tests relationships between all plot pairs within each studied year, whilst temporal dissimilarity compares relationships for each plot between each pair of study years (e.g. 2017 – 2018, 2017 – 2019 and 2017 – 2020; the dotted line represents the mean dissimilarity). Mantel R and *p* statistics for each year (spatial comparisons only) and averaged over all years (R bar; temporal comparisons only) are provided below the relevant panels (**Section 4.2.5**). Linear regression lines are provided as a visual fit of the data.

Again, similarly to spectral dissimilarity, spatial relationships between NDVI and biomass dissimilarity were stronger with NDVI relating significantly and strongly to biomass dissimilarity (*p*: < 0.001; R: 0.289 ~ 0.542; **Figure 4.5e**). Finally, as with full-range spectra, temporal relationships between NDVI dissimilarity and the *in situ* metrics were weaker to non-existent when compared to the spatial ones, with the taxonomic temporal link proving greater than either function or biomass (**Figure 4.5b**; **4.4b,d**). When comparing the strength of the results over space, spectral dissimilarity explains somewhat more variation in both functional and biomass dissimilarity in all years than NDVI dissimilarity, although NDVI dissimilarity in turn explains a greater proportion of the taxonomic dissimilarity between 2018 ~ 2020 (**Figure 4.6**).

4.4 Discussion

4.4.1 Spectral dissimilarity related to functional β-diversity

Our results highlight the potential utility of using hyperspectral imagery in the detection of fine-scale functional (and taxonomic) β-diversity across space within a single alpine tundra habitat. This supports the much-anticipated promise of using spectral reflectance in functional change detection (Jetz et al., 2016) and the results of other studies that highlighted significant links

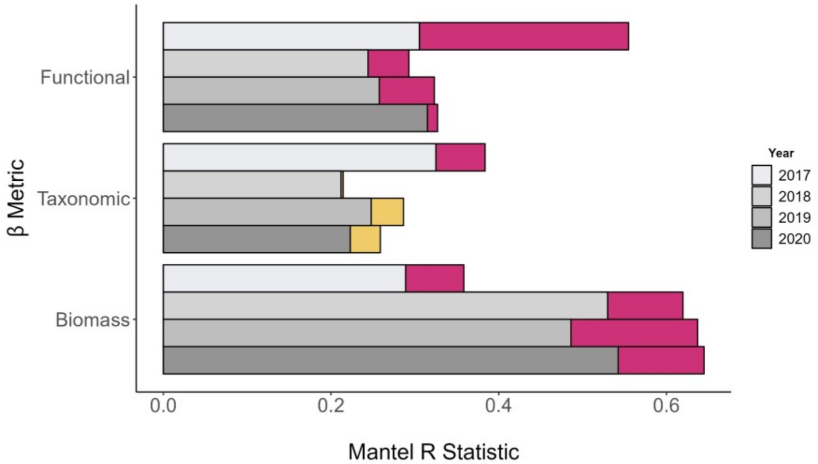

Figure 4.6 | A substantial proportion of the variation in functional composition, taxonomic composition and biomass among plots explained by hyperspectral dissimilarity can be explained by NDVI alone. Difference in strength of relationship between the three variables and spectral and NDVI dissimilarity respectively; grey bars illustrate the variation explained by both metrics, purple the additional variation explained when using full spectra over NDVI, and orange the additional variation explained when using NDVI over full spectra.

between spectral reflectance and elements of taxonomic (Baldeck and Asner, 2013; Laliberté et al., 2020; Marzialetti et al., 2021) and functional β-diversity (Asner et al., 2017). Spectral dissimilarity was significantly related to functional and taxonomic dissimilarity across space, although the relationships were only of moderate strength and exhibited considerable scatter (**Figure 4.3a**; **4.4a**). This suggests that whilst both these factors are clearly related, spectral differences are picking up additional factors beyond taxonomic and functional composition. Depending on the intended application, this may be advantageous. For example, our attempts to measure one ecosystem function directly (above-ground biomass) indicated *in situ* biomass generally showed a stronger spatial association with spectral reflectance than functional dissimilarity did. Relationships between *in situ* metrics and spectral dissimilarity across years however, were weaker to non-existent. Furthermore, whilst the associated R values suggest a moderately strong relationship between taxonomic and spectral dissimilarity over time, the almost complete removal of that relationship when using top hits only suggests a lack of robustness and reduces the confidence with which we view that result. This may mean that in slow-growing alpine tundra environments, detection of small directional shifts in taxonomic or functional change over time from aerial hyperspectral data may prove difficult, and anticipated promise of monitoring fine-scale β-diversity using spectra alone should be treated with caution (Nelson et al., 2022).

4.4.2 Why spatial scale matters

Scale issues, over both space and time, likely contribute to the only moderate relationships observed between spectral and functional and taxonomic dissimilarity in this study. Spatially, a core issue comes from the grain size at which comparisons of dissimilarity within the *in situ* plots and spectral reflectance occur. Past studies have shown that spectral variability best relates to species β-diversity at larger spatial grains. For instance, (Rocchini et al., 2010) found stronger correlations at 20 – 50 m as opposed to 10 m spatial grains in highland Savannahs. This stems from lower grain sizes typically incorporating higher noise when calculating β-diversity metrics (Rocchini et al., 2010). Past studies often utilise large plots (Laliberté et al., 2020; Rocchini, 2007; Schweiger and Laliberté, 2022; Wang et al., 2016a), although this hinders the fine-scale delineation of vegetation diversity through spectra. The small grain size used in our study (1 x 1 m) reflects the standard plot size for vegetation monitoring in most herbaceous systems. However, this grain size may decrease the signal-to-noise ratio and diminishes the strength of relationships between spectral dissimilarity and functional dissimilarity. Smaller spectral pixel sizes, typically 1 mm – 10 cm, are thought to be most appropriate for delineating aspects of fine-scale biodiversity, the size of individual herbaceous plants (Lopatin et al., 2017; Wang et al., 2018). The spectral grain size utilised also precludes the use of a ‘spectral species’ approach in this study, given that individual tundra plants are typically significantly smaller than the 1 x 1 m grain size, thereby preventing assessments of β-diversity through pixel clustering algorithms (Féret and Asner, 2014; Rossi et al., 2022). In spite of this, there remains no spatial scale universally considered for the remote detection of biodiversity (Wang et al., 2018).

Spatial mismatches also exist vertically in spectral studies of plant diversity. As outlined in the methods (**Section 4.2.2**), whilst field measurements sample both canopy and sub-canopy species, thereby better characterising community function, the limited ability of optical remote sensing to penetrate the canopy results in an underrepresentation of sub-canopy species and their associated traits within each plots’ spectral profile (Ma et al., 2020). As such, the spectra may not accurately capture plots’ functional composition, weakening relationships between spectral reflectances and *in situ* estimates of functional dissimilarity and limiting the utility of hyperspectral imagery in such analyses. That said, in our study, when our analyses were re-run with top hits only (**Figure S4.1**), the strength and significance of the observed relationships between spectral and functional and taxonomic dissimilarity typically remained largely unchanged, suggesting that the hyperspectral imagery is doing a good job of capturing understorey vegetation in this study site. The only result to dramatically change was the taxonomic – spectral relationship across time, which surprisingly reduced in significance when using top hits only; as described above, spectra usually follow top hits better than all hits due to their typical lack of canopy penetration. Shrubby plots, where the underrepresentation of sub-canopy species is maximised, are however, sparse across the Saddle so their influence remains hard to determine. Moving forwards, if we are to comprehensively and accurately characterise vegetation β-diversity in the future from remotely sensed means, consideration of such factors must continue to be taken into account.

4.4.3 The importance of timing

Despite evidence for significant spatial relationships between spectral dissimilarity and functional and taxonomic dissimilarity throughout our study system, we found spectral and temporal dissimilarity were typically decoupled from spectral dissimilarity over time. This may stem in large part from the high plasticity, both intra- and interannually, displayed by plant traits that can lead to substantial variability in spectral signatures (Osnas et al., 2018; Rossi et al., 2022; Serbin and Townsend, 2020). Alpine tundra ecosystems are characterised by extreme climates and short growing seasons (Nelson et al., 2022), where all plants must progress through leaf development, expansion, flowering and senescence within a few short months. Intraspecific variation due to phenology may exceed interspecific variation for some plant traits (Fajardo and Siefert, 2016). In arctic tundra, deciduous shrubs, graminoids and forbs showed approximately two-fold variation in foliar nitrogen values over the growing season (Kelsey et al., 2023). As well, different species may progress through key phenological stages asynchronistically (Bloomfield et al., 2018; Fajardo and Siefert, 2016; McKown et al., 2013). As such, functional composition of the plots, as well as traits of constituent species, evolve over the growing season (Ma et al., 2020; Wang et al., 2022). Using spectral reflectance from a single point in a time in the growing season therefore presents challenges as different species within plots are captured at differing points in their respective phenological path, which may not be the most spectrally discriminative part of the growing season (Beamish et al., 2017).

In addition to individual species phenology, the presence and relative influence of other factors known to contribute to variability in spectral reflectance – factors such as the proportion of nonvascular species, standing litter within the plot and soil moisture concentrations – also evolve over the course of the growing season. For instance, high *in situ* soil moisture conditions can depress near-infrared (NIR) signals (Jiang et al., 2016), whilst high proportions of standing litter can disproportionately increase NIR reflectance (van Leeuwen and Huete, 1996), introducing further intra-annual variability in spectral reflectance. Between year differences in environmental conditions further compound plant species and traits phenological pathways, in turn reducing the inter-annual comparability of spectral data. Indeed, within our study site the 2017/18 and 2018/19 winter snowpacks were respectively very low and high, thus some aspects of drought stress may have be apparent in the leaf spectra in 2017/18, even at peak season, while the 2018/19 development was delayed relative to a more typical year.

Differences in the timing of spectral data acquisition among years exacerbate the challenges in using this technology for long-term monitoring. NEON aims to collect hyperspectral data at each site during peak greenness, however, shared equipment, solar angle and cloud cover requirements pose additional constraints such that approximately a quarter of acquisitions to date have occurred outside the actual peak greenness window (Musinsky et al., 2022). At Niwot, acquisitions have typically fallen outside of the optimum timing, with only the 2020 acquisitions beginning within both the (targeted) mean 2003 ~ 2021 peak greenness window (measured by MODIS) and the observed period of annual peak greenness (measured by phenocams in the tundra on Niwot Ridge; **Figure 4.2**). 2017 was a particularly poor year for data collection with acquisition not taking place until 47 days after the end of the measured peak greenness window (**Figure 4.2**) (Musinsky et al., 2022). This was evident in all our results where spectral and NDVI dissimilarities were notably low in 2017 (**Figure 4.3a**; **4.4a,b**; **4.5a,c,e**; **Figure S4.10**). It is likely that a substantial proportion of the annual growth in 2017 had senesced by the time of the NEON flights, which would contribute to the decoupling of spectral signals, particularly the inter-annual signal in NDVI versus field measurements of productivity (Wang et al., 2022). The hyperspectral mosaic product combines individual flights that may have been sampled days or even weeks apart (NEON, 2023a). This could introduce further variability to the hyperspectral comparisons and magnify the influence of intra-annual compositional and trait plasticity.

Targeting peak phenology periods in mountainous environments is particularly complicated by the strong elevational gradients evident in their phenology, which makes the distinguishing of a single period of peak phenology difficult (Dai et al., 2021; Inouye and Wielgolaski, 2013). When collection dates fall sufficiently late in the season, as those in 2017 did, the spectral data collection may miss the majority of the alpine tundra growing season entirely. As such, key discriminatory signals in the spectra may be lost. Furthermore, whilst the day of peak greenness is relatively stable in tundra ecosystems compared to other ecosystem types (Musinsky et al., 2022), the consequences of flying outside the preferred window to data quality are likely greater. This is because of the steep, rapid changes in both tundra spectra and traits after the peak season with the onset and rapid progression of vegetation senescence (May et al., 2017). Furthermore, even on the selected day of acquisition, factors such as atmospheric conditions, bidirectional reflectance distribution function (BRDF) effects and the timing of the solar noon add further complications to the collection of spectral time series data comparable across years (Jafarbiglu and Pourreza, 2023; Roy et al., 2016).

Characteristics of the in-situ measurement campaigns used here likely also contribute to temporal mismatches. Characterisation of functional composition relies on two primary data sources: composition data and trait data (Ricotta and Pavoine, 2022). Ideally, both plant trait and composition data could be collected at regular intervals across the growing season to facilitate consistent analyses of spectra (Ma et al., 2020). The collection of *in situ* plant trait data however is extremely time consuming and laborious (Ma et al., 2020) so trait data is rarely collected with such temporal resolution (Jetz et al., 2016). It is typical therefore to rely on taxonomically and spatially gap-filled datasets (**Chapter 2**; **Figure S4.2**) collected at a limited number of time points. For example, in our study, we relied on data collected at irregular intervals throughout 2008 ~ 2009, 2017 ~ 2018 and 2021, instead of annually coinciding with the 2017 ~ 2020 flight campaigns. The temporal offset in the trait data likely diminishes its quality for use as *in situ* functional calibration data (Sandel et al., 2015). Thus it is possible that with more temporally intensive *in situ* field campaigns the relationships between spectral and functional β-diversity might be improved. Minimising GPS inaccuracies is also essential to ensure maximum comparability between *in situ* and remotely sensed data, although negligible differences in spectra extracted using 0 m, 1 m and 3 m buffers (**Figure S4.3**) suggest that this was not an issue in this study. To say with certainty whether spectral dissimilarity can or cannot be used to monitor changes in functional β-diversity may require more intensive and temporally coherent within-season temporal sampling for both the remote- and both *in situ* components of the study (Gholizadeh et al., 2019). If we are to reach the point where universal scaling rules can be developed to achieve vegetation characterisation from remote sensing platforms (Baldeck and Asner, 2013; Féret and Asner, 2014; Rocchini et al., 2016; Schweiger and Laliberté, 2022), collecting accurate *in situ* calibration data now is a necessity.

4.4.4 Spectra perform well with biomass

In this study, spectral dissimilarity was more strongly related to biomass dissimilarity than either functional or taxonomic dissimilarity across space. Past studies have successfully established relationships between spectral reflectance and biomass so this result is perhaps unsurprising (Wang et al., 2016b). A plant community's spectral reflectance is defined by the corresponding scattering and absorption of light within, which in turn drives both its chemical and three-dimensional physical structures (Schweiger et al., 2015; Ustin et al., 2004). It therefore follows that the greater the difference in biomass between plots, the greater the likely difference in physical structure and corresponding reflectance. As such, the spectral dissimilarity will be bigger, reflecting the difference in biomass within. Our study supports this application, although only over space where the strength of relationships observed was strong. Tundra landscapes typically include large proportions of dead plant material, bare ground and disturbance (Nelson et al., 2022; Yang et al., 2020), all factors that may weaken relationships between spectral reflectance, biomass and biodiversity (Rossi et al., 2022; Schweiger et al., 2015).

4.4.5 What are the alternatives?

Given the moderate strength of the spatial relationships between spectral, functional and taxonomic dissimilarity in this study, and lack of relationships over time, it is worth considering spectral scale and whether the investment in equipment that can capture full-range spectral data is even necessary to monitor change in β-diversity, or whether simpler, pre-existing technology and metrics would characterise the relationships equally well. In our study, functional, taxonomic and biomass dissimilarity displayed similar relationships with NDVI dissimilarity as they did with spectral dissimilarity in terms of the direction of the relationships and statistical significance. The strength of the relationships between NDVI dissimilarity, and functional and biomass dissimilarity was however, notably weaker in all years. This suggests that spectral dissimilarity does capture functionally relevant information beyond that reflected in NDVI. Past studies have found mixed evidence to this end (Rossi et al., 2022), with some (i.e., Rocchini, 2007) supporting the conclusion that adding spectral bands beyond those present in multispectral imagery enhances the accuracy of spectral biodiversity characterisation, and others not (i.e., Wang et al., 2018).

Whether the improvements justify the increased cost and complexity of the additional bands likely depends on the intended monitoring application. For characterising beta-diversity across study sites with dramatic variability in above-ground structure – such as across the sub-alpine/tundra ecotone – we would expect to see strong relationships between spectral and taxonomic or functional β-diversity. Indeed, a comparative study across all NEON sites found that spectral-taxonomic dissimilarity relationships were among the strongest at Niwot Ridge of all NEON sites (Schweiger and Laliberté, 2022). Notably, Schweiger and Laliberte's analysis included plots that span multiple ecosystem types (forest, tundra etc.) within a single study area. Whether taxonomic β-diversity across these broad gradients could be detected equally well using NDVI alone, or in conjunction with LiDAR, has not been tested. We calculated NDVI using the same wavelengths as that calculated from Sentinel-2 multispectral imagery (European Space Agency, 2023a), a free, global and temporally dense dataset with 10m spatial resolution and a return interval of 5 days. Given the wide availability and relative simplicity of multispectral imagery over hyperspectral, perhaps in certain scenarios, using the simpler measure over a larger temporal and geographical expanse is a more worthwhile endeavour, despite the moderate reduction in signal strength.

Even beyond NDVI, other simpler, cheaper methods have proved valuable in the remote characterisation of community diversity. For instance, using specific highly discriminant bands from full-range spectra have proven valuable in characterising tundra diversity (Bratsch et al., 2016; Rossi et al., 2022; Schweiger et al., 2018), whilst airborne LiDAR data, readily available across NEON sites (NEON, 2023b), have been proven to accurately predict tundra shrub biomass (Greaves et al., 2016). Perhaps then the significant expense and complexity of full-range spectrometers are not justified in some instances, and simpler multispectral, LiDAR, or even RGB methods (Beamish et al., 2018) may be similarly effective at delineating aspects of tundra diversity in certain scenarios (Harris et al., 2018). We acknowledge that this is a rapidly developing field and ever-improving processes, methodologies and datasets will only increase the utility of hyperspectral data in biodiversity characterisation in the future. As well, spectral data may prove more useful for other applications than those explored here, such as quantifying canopy nitrogen or water content (Asner and Martin, 2009; Wang et al., 2018). We encourage future studies evaluating the utility of hyperspectral data for monitoring applications to assess not only the performance of hyperspectral data, but also the relative gains over other methods that do not rely on full-spectra data.

The question of alternative methods also raises the possibility of boosting performance by the incorporation of additional, non-spectral data sources (Ma et al., 2020). For instance, the fusion of spectral and LiDAR data from remotely sensed platforms has been shown to enhance the characterisation of key vegetation parameters, such as biomass and productivity (Asner et al., 2012; Sankey et al., 2018; Torabzadeh et al., 2014). Fusing spectral data with data on the ecosystem’s vertical structure can dramatically enhance the ecological interpretation of the spectra by facilitating the incorporation of sub-canopy information (Jetz et al., 2016), thereby negating a key limitation of optical data (Ma et al., 2020). LiDAR data is readily available across all NEON sites, although the data from Niwot is insufficient for use in these analyses due to NEON’s processing algorithm which rounds all vegetation heights below 2 m to 0 m due to uncertainties in the collected data (Scholl, 2019). Such fusion approaches may be the key to unlocking new satellite-borne hyperspectral platforms – such as ‘EnMAP’ (EnMAP, 2023) and the scheduled ‘CHIME’ (European Space Agency, 2023b). As such, data fusion may enhance the utility of hyperspectral imagery and allow it to fulfil its anticipated promise as the means through which function and biodiversity can be characterised at the biome-scale.

4.4.6 Concluding thoughts

In sum, our data support the use of spectral dissimilarity based on hyperspectral campaigns to detect taxonomically and functionally unique areas of the landscape. We do, however, acknowledge that this application is in part likely to be affected by a degree of noise, highlighted by the moderate relationships between spectral reflectance and *in situ* dissimilarity metrics over space. Still, we envision that spectral dissimilarity could be readily applied to prioritise spectrally distinct areas for *in situ* monitoring campaigns. However, the utility of hyperspectral imagery in detecting interannual change in alpine tundra composition, functional or taxonomic, remains limited due to methodological limitations, data deficiencies, and inherent mismatches in the acquisition of data across and between growing seasons. The lack of robust relationships identified over time is also a cautionary tale for those attempting to adopt the principles of space-for-time substitution in hyperspectral studies, as with many domains (Blois et al., 2013; Davison et al., 2021). It is important to consider and revisit these identified temporal issues as longer time series emerge to see how much of the anticipated promise of hyperspectral imagery is manifest in long-term monitoring. The lack of robust temporal patterns observed and issues surrounding temporal monitoring using airborne hyperspectral imagery however, do not negate the validity of our study. This work is amongst the first to use a hyperspectral time series to observe change in vegetation β-diversity over time (Gholizadeh et al., 2020) and paves the way for future studies incorporating longer, more rigorous and more comparable time series.

We attempted to detect and characterise fine-scale changes within a small area of a single tundra vegetation community, an environment known to encompass considerable sub-pixel heterogeneity in composition and function and strong interspecific phenological variation (Bloomfield et al., 2018; Fajardo and Siefert, 2016; McKown et al., 2013; Nelson et al., 2022; Yang et al., 2020). Whilst our ability to characterise such fine-scale change was limited, others have shown spectral and taxonomic β-diversity to strongly relate to one another at larger scales. This includes (Schweiger and Laliberté, 2022) who at the same field location, Niwot Ridge, utilised considerably larger plots (~ 20 x 20 m) across strongly dissimilar ecosystem types (encompassing both tundra and boreal forest) to detect such relationships. Consequently, hyperspectral platforms' most useful avenues may currently lie in large-scale vegetation characterisation and monitoring of ecosystem change. This includes the characterisation of processes such as treeline expansion and warming-induced shrubification (Grigoriev et al., 2022; Jia et al., 2022) but more widely vegetation classification and the direct observation of tundra functional traits (Thomson et al., 2021). As such, it may be that the airborne hyperspectral data are not currently appropriate for studies such as ours, with a narrow spatial and temporal focus, individuals of a greatly smaller size than that of the pixels, and an environment characterised by subtle, fine-scale change. It could be argued that platforms including LiDAR and simpler optical measures (e.g. NDVI) perform these functions equally well already (Berner et al., 2020; Myers-Smith et al., 2020) and that the added utility of hyperspectral imaging does not yet justify its utility. This study suggests that hyperspectral imagery does provide notable additional benefits in the characterisation of fine-scale tundra functional β-diversity across space, but that advances are required in methodology and data acquisition if we are to extract the full potential of hyperspectral time series in biodiversity science.

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5

Synthesis

In the final chapter, I both summarise the main findings of this thesis (**Section 5.1**), and draw out three overarching, cross-chapter themes (**Section 5.2**), namely: 1) *laying the groundwork*; 2) *what about time?*; and 3) *a roadmap for functional diversity*. From these themes, I distil my key findings before rounding off the thesis in my concluding remarks (**Section 5.3**).

5.1 Summary of results

In **Chapter 2** – *considering geographic proximity improves gap-filling performance in tundra plant traits* – I highlight the significance of incorporating explicit spatial hierarchies into tundra trait gap-filling. Gap-filled trait values increasingly differed from true values at higher spatial hierarchies, although patterns were not monotonic. There was a step-change reduction in gap-filling performance at the regional level and comparatively better performance in using family-level values over genus below this threshold. Patterns across hierarchies showed high between-trait specificity. My results provide a number of key suggestions for how to incorporate explicit spatial hierarchies to better enhance gap-filling performance and tundra trait data collection to facilitate more accurate assessments of tundra functional ecology in the future, thereby ensuring we achieved the aims set out in **Section 1.2.1**.

In **Chapter 3** – *functional diversity of tundra vascular plants across space and time* – I show that known global latitudinal gradients in functional diversity extend across the breadth of the tundra to the planet's far northern reaches. Such patterns were dictated by both abiotic (e.g., temperature) and biotic (e.g., functional group) factors. I found no net directional shift in tundra functional diversity over time. I did, however, find opposing patterns through time between functional groups, with increased forbs positively correlating, and decreased graminoids and shrubs negatively correlating with increased functional richness and evenness. Given expected tundra-wide shrubification (Myers-Smith et al., 2011; Myers-Smith and Hik, 2017), this finding is a key concern. Such shrub increases appear likely to drive declines in functional richness and evenness across the biome, threatening tundra ecosystem function and services in turn. When considered more broadly, these findings allowed us to achieve our original aim (**Section 1.2.1**) of quantifying biome-scale distributions in tundra functional diversity for the very first time, whilst also determining key drivers and change over time in the process.

Finally, in **Chapter 4** – *evaluating the utility of hyperspectral data to monitor local-scale β-diversity across space and time* – I find initial evidence to support the use of hyperspectral dissimilarity to characterise local-scale functional and taxonomic β-diversity across space. Relationships incorporated a high degree of noise however, likely a result of using medium-grain size spectral methods to measure fine-scale vegetation variability. Relationships between functional dissimilarity and other simpler spectral measures (e.g., NDVI) were similar to those with full-range spectra, perhaps suggesting that the added utility of hyperspectral imaging does not yet justify its cost. Finally, I found that currently available hyperspectral time series remain insufficient to detect temporal change in functional composition due to methodological limitations and mismatches in the timing of data acquisition both within and between years. We therefore met our aim set out in **Section 1.2.1** to determine the feasibility of using spectra to remotely track spectra and conclude that methodological advances are required to leverage the full capabilities of hyperspectral data across time in functional ecology in the future.

5.2 Cross-chapter synthesis

5.2.1 Laying the groundwork

Prior to completing this thesis, large aspects of the wider tundra functional diversity picture remained a relative unknown. Studies had begun to investigate functional diversity at local and regional scales (e.g., Niittynen et al., 2020; Rissanen et al., 2023) but to the best of my knowledge, no studies yet characterised tundra functional diversity at the biome scale. In a biome experiencing rapid, accelerating warming (Palazzi et al., 2019; Rantanen et al., 2022), the potential for change in communities' species and functional traits is rife and indeed, such changes are already being witnessed (Bjorkman et al., 2018a; García Criado et al., 2023). Any resultant shifts in functional diversity would threaten key ecosystem functions (Hagan et al., 2023; Miedema Brown and Anand, 2022; Niittynen et al., 2020; Villéger et al., 2008) and risk ecosystems passing tipping points beyond which the provision of their ecosystem services could not adapt and respond (Myers-Smith et al., 2019; Schweiger and Laliberté, 2022; Villéger et al., 2013, 2008).

The knowledge paucity surrounding tundra functional diversity therefore seemed like a critical knowledge gap that required filling as a matter of urgency, and this, I believe, is a task this thesis accomplished. Whilst there is much to learn and many more avenues to explore, this thesis *laid the groundwork* for assessments of tundra functional diversity, tackling key aspects across each of its chapters.

Each of the three chapters in this thesis tackled a distinct but complementary unknown aspect of the wider tundra functional diversity picture to help set forth a cohesive understanding for the very first time. To begin, I determined where tundra functional diversity is distributed, why it follows the patterns it does and how such factors play out over time. My findings that it follows known global patterns across latitudes were perhaps expected (Oliveira et al., 2016; Schumm et al., 2019) but its divergent relationships with different functional groups were most likely not (Thomas et al., 2018). Future studies can build on these findings to explore the influence of further biotic and abiotic drivers, such as species rarity (Jain et al., 2014) and snow cover (Rissanen et al., 2023), on tundra functional diversity. Next, when investigating the performance of trait matrix gap-filling methodologies, I highlighted the fundamental role of incorporating explicit spatial hierarchies. My finding that intraspecific spatial variability comprises a significant proportion of overall trait variation was known prior (Cordlandwehr et al., 2013; Jónsdóttir et al., 2023), but the significant role it plays in determining gap-filling performance across spatial scales was most certainly not. Following analyses should aim to assimilate our approach with other key methods, such as trait-trait and trait-environment relationships (Joswig et al., 2023; Schrodt et al., 2015), to further enhance gap-filling accuracy in the future. Finally, I tested the suitability of using spectra to delineate functional variation across tundra space and time, a method long touted by many as an almost ‘holy grail’ in vegetation functional ecology (Jetz et al., 2016). Its utility in other biomes globally has been lauded in recent years (e.g. Schweiger et al., 2018; Wang et al., 2022, 2018) but in the tundra its utility across space, and lack of it across time, has seldom been tested. These results provide actionable suggestions for how enhanced hyperspectral time series could improve the characterisation of functional diversity across time in future studies. Therefore, in every instance, across every chapter, knowledge, assumptions and expectations were simultaneously incorporated and challenged to elucidate new understanding of functional diversity across the tundra. In doing so, this thesis helped *lay the groundwork* for all future work in tundra functional diversity and ecology.

5.2.2 What about time?

One of the key themes, or perhaps issues, that runs throughout this thesis is that of time. Specifically, the question is: when observing change across time, or more accurately, a lack of change across time (see **Chapters 2** and **4**), to what extent are these temporal patterns a product of true ecological processes rather than unavoidable inaccuracies in the datasets and methodologies used to investigate them? Tundra plants are known to exhibit high trait plasticity both intra- and interannually (Osnas et al., 2018; Rossi et al., 2022; Serbin and Townsend, 2020) and pass through key phenological stages asynchronistically in the short high latitude or altitude growing season (Bloomfield et al., 2018; Fajardo and Siefert, 2016; McKown et al., 2013). As such, the datasets we use to understand such nuanced change must be of similarly high temporal resolution and measured with consistent intra- and interannual repeats to ensure comparable measurements for all species across time. As this thesis highlights, however, tundra trait and associated datasets rarely conform to such criteria, greatly inhibiting our ability to characterise temporal change in functional diversity.

In my biome-scale analyses (**Chapter 3**), I found no net directional change in tundra functional diversity over the 38 year assessed period. On the face of things, this matches expectations. Biome-wide shifts in key traits (Bjorkman et al., 2018a) and species diversity (Stewart et al., 2016) lag behind rates of warming with the latest assessments illustrating no net change in tundra species richness throughout recent decades (García Criado et al., 2023). My findings conform to these conclusions and suggest time lags in shifts in tundra functional diversity. However, the question arises, to what extent these temporal patterns are the product of true ecological processes, rather than inadequacies in the datasets and methodologies used. **Chapter 2** (and **Chapter 3**) relied on the TRY and TTT databases, which constitute thousands of tundra trait records from across the biome (Bjorkman et al., 2018b; Kattge et al., 2020, 2011). Whilst the collection of such trait records spans decades, the collection was not done in a coherent manner, nor did it follow any standardised protocol (Joswig et al., 2023; Schrodt et al., 2015). As such, sites rarely, if ever, exhibit consistent repeat measurements between years or across sites, and records occur sporadically across years and space (Poyatos et al., 2018; Shan et al., 2012). This prohibits the joining of plant composition records – often measured with consistent repeats as part of long-term time series (e.g., ITEX+, Bjorkman et al., In prep.) – to plant trait records at specific locations and time points. Instead, averaged trait values across years must be assigned to composition records, thereby removing any between-year trait variation from analyses and ensuring ‘interannual’ assessments reflect only composition, not trait, change.

Our inability to detect signals of fine-scale functional change across time through spectra in **Chapter 4** was similarly hampered by temporal data paucities. NEON aims to capture airborne hyperspectral imagery, as used in this study, at, or close to, the point of peak greenness each year, thereby facilitating accurate interannual comparisons of vegetation spectra (Musinsky et al., 2022; NEON, 2023). Whilst NEON strives to achieve this goal, operational and environmental constraints severely limit their ability to reliably do so. As such, the NEON hyperspectral imagery used in this study, collected between 2017 and 2020, exhibited significant interannual inconsistencies with annual capture dates spread over a period of 62 days, or two months, between years (**Figure 4.2**; Musinsky et al., 2022; NEON, 2023). As described, tundra plants exhibit high trait plasticity both intra- and interannually (Osnas et al., 2018; Rossi et al., 2022; Serbin and Townsend, 2020) and pass through key phenological stages rapidly and asynchronistically (Bloomfield et al., 2018; Fajardo and Siefert, 2016; McKown et al., 2013). Spectral profiles of tundra species hence change rapidly and asynchronistically in response, both within and between years (Beamish et al., 2017; Osnas et al., 2018). Therefore, when spectral acquisition dates differ by as much as two months each year, the spectral profiles of species are captured at disparate points of their respective phenological pathways, confounding between year signals with within year signals. When further combined with the lack of consistently sampled *in situ* trait data with which to ground truth spectral-functional relationships, inferring temporal change in functions through spectra becomes nearly impossible.

The inability to confidently and definitively deduce change in tundra functional diversity over time due to data deficiencies is a fundamental issue present across the breadth of this thesis. Given the known significance of functional diversity to ecosystem services and functions in a biome subject to rapid and unchecked warming (Imbert et al., 2021; Miedema Brown and Anand, 2022; Rantanen et al., 2022), this is a critical knowledge gap. How certain am I that I am not missing something key? What patterns are going unnoticed? How confident can I be in my current conclusions? All of these queries currently go unanswered when asking the question, *what about time*? It is the identification of issues such as these that is perhaps, counterintuitively, the strongest aspect of this thesis. Data collection must be dramatically enhanced in the near future to begin to accurately characterise shifts in tundra functional diversity through time. By tackling questions such as *what about time* through a critical lens, this thesis has identified key areas of potential improvement in functional ecological assessments and acts as a *roadmap for change* when assessing functional diversity across the tundra in the near future (**Section 5.2.3**).

5.2.3 A roadmap for change

As discussed above, this thesis has *laid the groundwork* for future studies in tundra functional diversity. It has also highlighted a number of issues regarding current methodologies and data deficiencies that must be addressed. In my eyes, tackling these concerns should comprise the primary focus of future work on tundra functional diversity. Tackling these concerns will enhance the accuracy of functional analyses. By increasing accuracy and confidence in our current understanding of tundra functional diversity, you increase the potential to be able to accurately predict future change in turn. Given the rate of warming in the tundra, and potential magnitude of change, such possibilities appear invaluable. This thesis therefore acts as *a roadmap for change* and provides suggestions on how it can be achieved.

Some changes I suggest are clear and have been spoken about at length already in this thesis. For instance, in **Chapter 3**, I highlight the lack of non-vascular and below-ground trait data currently available for use in tundra studies. The influence of non-vascular species in the tundra shouldn't be understated. Moss species are known to significantly influence key ecosystem processes such as nutrient, carbon and water cycling whilst exerting longer-term controls on key ecosystem components such as permafrost thaw and carbon accumulation (Turetsky et al., 2012). They are especially important in communities with low vascular plant cover (Eldridge et al., 2023), common in the tundra, and are thought to potentially offer high resilience to extreme environmental change (Turetsky et al., 2012). As such, incorporating burgeoning datasets in these areas (e.g. Klimešová et al., 2017, 2012; Lett et al., 2021; Lewis et al., 2017) will allow us to paint a more holistic picture of functional diversity across full tundra plant communities in the future. In **Chapter 2**, I highlight the need for, and potential methods to obtain, trait data that meets scale-specific geographical and taxonomic needs. Collecting such data will facilitate increasingly accurate gap-filling of trait matrices, the fundamental underpinning to many studies investigating functional diversity. Finally, in **Chapter 4**, I detail the urgent need for hyperspectral imagery captured across broad spatial-scales and at regular intervals across the tundra (Musinsky et al., 2022). Only when such data become available, in combination with the consistent collection of trait data over multiple years, will attempts to detect functional diversity across space and time through remote means become possible. The implementation of suggestions such as these hence have the potential to dramatically increase our ability to undertake nuanced assessments of tundra functional diversity across space and time.

My suggested improvements go beyond just data deficiencies however, and begin to suggest ways in which we can better employ existing data to maximise the possibilities that functional ecology entails. For instance, in **Chapter 3**, I trialled the use of incorporating explicit spatial hierarchies into gap-filling approaches to better estimate missing records in sparse trait matrices (**Section 3.4**). My work in **Chapter 2** confirmed the value of such methods, so much so that the method has now been used in two further studies considering tundra traits (Björnsdóttir et al., In prep.) and functional diversity (Scharn et al., In prep.). In **Chapter 3**, I also raise the potential for losses in tundra functional diversity in response to expected shrub advances. I believe future studies should aim to quantify the magnitude, locations and timings of any losses that such shrub expansions may entail. Similarly, in **Chapter 4,** I highlight the tantalising possibility of using hyperspectral platforms to facilitate much needed assessments of tundra functional diversity across broader spatial scales with consistent temporal repeats. I believe my methods in **Chapter 4** can be built on and diversified to encompass new technologies, such as the EnMAP hyperspectral platform (EnMAP, 2023), to achieve such goals.

Finally, and perhaps most critically of all, this thesis began by detailing the significance of functional diversity in the tundra, specifically its fundamental role in defining the variety and stability of ecosystem services across the biome. Whilst this link is well known (Hagan et al., 2023; Miedema Brown and Anand, 2022), I believe future work must begin to prioritise the quantification of such relationships between tundra functional diversity and specific ecosystem services. Only then can conclusions regarding shifts in functional diversity be mechanistically linked to changes in ecosystem services, be that soil fertility or climate feedbacks (Bjorkman et al., 2020; Ottoy et al., 2017). Given rates of warming in this dynamic, evolving biome, and its known significance to the wider earth system (e.g. Callaghan et al., 2011; Chapin et al., 1996; Euskirchen et al., 2009), understanding such feedbacks must be considered a priority.

5.3 Concluding remarks

Across the breadth of this thesis, I have attempted to shed new light on the tundra functional diversity picture, an under-researched subject of considerable importance. I carried out the first biome-scale assessment of tundra functional diversity, and in doing so, determined its spatial distribution, drivers and temporal change for the very first time. I challenged and built upon gap-filling methods commonly used in its assessment, providing suggestions and improvements through which it can be better characterised in the future. Finally, I broke new ground by exploring original approaches to more consistently detect change in functional diversity across greater expanses, critical in a changing world. Overall, I believe this work was both novel and timely, and has been invaluable in laying the groundwork on which future studies into tundra functional ecology can, and perhaps should, be built. Critically however, it also identified key issues and deficiencies in current approaches that must be addressed. Some of these I tackled, such as the incorporation of spatial hierarchies into gap-filling approaches. Some, however, fell beyond the scope of this study and now fall to others. All in all, I believe the functional diversity picture across the tundra is much clearer as a result of this thesis. This can only be a benefit to understanding how key functions, feedbacks and ecosystem services are likely to shift as warming accelerates throughout this changing, contemporary tundra.

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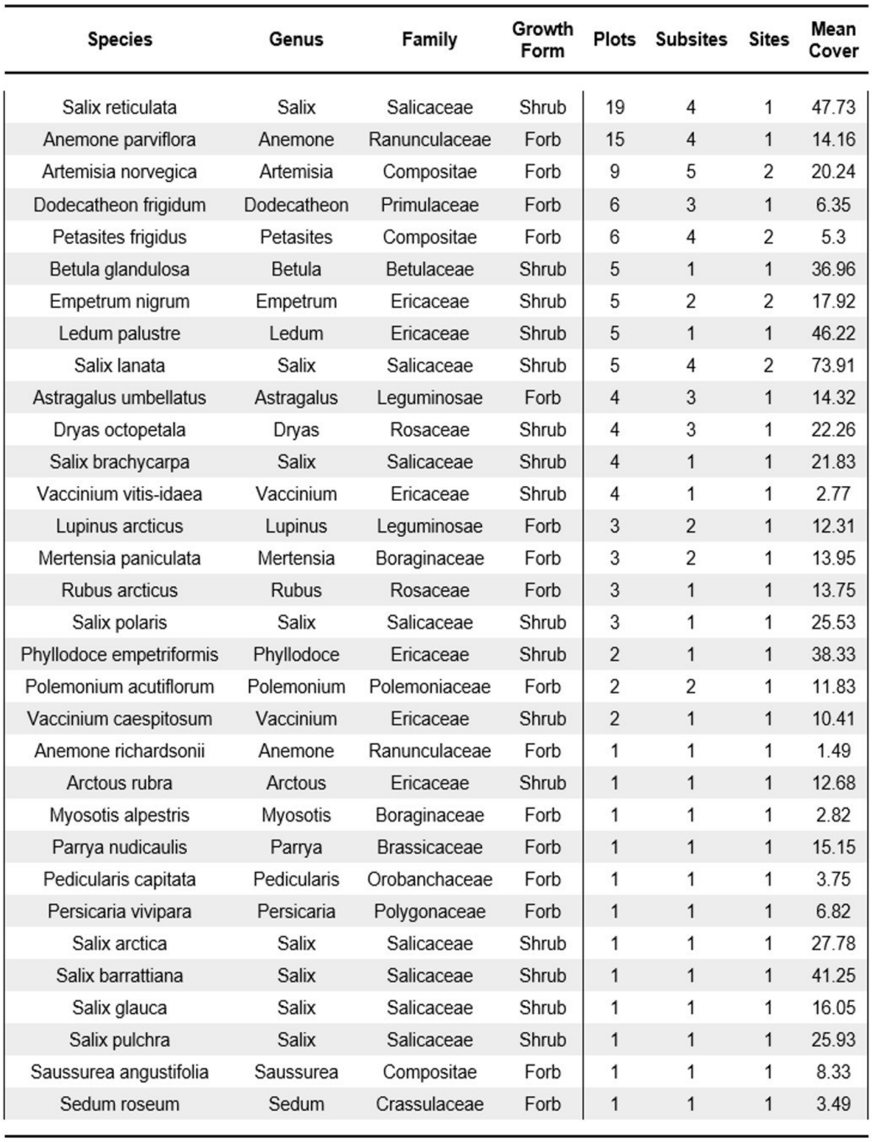
Appendices

6.1 Supplementary Materials [Chapter 2]

- **Gap-filling**

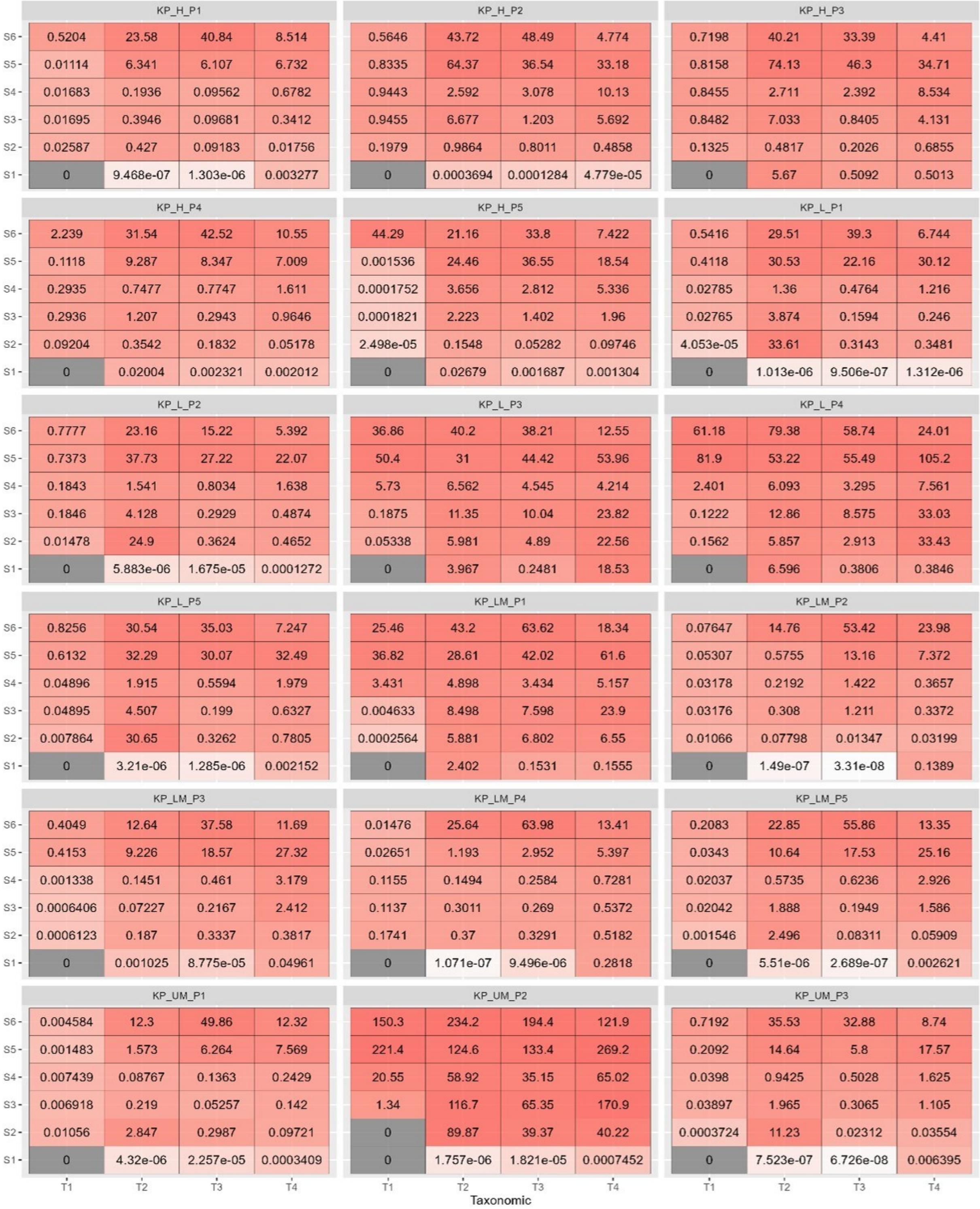
Table S2.1 Surveyed forb and shrub species



Species	Genus	Family	Growth Form	Plots	Subsites	Sites	Mean Cover
Salix reticulata	Salix	Salicaceae	Shrub	19	4	1	47.73
Anemone parviflora	Anemone	Ranunculaceae	Forb	15	4	1	14.16
Artemisia norvegica	Artemisia	Compositae	Forb	9	5	2	20.24
Dodecatheon frigidum	Dodecatheon	Primulaceae	Forb	6	3	1	6.35
Petasites frigidus	Petasites	Compositae	Forb	6	4	2	5.3
Betula glandulosa	Betula	Betulaceae	Shrub	5	1	1	36.96
Empetrum nigrum	Empetrum	Ericaceae	Shrub	5	2	2	17.92
Ledum palustre	Ledum	Ericaceae	Shrub	5	1	1	46.22
Salix lanata	Salix	Salicaceae	Shrub	5	4	2	73.91
Astragalus umbellatus	Astragalus	Leguminosae	Forb	4	3	1	14.32
Dryas octopetala	Dryas	Rosaceae	Shrub	4	3	1	22.26
Salix brachycarpa	Salix	Salicaceae	Shrub	4	1	1	21.83
Vaccinium vitis-idaea	Vaccinium	Ericaceae	Shrub	4	1	1	2.77
Lupinus arcticus	Lupinus	Leguminosae	Forb	3	2	1	12.31
Mertensia paniculata	Mertensia	Boraginaceae	Forb	3	2	1	13.95
Rubus arcticus	Rubus	Rosaceae	Forb	3	1	1	13.75
Salix polaris	Salix	Salicaceae	Shrub	3	1	1	25.53
Phyllodoce empetriformis	Phyllodoce	Ericaceae	Shrub	2	1	1	38.33
Polemonium acutiflorum	Polemonium	Polemoniaceae	Forb	2	2	1	11.83
Vaccinium caespitosum	Vaccinium	Ericaceae	Shrub	2	1	1	10.41
Anemone richardsonii	Anemone	Ranunculaceae	Forb	1	1	1	1.49
Arctous rubra	Arctous	Ericaceae	Shrub	1	1	1	12.68
Myosotis alpestris	Myosotis	Boraginaceae	Forb	1	1	1	2.82
Parrya nudicaulis	Parrya	Brassicaceae	Forb	1	1	1	15.15
Pedicularis capitata	Pedicularis	Orobanchaceae	Forb	1	1	1	3.75
Persicaria vivipara	Persicaria	Polygonaceae	Forb	1	1	1	6.82
Salix arctica	Salix	Salicaceae	Shrub	1	1	1	27.78
Salix barrattiana	Salix	Salicaceae	Shrub	1	1	1	41.25
Salix glauca	Salix	Salicaceae	Shrub	1	1	1	16.05
Salix pulchra	Salix	Salicaceae	Shrub	1	1	1	25.93
Saussurea angustifolia	Saussurea	Compositae	Forb	1	1	1	8.33
Sedum roseum	Sedum	Crassulaceae	Forb	1	1	1	3.49

Table S2.1 | Surveyed forb and shrub species. This table details all the forb and shrub species encountered in our network of 30 composition plots across the Canadian NW in summer of 2022 (**Figure 2.1**). It details both their taxonomic nomenclature, the number of plots, subsites and sites in which they were surveyed, and finally the mean relative cover with which they were found in each plot (**Section 2.2.2**).

Figure S2.1 Mahalanobis distance by plot



KP_H_P1

	T1	T2	T3	T4
S6	0.5204	23.58	40.84	8.514
S5	0.01114	6.341	6.107	6.732
S4	0.01683	0.1936	0.09562	0.6782
S3	0.01695	0.3946	0.09681	0.3412
S2	0.02587	0.427	0.09183	0.01756
S1	0	9.468e-07	1.303e-06	0.003277

KP_H_P2

	T1	T2	T3	T4
S6	0.5646	43.72	48.49	4.774
S5	0.8335	64.37	36.54	33.18
S4	0.9443	2.592	3.078	10.13
S3	0.9455	6.677	1.203	5.692
S2	0.1979	0.9864	0.8011	0.4858
S1	0	0.0003694	0.0001284	4.779e-05

KP_H_P3

	T1	T2	T3	T4
S6	0.7198	40.21	33.39	4.41
S5	0.8158	74.13	46.3	34.71
S4	0.8455	2.711	2.392	8.534
S3	0.8482	7.033	0.8405	4.131
S2	0.1325	0.4817	0.2026	0.6855
S1	0	5.67	0.5092	0.5013

KP_H_P4

	T1	T2	T3	T4
S6	2.239	31.54	42.52	10.55
S5	0.1118	9.287	8.347	7.009
S4	0.2935	0.7477	0.7747	1.611
S3	0.2936	1.207	0.2943	0.9646
S2	0.09204	0.3542	0.1832	0.05178
S1	0	0.02004	0.002321	0.002012

KP_H_P5

	T1	T2	T3	T4
S6	44.29	21.16	33.8	7.422
S5	0.001536	24.46	36.55	18.54
S4	0.0001752	3.656	2.812	5.336
S3	0.0001821	2.223	1.402	1.96
S2	2.498e-05	0.1548	0.05282	0.09746
S1	0	0.02679	0.001687	0.001304

KP_L_P1

	T1	T2	T3	T4
S6	0.5416	29.51	39.3	6.744
S5	0.4118	30.53	22.16	30.12
S4	0.02785	1.36	0.4764	1.216
S3	0.02765	3.874	0.1594	0.246
S2	4.053e-05	33.61	0.3143	0.3481
S1	0	1.013e-06	9.506e-07	1.312e-06

KP_L_P2

	T1	T2	T3	T4
S6	0.7777	23.16	15.22	5.392
S5	0.7373	37.73	27.22	22.07
S4	0.1843	1.541	0.8034	1.638
S3	0.1846	4.128	0.2929	0.4874
S2	0.01478	24.9	0.3624	0.4652
S1	0	5.883e-06	1.675e-05	0.0001272

KP_L_P3

	T1	T2	T3	T4
S6	36.86	40.2	38.21	12.55
S5	50.4	31	44.42	53.96
S4	5.73	6.562	4.545	4.214
S3	0.1875	11.35	10.04	23.82
S2	0.05338	5.981	4.89	22.56
S1	0	3.967	0.2481	18.53

KP_L_P4

	T1	T2	T3	T4
S6	61.18	79.38	58.74	24.01
S5	81.9	53.22	55.49	105.2
S4	2.401	6.093	3.295	7.561
S3	0.1222	12.86	8.575	33.03
S2	0.1562	5.857	2.913	33.43
S1	0	6.596	0.3806	0.3846

KP_L_P5

	T1	T2	T3	T4
S6	0.8256	30.54	35.03	7.247
S5	0.6132	32.29	30.07	32.49
S4	0.04896	1.915	0.5594	1.979
S3	0.04895	4.507	0.199	0.6327
S2	0.007864	30.65	0.3262	0.7805
S1	0	3.21e-06	1.285e-06	0.002152

KP_LM_P1

	T1	T2	T3	T4
S6	25.46	43.2	63.62	18.34
S5	36.82	28.61	42.02	61.6
S4	3.431	4.898	3.434	5.157
S3	0.004633	8.498	7.598	23.9
S2	0.0002564	5.881	6.802	6.55
S1	0	2.402	0.1531	0.1555

KP_LM_P2

	T1	T2	T3	T4
S6	0.07647	14.76	53.42	23.98
S5	0.05307	0.5755	13.16	7.372
S4	0.03178	0.2192	1.422	0.3657
S3	0.03176	0.308	1.211	0.3372
S2	0.01066	0.07798	0.01347	0.03199
S1	0	1.49e-07	3.31e-08	0.1389

KP_LM_P3

	T1	T2	T3	T4
S6	0.4049	12.64	37.58	11.69
S5	0.4153	9.226	18.57	27.32
S4	0.001338	0.1451	0.461	3.179
S3	0.0006406	0.07227	0.2167	2.412
S2	0.0006123	0.187	0.3337	0.3817
S1	0	0.001025	8.775e-05	0.04961

KP_LM_P4

	T1	T2	T3	T4
S6	0.01476	25.64	63.98	13.41
S5	0.02651	1.193	2.952	5.397
S4	0.1155	0.1494	0.2584	0.7281
S3	0.1137	0.3011	0.269	0.5372
S2	0.1741	0.37	0.3291	0.5182
S1	0	1.071e-07	9.496e-06	0.2818

KP_LM_P5

	T1	T2	T3	T4
S6	0.2083	22.85	55.86	13.35
S5	0.0343	10.64	17.53	25.16
S4	0.02037	0.5735	0.6236	2.926
S3	0.02042	1.888	0.1949	1.586
S2	0.001546	2.496	0.08311	0.05909
S1	0	5.51e-06	2.689e-07	0.002621

KP_UM_P1

	T1	T2	T3	T4
S6	0.004584	12.3	49.86	12.32
S5	0.001483	1.573	6.264	7.569
S4	0.007439	0.08767	0.1363	0.2429
S3	0.006918	0.219	0.05257	0.142
S2	0.01056	2.847	0.2987	0.09721
S1	0	4.32e-06	2.257e-05	0.0003409

KP_UM_P2

	T1	T2	T3	T4
S6	150.3	234.2	194.4	121.9
S5	221.4	124.6	133.4	269.2
S4	20.55	58.92	35.15	65.02
S3	1.34	116.7	65.35	170.9
S2	0	89.87	39.37	40.22
S1	0	1.757e-06	1.821e-05	0.0007452

KP_UM_P3

	T1	T2	T3	T4
S6	0.7192	35.53	32.88	8.74
S5	0.2092	14.64	5.8	17.57
S4	0.0398	0.9425	0.5028	1.625
S3	0.03897	1.965	0.3065	1.105
S2	0.0003724	11.23	0.02312	0.03554
S1	0	7.523e-07	6.726e-08	0.006395

KP_UM_P4

	T1	T2	T3	T4
S6	0.2066	12.08	40.56	7.951
S5	0.07774	12.34	12.88	17.8
S4	0.003541	0.4035	0.1762	1.095
S3	0.003366	1.324	0.1293	0.4874
S2	0.007125	16.61	0.07573	0.1293
S1	0	7.643e-06	2.696e-06	0.01794

KP_UM_P5

	T1	T2	T3	T4
S6	2.046	30.85	26.66	18.91
S5	1.878	15.05	7.856	31.31
S4	1.09	4.465	2.048	3.473
S3	1.087	6.011	1.731	2.709
S2	0.2066	8.418	0.2693	0.06946
S1	0	6.247e-06	2.411e-06	0.005271

SG_L_P1

	T1	T2	T3	T4
S6	0.01446	54.77	38.15	171.5
S5	0.003056	0.1053	27.04	2.104
S4	0.001941	0.005005	0.128	3.165
S3	0.001941	0.009081	0.05066	2.956
S2	0.001941	0.00456	0.1454	2.598
S1	0	2.807e-05	0.1878	0.6985

SG_L_P2

	T1	T2	T3	T4
S6	0.007672	29.51	43.12	23.22
S5	0.0004561	13.18	41.28	26.84
S4	0.0001752	5.275	0.08389	4.567
S3	0.0001752	5.142	0.06885	4.567
S2	0.0001752	4.623	0.1076	4.567
S1	0	5.011e-06	3.376e-06	0.003602

SG_L_P3

	T1	T2	T3	T4
S6	0.3341	21.44	34.73	44.75
S5	0.3964	2.041	36.89	6.205
S4	0.0569	0.9352	0.6206	10.1
S3	0.0569	0.9774	0.4808	9.917
S2	0.0569	1.035	0.7372	10.47
S1	0	9.794e-05	3.527e-05	8.128e-05

SG_L_P4

	T1	T2	T3	T4
S6	0.1352	10.41	12.71	689.9
S5	0.08377	3.641	6.625	2.939
S4	0.08377	0.8441	1.84	1.292
S3	0.08377	1.102	2.07	1.417
S2	0.08377	0.8896	1.409	1.594
S1	0	1.362e-05	2.451e-05	1.719e-05

SG_L_P5

	T1	T2	T3	T4
S6	127.8	245.6	226.3	167.1
S5	192.1	156	194.9	272.1
S4	0.0002496	126.7	69.45	246.9
S3	0.0002496	125.1	71.92	246.9
S2	0.0002496	129.6	69.68	246.9
S1	0	96.72	6.125	250.4

T_L_P1

	T1	T2	T3	T4
S6	4.021	1.138	26.51	1550
S5	3.283	10.64	210.8	0.2737
S4	8.527e-05	0.000118	0.08662	0.896
S3	8.527e-05	0.0003459	0.08764	0.8944
S2	8.527e-05	0.0001292	0.05434	1.264
S1	0	1.175e-07	0.004041	0.0004671

T_L_P2

	T1	T2	T3	T4
S6	1.164	0.09282	3.8	2918
S5	0.6819	0.7946	24.97	0.03645
S4	0.002534	0.00648	0.02233	0.04142
S3	0.002534	0.00278	0.01728	0.06219
S2	0.002534	0.002793	0.02091	0.1246
S1	0	1.829e-06	0.004812	0.0015

T_L_P3

	T1	T2	T3	T4
S6	10.4	1.684	129	250.5
S5	8.718	53.79	1327	0.9591
S4	0.01528	0.01005	0.0007605	0.9642
S3	0.01528	0.01627	0.001377	0.9602
S2	0.01528	0.03287	0.0002861	1.035
S1	0	1.351e-05	0.001029	0.0009218

T_L_P4

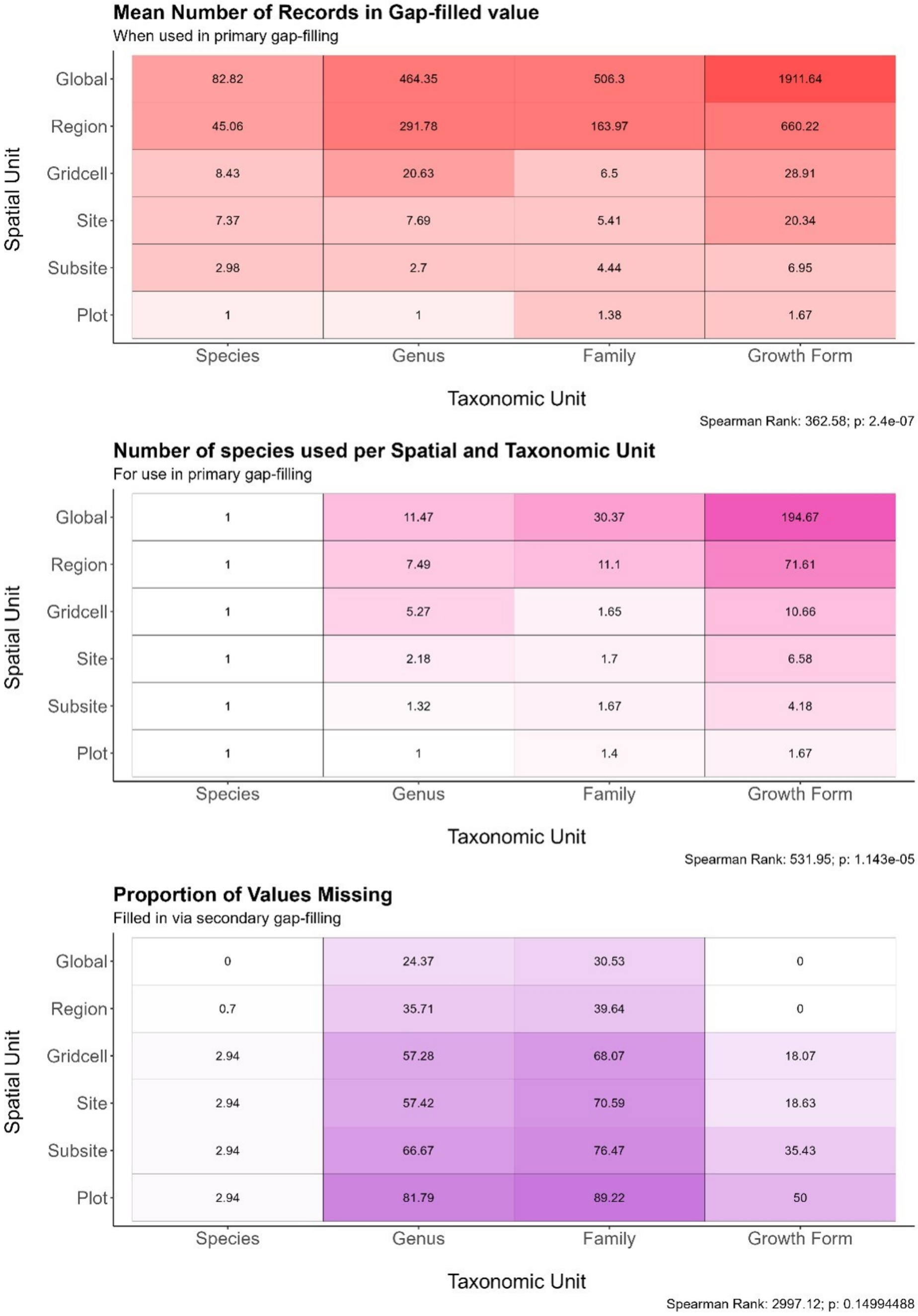
	T1	T2	T3	T4
S6	12.14	1.561	5.618	143.3
S5	6.3	1.735	19.39	2.997
S4	5.525e-07	6.61e-05	0.0008079	0.01963
S3	5.525e-07	0.0001798	0.0009895	0.02087
S2	5.525e-07	0.0007505	0.0008901	0.01939
S1	0	9.241e-05	0.001343	0.01607

T_L_P5

	T1	T2	T3	T4
S6	15.43	5.361	133.3	361.1
S5	13.54	69.56	1263	1.654
S4	0.01888	0.02253	0.07026	4.231
S3	0.01888	0.01415	0.08282	4.495
S2	0.01888	0.01288	0.09904	4.309
S1	0	5.132e-07	0.006479	0.0008622

Figure S2.1 | Mahalanobis distances by individual plot. This figure details the individual pairwise squared generalised Mahalanobis distances calculated across all spatial and taxonomic hierarchical levels for each of the 30 composition plots across the Canadian NW in summer of 2022 (**Figure 2.1**). Values from each hierarchical level across each of the 30 plots were averaged to produce the mean output seen in **Figure 2.3**.

Figure S2.2 Summary gap-filling statistics



Mean Number of Records in Gap-filled value
When used in primary gap-filling

Spatial Unit	Species	Genus	Family	Growth Form
Global	82.82	464.35	506.3	1911.64
Region	45.06	291.78	163.97	660.22
Gridcell	8.43	20.63	6.5	28.91
Site	7.37	7.69	5.41	20.34
Subsite	2.98	2.7	4.44	6.95
Plot	1	1	1.38	1.67

Taxonomic Unit

Spearman Rank: 362.58; p: 2.4e-07

Number of species used per Spatial and Taxonomic Unit
For use in primary gap-filling

Spatial Unit	Species	Genus	Family	Growth Form
Global	1	11.47	30.37	194.67
Region	1	7.49	11.1	71.61
Gridcell	1	5.27	1.65	10.66
Site	1	2.18	1.7	6.58
Subsite	1	1.32	1.67	4.18
Plot	1	1	1.4	1.67

Taxonomic Unit

Spearman Rank: 531.95; p: 1.143e-05

Proportion of Values Missing
Filled in via secondary gap-filling

Spatial Unit	Species	Genus	Family	Growth Form
Global	0	24.37	30.53	0
Region	0.7	35.71	39.64	0
Gridcell	2.94	57.28	68.07	18.07
Site	2.94	57.42	70.59	18.63
Subsite	2.94	66.67	76.47	35.43
Plot	2.94	81.79	89.22	50

Taxonomic Unit

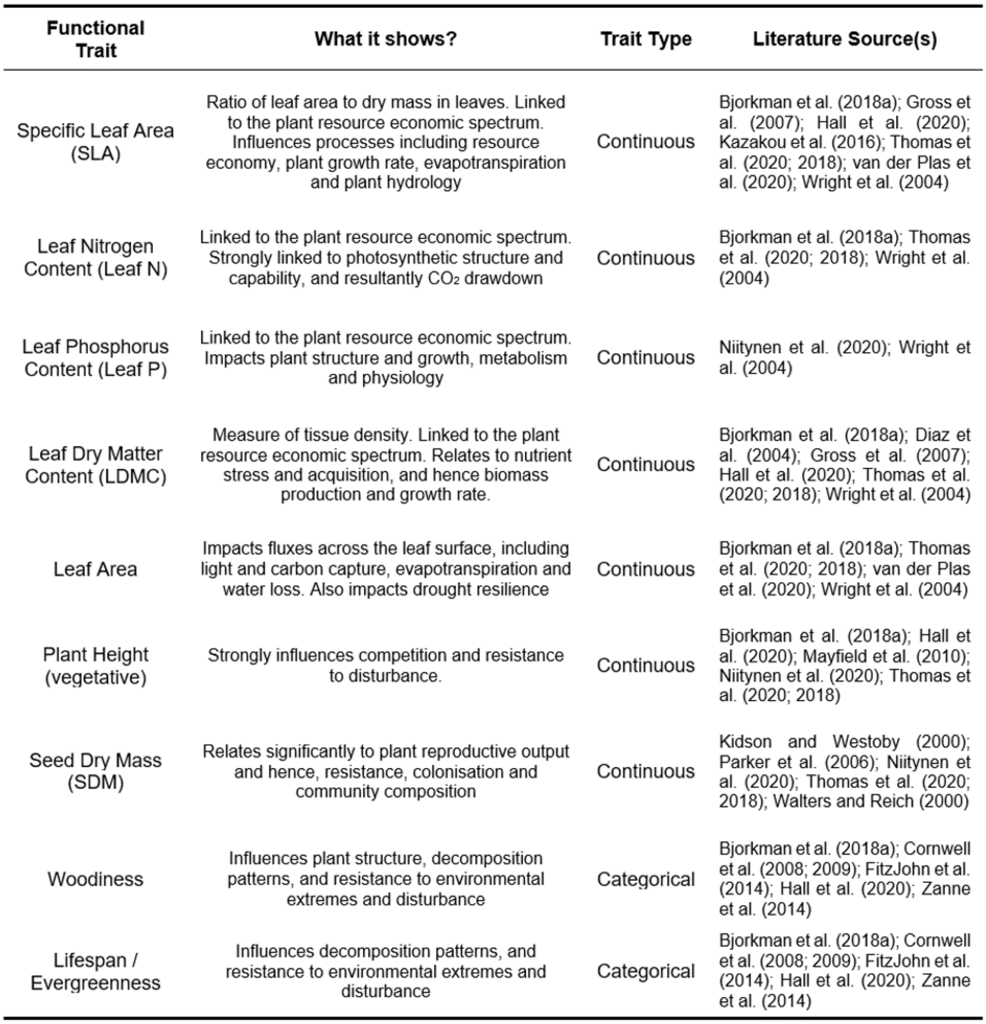
Spearman Rank: 2997.12; p: 0.14994488

Figure S2.2 | Calculated Mahalanobis distances correlated with number of records and species used in primary gap-filling. Mahalanobis distance was seen to be significantly related ($p < 0.05$) to the number of records used in primary gap-filling, and the number of species from which those records were drawn, suggesting that more records used and species used leads to more inaccurate gap-filling values. Conversely, the proportion of missing values (a proxy for the amount of times the secondary gap-filling procedure was used) was not significantly correlated with Mahalanobis distance, suggesting that the secondary gap-filling process was not responsible for the patterns seen.

6.2 Supplementary Materials [Chapter 3] - **Functional Diversity**

Table S3.1 Assessed functional traits

Table S3.1 | Assessed functional traits. A summary of the nine plant functional traits selected for the calculation of functional diversity metrics, examples of their relative function in the ecosystem, and relevant literature sources.



Functional Trait	What it shows?	Trait Type	Literature Source(s)
Specific Leaf Area (SLA)	Ratio of leaf area to dry mass in leaves. Linked to the plant resource economic spectrum. Influences processes including resource economy, plant growth rate, evapotranspiration and plant hydrology	Continuous	Bjorkman et al. (2018a); Gross et al. (2007); Hall et al. (2020); Kazakou et al. (2016); Thomas et al. (2020; 2018); van der Plas et al. (2020); Wright et al. (2004)
Leaf Nitrogen Content (Leaf N)	Linked to the plant resource economic spectrum. Strongly linked to photosynthetic structure and capability, and resultantly CO_2 drawdown	Continuous	Bjorkman et al. (2018a); Thomas et al. (2020; 2018); Wright et al. (2004)
Leaf Phosphorus Content (Leaf P)	Linked to the plant resource economic spectrum. Impacts plant structure and growth, metabolism and physiology	Continuous	Niitynen et al. (2020); Wright et al. (2004)
Leaf Dry Matter Content (LDMC)	Measure of tissue density. Linked to the plant resource economic spectrum. Relates to nutrient stress and acquisition, and hence biomass production and growth rate.	Continuous	Bjorkman et al. (2018a); Diaz et al. (2004); Gross et al. (2007); Hall et al. (2020); Thomas et al. (2020; 2018); Wright et al. (2004)
Leaf Area	Impacts fluxes across the leaf surface, including light and carbon capture, evapotranspiration and water loss. Also impacts drought resilience	Continuous	Bjorkman et al. (2018a); Thomas et al. (2020; 2018); van der Plas et al. (2020); Wright et al. (2004)
Plant Height (vegetative)	Strongly influences competition and resistance to disturbance.	Continuous	Bjorkman et al. (2018a); Hall et al. (2020); Mayfield et al. (2010); Niitynen et al. (2020); Thomas et al. (2020; 2018)
Seed Dry Mass (SDM)	Relates significantly to plant reproductive output and hence, resistance, colonisation and community composition	Continuous	Kidson and Westoby (2000); Parker et al. (2006); Niitynen et al. (2020); Thomas et al. (2020; 2018); Walters and Reich (2000)
Woodiness	Influences plant structure, decomposition patterns, and resistance to environmental extremes and disturbance	Categorical	Bjorkman et al. (2018a); Cornwell et al. (2008; 2009); FitzJohn et al. (2014); Hall et al. (2020); Zanne et al. (2014)
Lifespan / Evergreenness	Influences decomposition patterns, and resistance to environmental extremes and disturbance	Categorical	Bjorkman et al. (2018a); Cornwell et al. (2008; 2009); FitzJohn et al. (2014); Hall et al. (2020); Zanne et al. (2014)

Table S3.2 Bayesian model outputs

Table S3.2 | Bayesian model structures and outputs. Details of the model structures, including response variables, fixed effects and variable types, covariates (when categoric), model type, estimates and 95% CIs for all spatial and temporal models run in the analysis for **Chapter 3**. Details of the random effects and distributions used, and the reasoning for all model decisions can be found in **Section 3.2.6**.

Response Variable	Fixed Effect	Fixed Var. Type	Covariate	Type	Estimate	Lower CI (95%)	Upper CI (95%)
FEve change	1	NA	NA	Linear	-9.00E-04	-0.0033	0.0014
FRic change	1	NA	NA	Linear	-0.0307	-0.1274	0.0665
Forb change	1	NA	NA	Linear	0.0056	-0.2312	0.2654
Gram. change	1	NA	NA	Linear	-0.1542	-0.4837	0.191
SR change	1	NA	NA	Linear	-0.0073	-0.039	0.0267
Shrub change	1	NA	NA	Linear	0.1477	-0.2594	0.5352
FEve	Dominant FG	Categoric	Reference	Linear	0.5986	0.5489	0.6466
FEve	Dominant FG	Categoric	Graminoid	Linear	-0.0383	-0.0789	0.0042
FEve	Dominant FG	Categoric	None	Linear	0.0377	-0.0067	0.082
FEve	Dominant FG	Categoric	Shrub	Linear	-0.0123	-0.054	0.03
FRic	Dominant FG	Categoric	Reference	Censored	2.8744	2.6984	3.0471
FRic	Dominant FG	Categoric	Graminoid	Censored	-0.1533	-0.236	-0.0688
FRic	Dominant FG	Categoric	None	Censored	0.0278	-0.0583	0.115
FRic	Dominant FG	Categoric	Shrub	Censored	-0.084	-0.1668	-0.0027
SR	Dominant FG	Categoric	Reference	Linear	2.0229	1.8557	2.1872
SR	Dominant FG	Categoric	Graminoid	Linear	-0.1012	-0.2008	-0.0058
SR	Dominant FG	Categoric	None	Linear	0.0679	-0.0338	0.1705
SR	Dominant FG	Categoric	Shrub	Linear	-0.0321	-0.1276	0.0669
FEve change	Forb change	Continuous	NA	Linear	0.0023	0.0014	0.003
FRic change	Forb change	Continuous	NA	Linear	0.1046	0.0812	0.1277
SR change	Forb change	Continuous	NA	Linear	0.0348	0.027	0.0428
FEve	Forbs	Categoric	1st Order	Quadratic	0.0018	9.00E-04	0.0028
FEve	Forbs	Categoric	2nd Order	Quadratic	0	0	0
FRic	Forbs	Continuous	NA	Censored	0.0059	0.0048	0.0071
SR	Forbs	Continuous	NA	Linear	0.0049	0.0036	0.0063
FEve change	Gram. change	Continuous	NA	Linear	-8.00E-04	-0.0014	-2.00E-04
FRic change	Gram. change	Continuous	NA	Linear	-0.0233	-0.042	-0.0045
SR change	Gram. change	Continuous	NA	Linear	-0.0037	-0.0099	0.0025
FEve	Graminoids	Categoric	1st Order	Quadratic	6.00E-04	2.00E-04	0.001
FEve	Graminoids	Categoric	2nd Order	Quadratic	0	-1.00E-04	0
FRic	Graminoids	Continuous	NA	Censored	-0.0019	-0.0026	-0.0011
SR	Graminoids	Continuous	NA	Linear	-0.0018	-0.0027	-8.00E-04
FEve	LAT	Continuous	NA	Linear	0.0042	-2.00E-04	0.0086
FEve change	LAT	Continuous	NA	Linear	4.00E-04	0	8.00E-04
FRic	LAT	Continuous	NA	Censored	-0.0287	-0.053	-0.0041
FRic change	LAT	Continuous	NA	Linear	-0.0053	-0.0225	0.0114
SR	LAT	Continuous	NA	Linear	-0.0282	-0.0515	-0.0048
SR change	LAT	Continuous	NA	Linear	-0.0031	-0.0093	0.0026

FEve	MOISTURE	Categoric	Reference	Linear	0.5715	0.5316	0.6134
FEve	MOISTURE	Categoric	Moist	Linear	0.0071	-0.0377	0.0519
FEve	MOISTURE	Categoric	Wet	Linear	-0.0231	-0.0769	0.0316
FRic	MOISTURE	Categoric	Reference	Censored	2.7685	2.5909	2.9591
FRic	MOISTURE	Categoric	Moist	Censored	0.1251	-0.0364	0.2847
FRic	MOISTURE	Categoric	Wet	Censored	-0.0438	-0.2351	0.155
SR	MOISTURE	Categoric	Reference	Linear	1.9795	1.8044	2.1646
SR	MOISTURE	Categoric	Moist	Linear	0.1374	-0.0373	0.3083
SR	MOISTURE	Categoric	Wet	Linear	-0.1051	-0.3373	0.1141
FEve	PrecipAnn	Continuous	NA	Linear	0	-1.00E-04	0
FRic	PrecipAnn	Continuous	NA	Censored	3.00E-04	0	6.00E-04
SR	PrecipAnn	Continuous	NA	Linear	3.00E-04	0	6.00E-04
FEve	Region	Categoric	Reference	Linear	0.5243	0.4816	0.5678
FEve	Region	Categoric	GreenIceland	Linear	0.0416	-0.0099	0.0921
FEve	Region	Categoric	N. America-E	Linear	0.0972	0.0255	0.163
FEve	Region	Categoric	N. America-W	Linear	0.0996	0.0371	0.1583
FRic	Region	Categoric	Reference	Censored	2.7146	2.4399	2.9697
FRic	Region	Categoric	GreenIceland	Censored	0.218	-0.1072	0.5493
FRic	Region	Categoric	N. America-E	Censored	-0.0668	-0.4388	0.3668
FRic	Region	Categoric	N. America-W	Censored	0.0461	-0.3832	0.4677
SR	Region	Categoric	Reference	Linear	1.9717	1.7219	2.2244
SR	Region	Categoric	GreenIceland	Linear	0.1116	-0.1992	0.4191
SR	Region	Categoric	N. America-E	Linear	-0.1326	-0.4883	0.2406
SR	Region	Categoric	N. America-W	Linear	0.0306	-0.3781	0.4317
FEve	SR	Continuous	NA	Linear	-0.0029	-0.006	3.00E-04
FRic	SR	Categoric	1st Order	Quadratic	0.1521	0.1484	0.1557
FRic	SR	Categoric	2nd Order	Quadratic	-0.0052	-0.0057	-0.0047
FEve change	Shrub change	Continuous	NA	Linear	-4.00E-04	-9.00E-04	2.00E-04
FRic change	Shrub change	Continuous	NA	Linear	-0.0342	-0.0513	-0.0174
SR change	Shrub change	Continuous	NA	Linear	-0.0147	-0.0203	-0.009
FEve	Shrubs	Categoric	1st Order	Quadratic	-4.00E-04	-7.00E-04	0
FEve	Shrubs	Categoric	2nd Order	Quadratic	0	-1.00E-04	0
FRic	Shrubs	Continuous	NA	Censored	-8.00E-04	-0.0015	0
SR	Shrubs	Continuous	NA	Linear	-6.00E-04	-0.0015	4.00E-04
FEve	TempAvSum	Continuous	NA	Linear	-0.014	-0.0207	-0.0072
FEve change	TempAvSum	Continuous	NA	Linear	-5.00E-04	-0.0012	1.00E-04
FRic	TempAvSum	Continuous	NA	Censored	0.0549	0.017	0.0932
FRic change	TempAvSum	Continuous	NA	Linear	0.004	-0.0253	0.033
SR	TempAvSum	Continuous	NA	Linear	0.0631	0.0269	0.1001
SR change	TempAvSum	Continuous	NA	Linear	0.005	-0.0039	0.0144

Figure S3.1 Automated and manual trait error checking

"Duplicate records, both within and between the TTT and TRY datasets were checked for and removed. Histograms were also generated for all species-trait combinations to identify significant outliers and clusters of erroneous data points requiring removal. All trait values that fell outside two standard deviations of the mean trait value for that species-trait combination were removed automatically, whilst rare clusters of clearly incorrect values were filtered from the dataset. Leaf area values displayed numerous clusters of incorrect values due to the apparent inclusion of 'leaflet areas' as 'single leaf areas'. To rectify this issue, k-means clustering (n = 2) was run on all species-leaf area combinations. If the distance between the means of the two respective clusters was greater than 50% of the spread of all the data for that species-leaf area combination, the cluster of larger areas was deemed likely to be a 'leaflet area' and was thus precautionarily removed. The combined dataset also contained both vegetative and reproductive plant height records so additional checks were run to ensure the most suitable height records were being retained. For each species, if the number of vegetative records was four or greater, only vegetative records were retained. If it was less than four, but there was four or more reproductive records, reproductive records were considered a more accurate representation and retained. If there were less than four records for both height types, all height records were removed for that species due to low confidence in the remaining values."

Figure S3.1 | Automated and manual trait error checking. A detailed description of the automated and manual error checking carried out on the combined tundra trait team (TTT; Bjorkman et al., 2018) and TRY (Kattge et al., 2020) trait dataset, as outlined in **Section 3.2.3** and **Section 2.2.4**.

Figure S3.2 Functional richness and evenness simulation plots

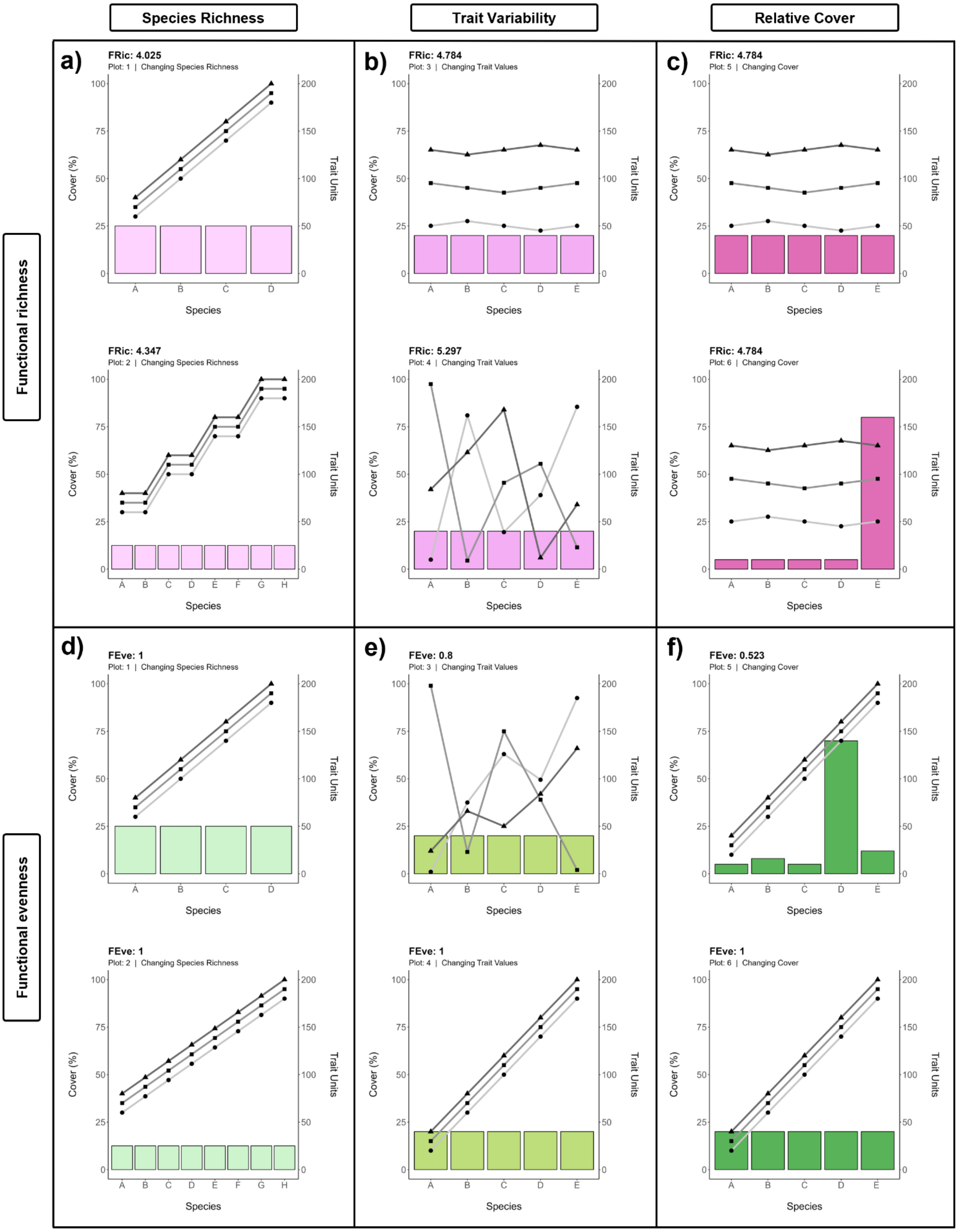


Figure S3.2 | Synthetic functional richness and evenness simulation plots. Simplified, synthetic plots were created to illustrate how changes in three key variables – (**a,d**) species richness; (**b,e**) trait variability; and (**c,f**) relative cover – impacted calculations of functional richness (FRic) and functional evenness (FEve) using the dbFD function (Laliberté et al., (2023); **Section 3.2.5**). To test each variable, six synthetic plots were created, each plot containing a number of simulated species (i.e. species A, species B…) with each species assigned hypothetical values for three simulated traits (i.e. trait 1, trait 2, …). These six plots were separated into three pairs, the first pair testing the impact of changing species richness on the designated metric, the second interspecific trait differences and the third relative cover. The two variables not being tested within a plot-pair were controlled to isolate the influence of the intended test variable. Functional richness and functional evenness were calculated in the synthetic plots using the same methods used to calculate the metrics in the full dataset, as described in **Section 3.2.5**. When calculated in simplified synthetic plots, we found that both greater species richness and greater input trait variability resulted in higher functional richness, whilst changes in species' relative cover had no effect (**a,b,c**). Contrastingly, we found that greater input trait variability and greater variability in species' relative cover resulted in lower functional evenness, whilst changing species richness had no effect (**d,e,f**).

Figure S3.3 Species richness vs functional evenness

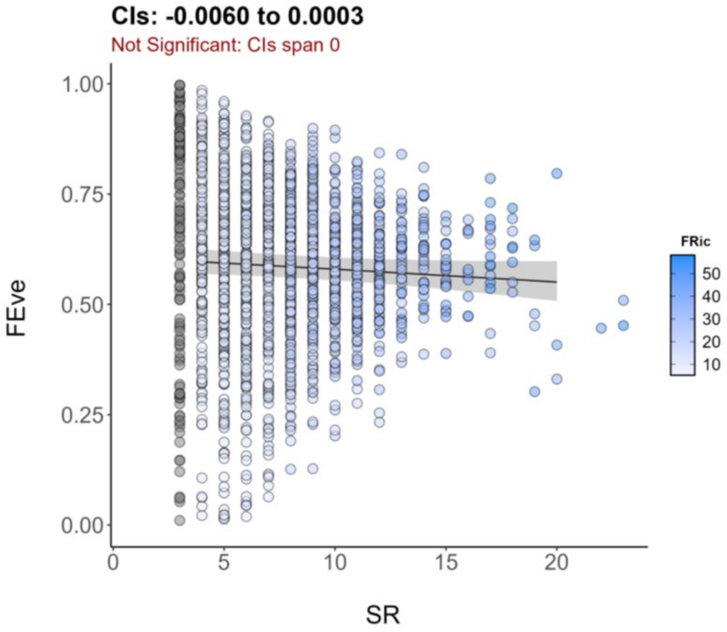


Figure S3.3 | Spatial patterns in functional evenness do not follow species richness across the tundra. Functional evenness (FEve) was not significantly correlated with species richness (SR) across our spatial plot network (n = 1,950). The detailed 95% confidence interval (CI) refers to the slope estimate of the first order model term. The line and ribbon are drawn from the model outputs in **Table S3.2**.

Figure S3.4 Region vs functional richness, evenness and species richness

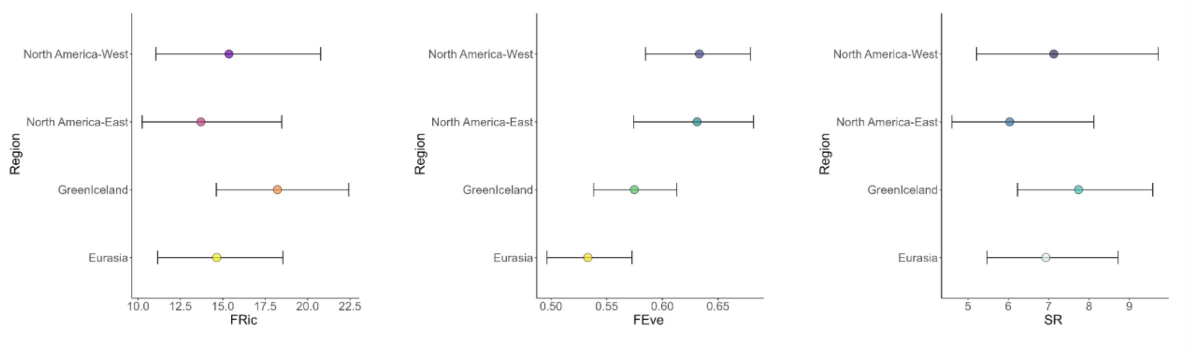


Figure S3.4 | Little difference in the assessed metrics across regions. With the exception of functional evenness, which was found to be significantly higher in both North American regions than in Eurasia, none of the assessed metrics differed significantly between biogeographic regions with all other 95% CIs spanning zero (as per the outputs in **Table S3.2**).

Figure S3.5 Precipitation vs functional richness, evenness and species richness

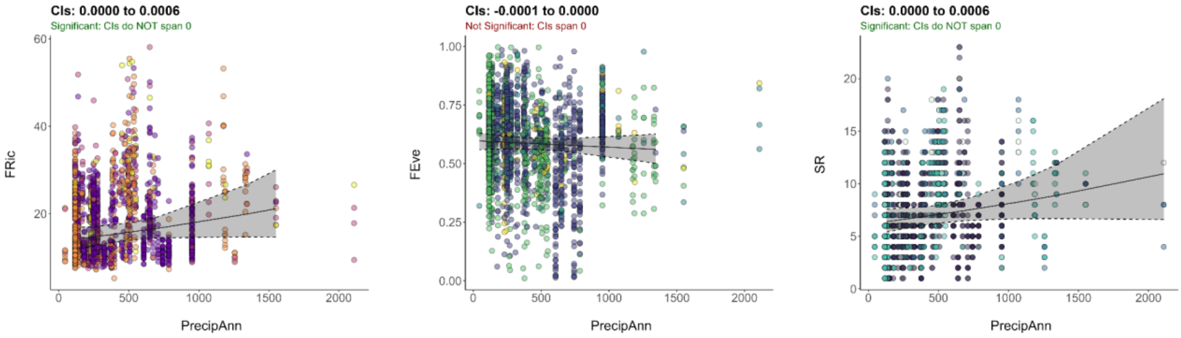


Figure S3.5 | Functional and species richness but not functional evenness increased with precipitation. Both functional richness (n = 1,822) and species richness (n = 2,087) exhibited moderate increases with annual precipitation across the spatial plot network. Functional evenness (n = 1,950) exhibited no notable change with change in precipitation. The line, ribbon and 95% confidence intervals (CIs) are drawn from the model outputs in **Table S3.2**.

Figure S3.6 Soil moisture vs functional richness, evenness and species richness

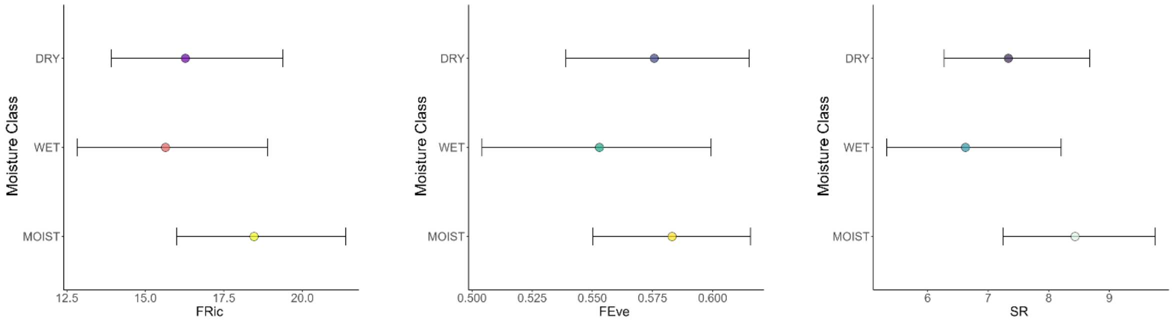


Figure S3.6 | None of the assessed metrics differed across soil moisture classes. None of the assessed metrics displayed any significant differences between the three soil moisture categorisations, with all 95% CIs spanning zero (as per the outputs in **Table S3.2**).

Figure S3.7 Dominant functional group vs functional richness, evenness and species richness

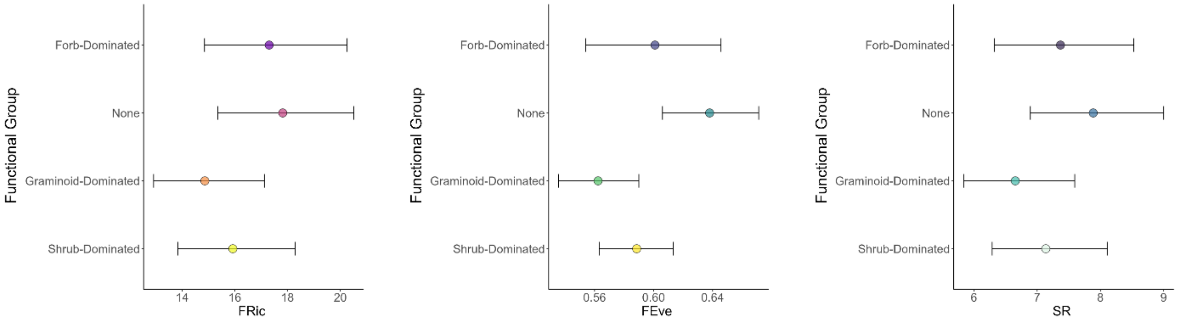


Figure S3.7 | Plots dominated by forbs displayed higher functional and species richness than those dominated by shrubs and graminoids. Functional and species richness were higher in plots dominated by forb species than those dominated by shrubs and graminoids, although such patterns were not found in functional evenness where 95% CIs spanned zero (reference level: *forbs*; as per the model outputs in **Table S3.2**).

Figure S3.8 Change in cover of forbs, shrubs and graminoids across time

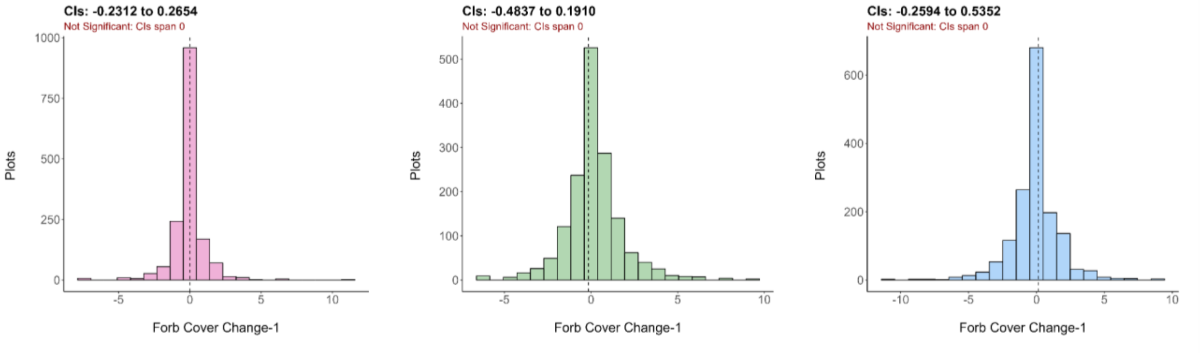


Figure S3.8 | No significant change in the cover of forbs, shrubs or graminoids over time. We found no net directional change in within-plot forb, shrub or graminoid cover across the assessed time period in plots surveyed at least twice over a period of at least five years (n = 1,777; as per the methods outlined in **Section 3.2.6.2**). Change in all three indices was calculated as the slope of functional richness per year per plot with 95% confidence intervals (CIs) drawn from the model outputs in **Table S3.2**.

Figure S3.9 Latitude vs change in functional richness, evenness and species richness

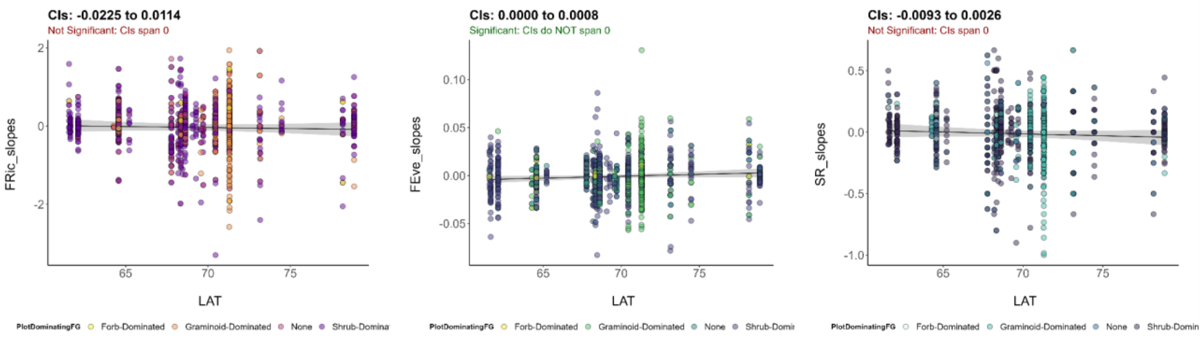


Figure S3.9 | Functional evenness increased marginally more in the higher latitudes. With the exception of functional evenness (FEve), which exhibited a marginally greater increase at higher latitudes, the assessed metrics displayed no difference in annual rates of change across latitudes. The line, ribbon and 95% confidence intervals (CIs) are drawn from the model outputs in **Table S3.2**.

Figure S3.10 Mean summer temperature vs change in functional richness, evenness and species richness

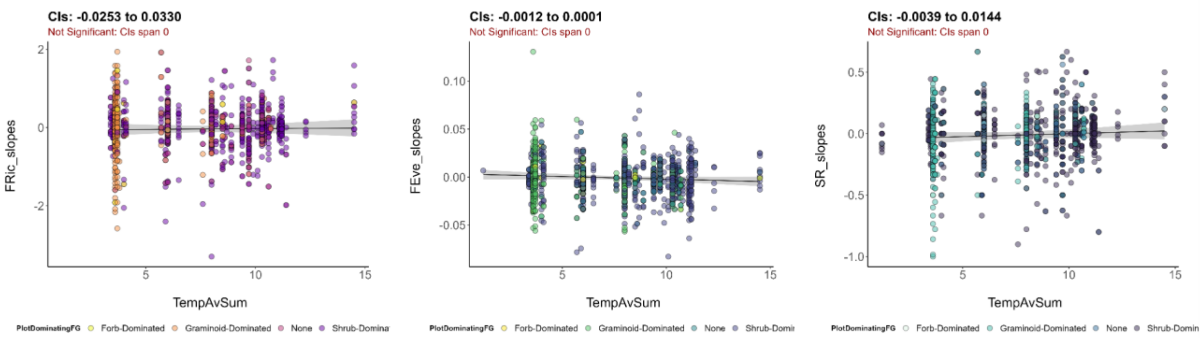


Figure S3.10 | Assessed metrics exhibited no difference in change across temperature gradients. None of the assessed metrics exhibited any significant difference in rates of annual change across gradients in temperature. The line, ribbon and 95% confidence intervals (CIs) are drawn from the model outputs in **Table S3.2**.

Figure S3.11 Principal Component Analysis by Functional Group

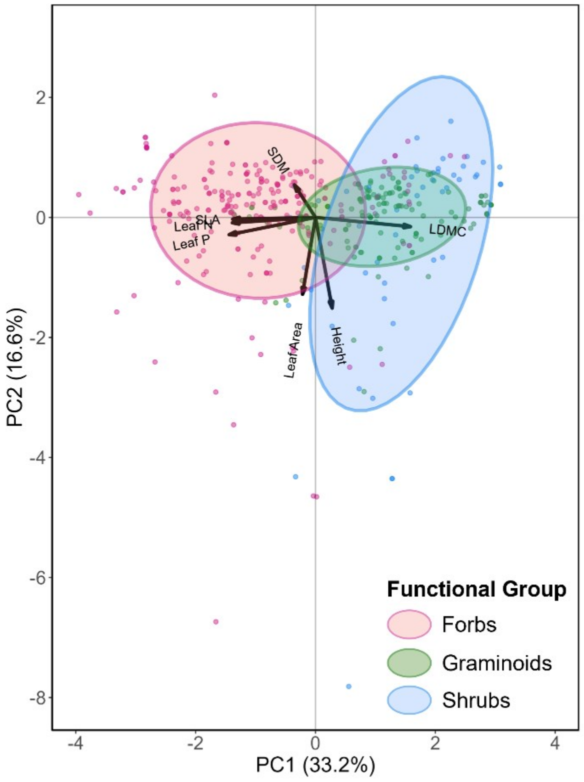


Figure S3.11 | Forb species typically exhibit distinct trait values from those of graminoid and shrub species. When assessed using a principal component analysis (PCA), using the average gap-filled trait values per species, forb species tended to exhibit largely distinct trait distributions from graminoid and shrub species, which exhibited large overlap. Trait distributions for forb species were predominantly determined by traits related to the leaf economic spectrum, whilst graminoid and shrub species were largely determined by structural plant traits

6.3 Supplementary Materials [Chapter 4] - **Hyperspectral Diversity**

Figure S4.1 Results with top-hits only

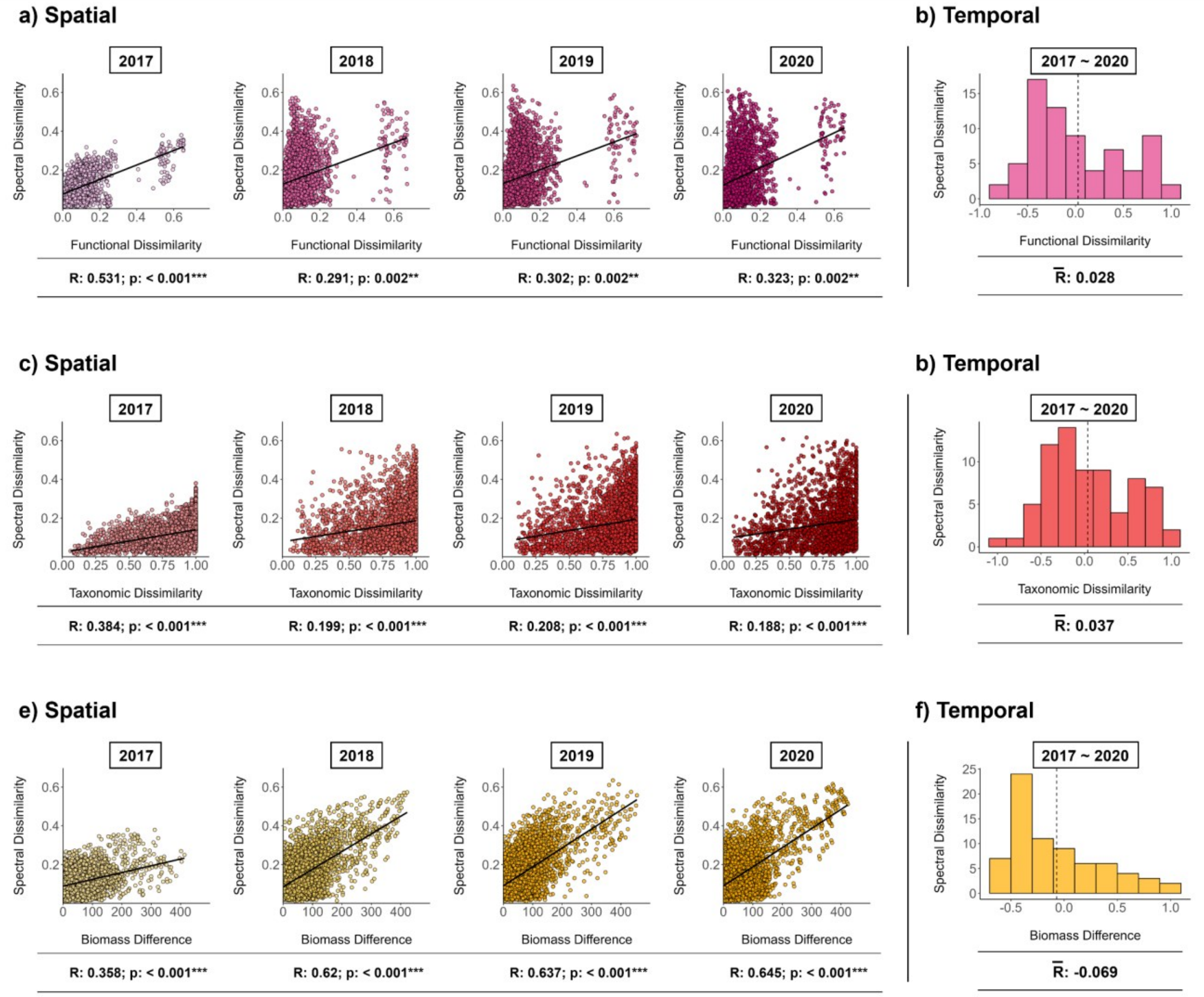


Figure S4.1 | Main spatial findings are robust to the exclusion of sub-canopy vegetation although temporal results remain uncertain. Functional, taxonomic and biomass dissimilarity versus spectral dissimilarity, and associated Mantel statistics with only top point-frame hits included. In the full dataset, 36% of the understorey vegetation records (removed here) were vascular plant species.

Figure S4.2 Gap-filled trait data

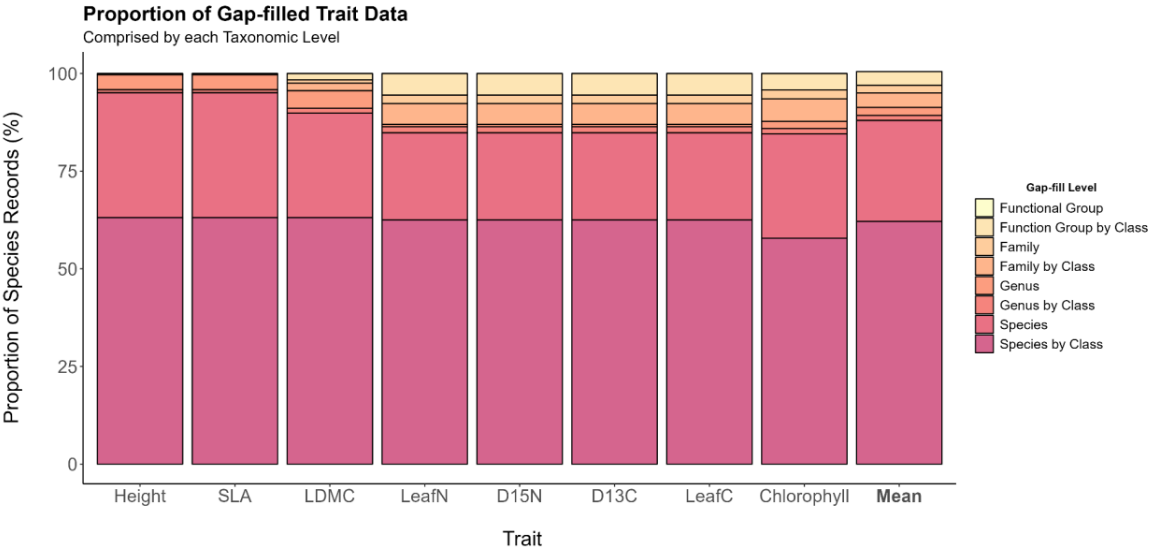


Figure S4.2 | The proportion of species trait values derived from the different stages of hierarchical gap-filling. Traits include: plant height (cm), leaf dry matter content (LDMC; mg g-1), specific leaf area (SLA; cm2 g-1), leaf nitrogen (LeafN; %), nitrogen isotopic composition δ15N (‰), carbon isotopic composition δ13C (‰), leaf carbon (LeafP; %) and leaf chlorophyll (μmol m2).

Figure S4.3 Buffer plots

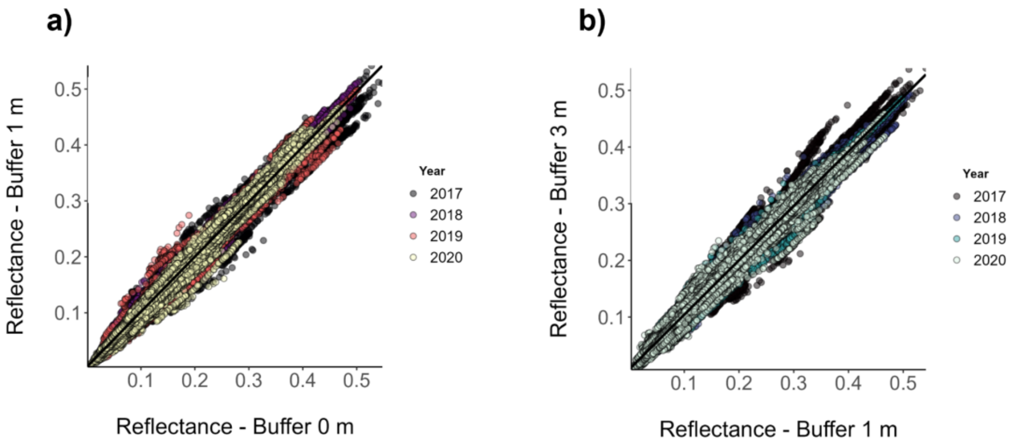
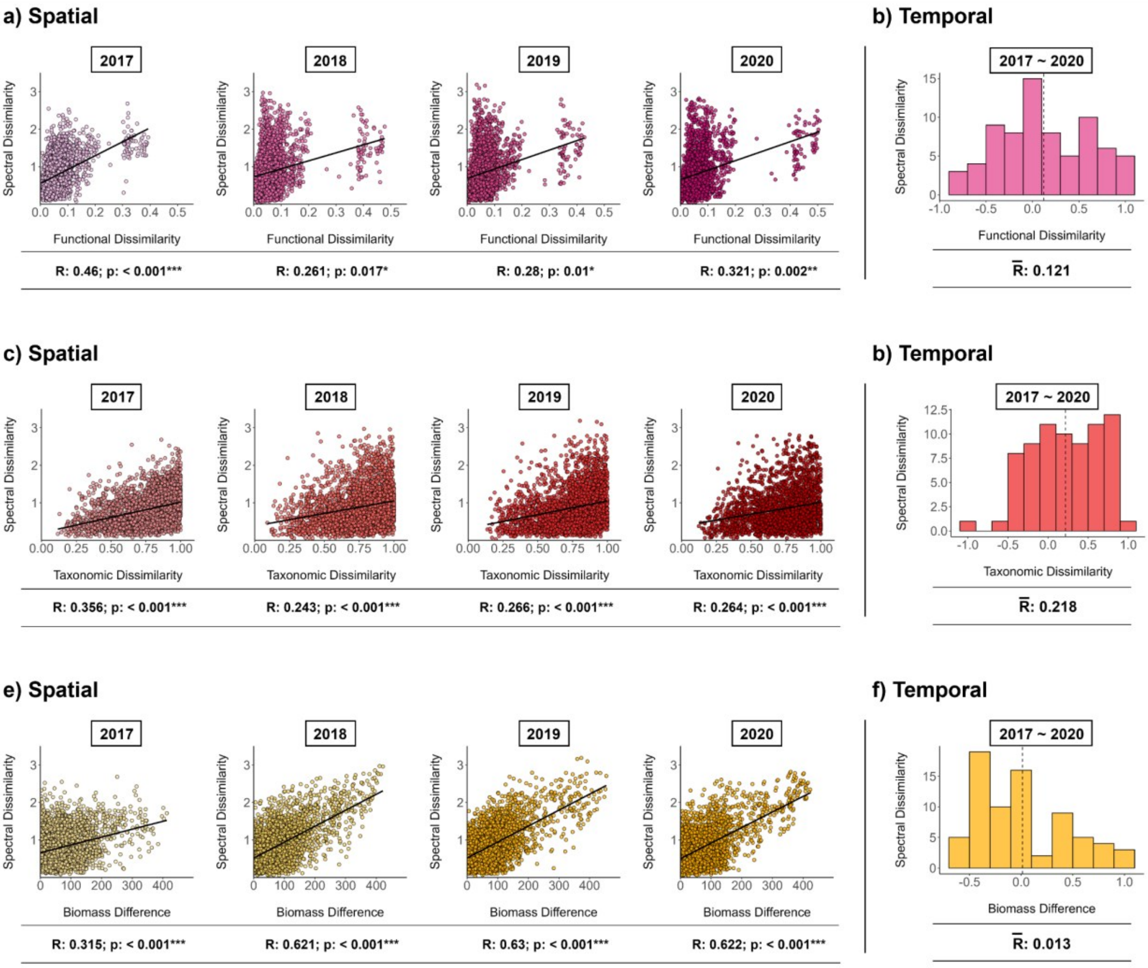
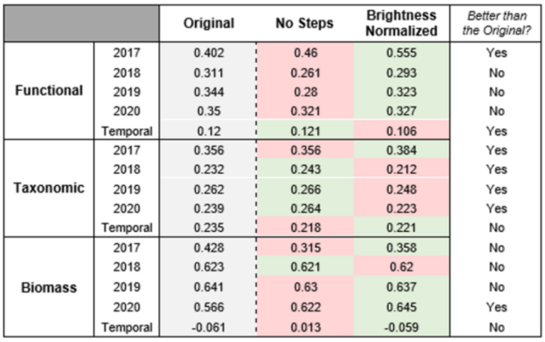


Figure S4.3 | Buffer plots. We used a 1 m buffer around each plot to account for geolocation uncertainty. However, pairwise spectral distances among plots were very similar for buffer sizes ranging from: (a) 0 m to (b) 3 m (b). R^2 values for the assessed relationships for each year of data collection were: 0 – 1 m (0.982 ~ 0.988), 1 – 3 m (0.978 ~ 0.984).

Figure S4.4 Non-brightness normalised spectra





		Original	No Steps	Brightness Normalized	*Better than the Original?*
Functional	2017	0.402	0.46	0.555	Yes
	2018	0.311	0.261	0.293	No
	2019	0.344	0.28	0.323	No
	2020	0.35	0.321	0.327	No
	Temporal	0.12	0.121	0.106	Yes
Taxonomic	2017	0.356	0.356	0.384	Yes
	2018	0.232	0.243	0.212	Yes
	2019	0.262	0.266	0.248	Yes
	2020	0.239	0.264	0.223	Yes
	Temporal	0.235	0.218	0.221	No
Biomass	2017	0.428	0.315	0.358	No
	2018	0.623	0.621	0.62	No
	2019	0.641	0.63	0.637	No
	2020	0.566	0.622	0.645	Yes
	Temporal	-0.061	0.013	-0.059	No

Figure S4.4 | Main spatial and temporal findings are robust whether brightness normalization is (manuscript; Figures 3-4) or is not (here) carried out. Functional, taxonomic and biomass dissimilarity versus spectral dissimilarity, and associated Mantel statistics with only top point-frame hits included. Comparisons of the mantel statistics between the non-brightness normalized and brightness normalized results can be found in the table and highlight the negligible differences between the two approaches.

Figure S4.5 Example smoothed spectra

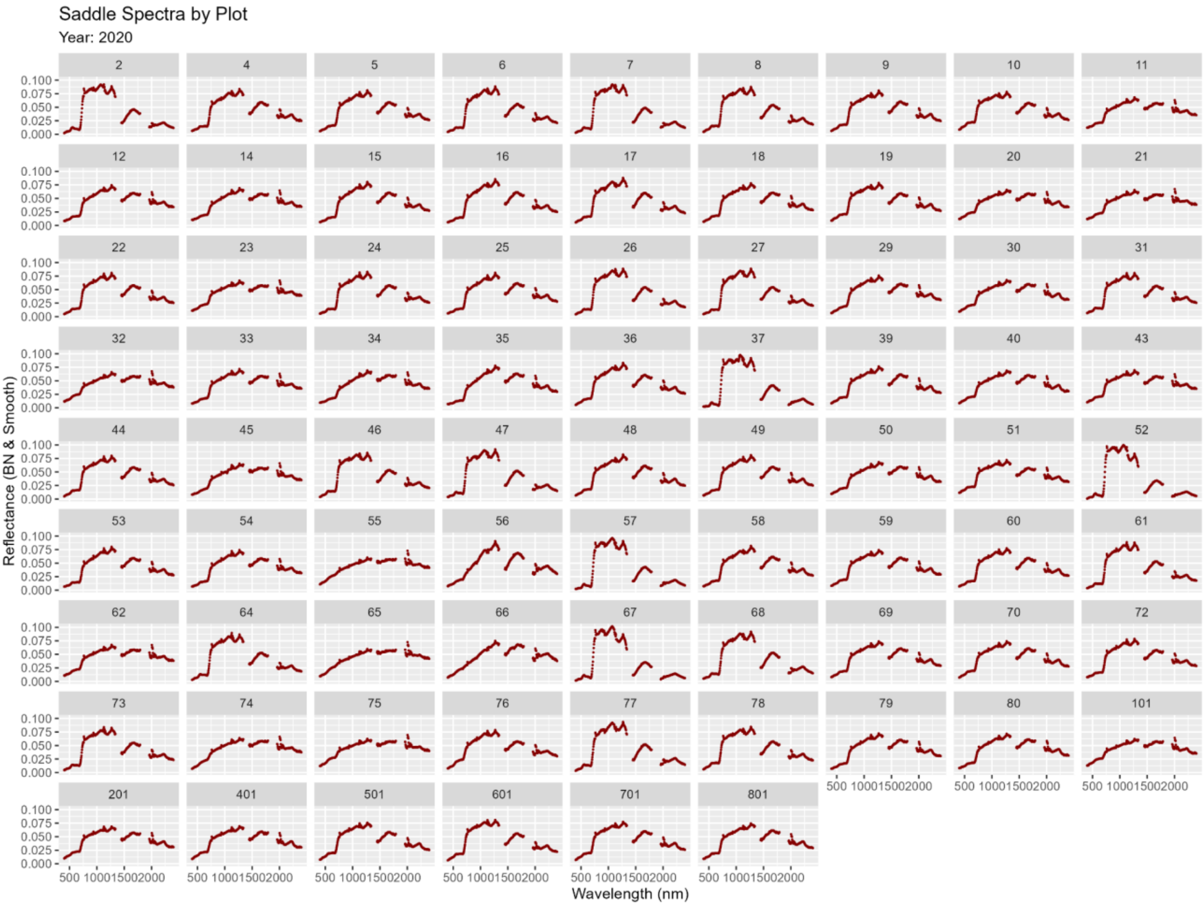


Figure S4.5 | Smoothed spectra. Example spectra for a single year (2020), extracted from the NEON hyperspectral tiles and subsequently scaled and brightness normalised before removing atmospheric water absorption bands and bands at the extremes.

Figure S4.6 Spectral distance metrics

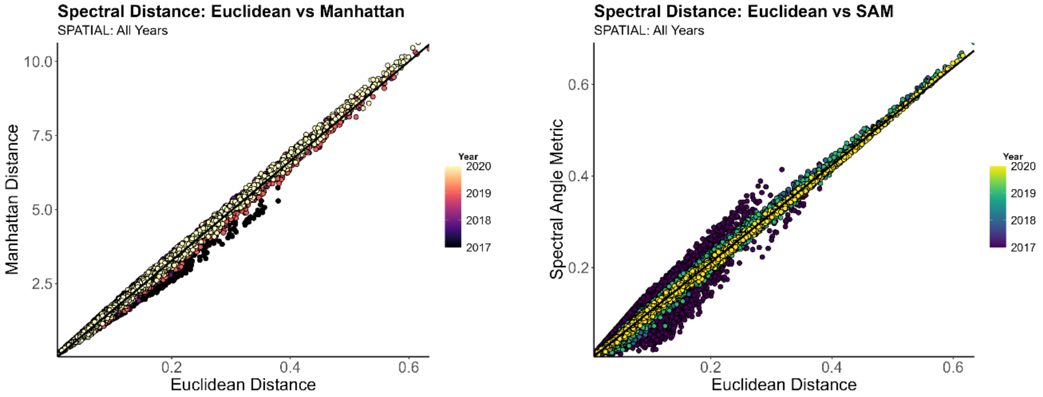
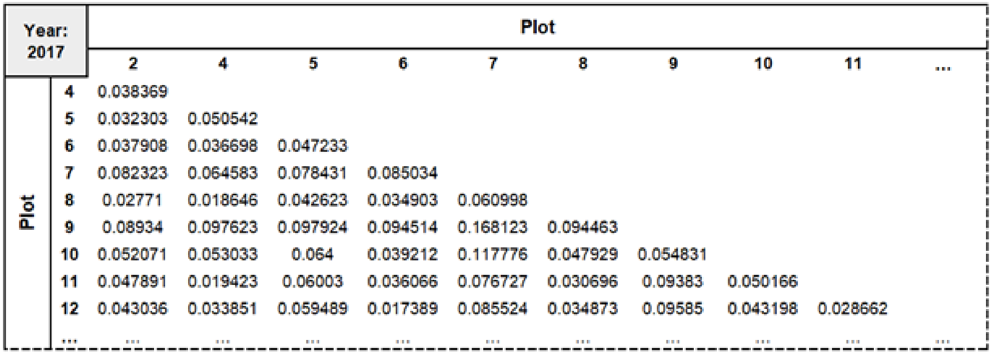


Figure S4.6 | Spectral distance metrics. We used Euclidean distance to quantify spectral dissimilarity among plots. However, pairwise spectral distances among plots were generally similar using Euclidean distance versus (a) Manhattan distance, or (b) the Spectral Angle Metric (SAM).

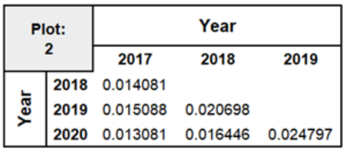
Figure S4.7 Example spatial matrix



Year: 2017		**Plot**									
		2	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**...**
Plot	**4**	0.038369									
	5	0.032303	0.050542								
	6	0.037908	0.036698	0.047233							
	7	0.082323	0.064583	0.078431	0.085034						
	8	0.02771	0.018646	0.042623	0.034903	0.060998					
	9	0.08934	0.097623	0.097924	0.094514	0.168123	0.094463				
	10	0.052071	0.053033	0.064	0.039212	0.117776	0.047929	0.054831			
	11	0.047891	0.019423	0.06003	0.036066	0.076727	0.030696	0.09383	0.050166		
	12	0.043036	0.033851	0.059489	0.017389	0.085524	0.034873	0.09585	0.043198	0.028662	
	...	...	...	...	...	...	...	...	...	...	...

Figure S4.7 | Spatial matrix. Example 'spatial' Euclidean distance matrix where plot pairs are compared within a single individual year.

Figure S4.8 Example temporal matrix



Plot: 2		**Year**		
		2017	**2018**	**2019**
Year	**2018**	0.014081		
	2019	0.015088	0.020698	
	2020	0.013081	0.016446	0.024797

Figure S4.8 | Temporal matrix. Example 'temporal' Euclidean distance matrix where individual plots are compared between year pairs.

Figure S4.9 Results without ‘Plot 37’

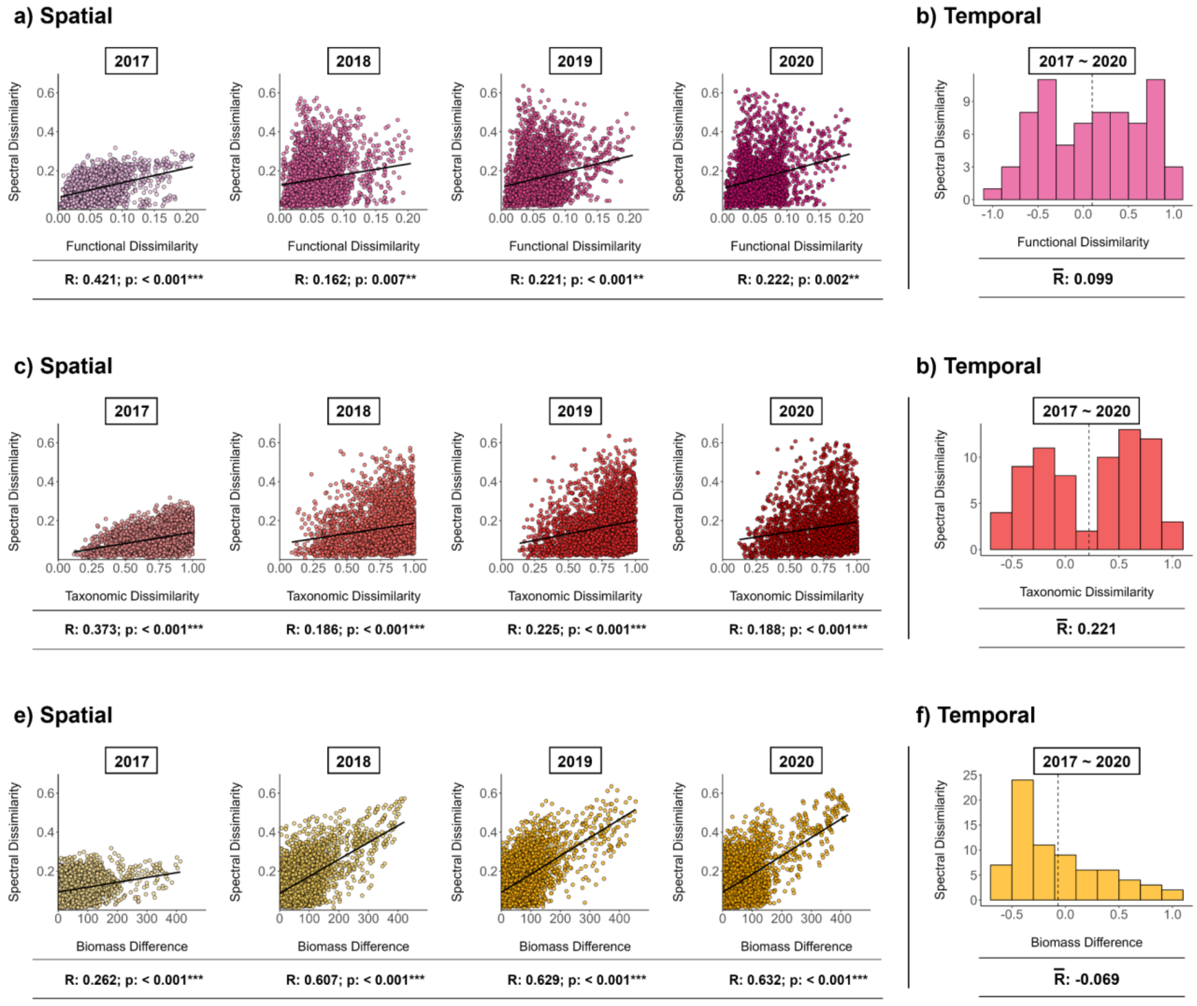


Figure S4.9 | Main findings are robust to the exclusion of the single shrub-dominated plot. Functional, taxonomic and biomass dissimilarity versus spectral dissimilarity, and associated Mantel statistics with plot 37 (a shrub-dominated plot) removed from the analyses.

Figure S4.10 Spectral distances between years

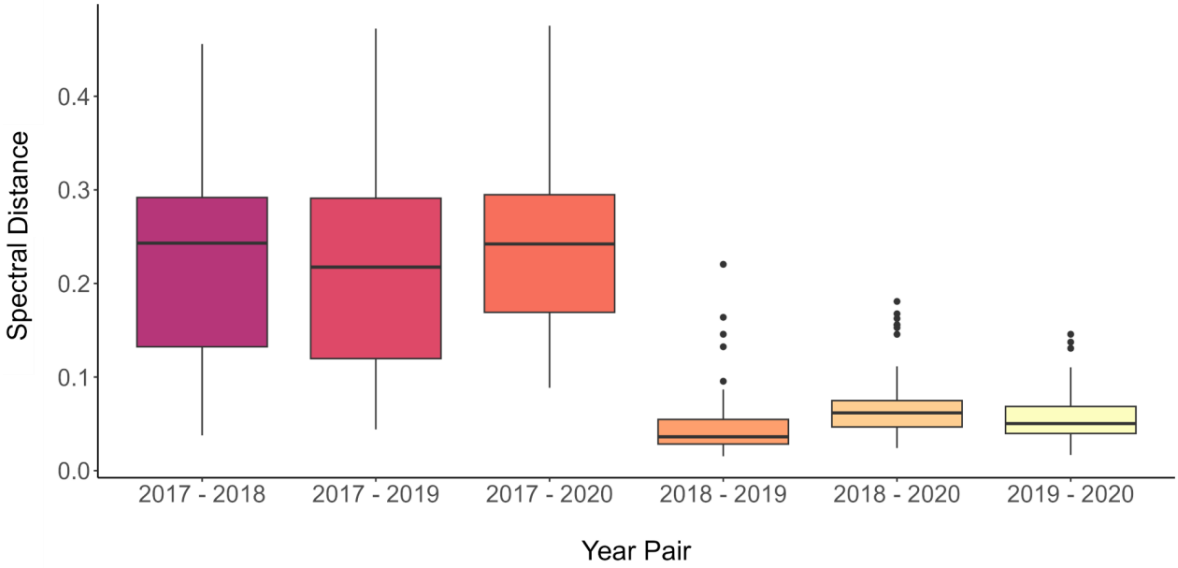


Figure S4.10 | Pairwise spectral dissimilarities were greatest between 2017 and any other year, compared to all other year-pair combinations. Interannual spectral differences were largest when 2017, the year in which hyperspectral measurements were made furthest from the period of peak greenness, was included within the year pair.