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Plant traits as predictors of ecosystem change and function in a warming tundra biome

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The University of Edinburgh
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Declaration

I declare that this thesis has been composed by myself and that the work has not been submitted for any other degree or professional qualification. I confirm that the work submitted is my own, except where work which has formed part of jointly-authored publications has been included. My contribution and those of the other authors to this work have been explicitly indicated below. I confirm that appropriate credit has been given within this thesis where reference has been made to the work of others.

The following work has been previously published or submitted for publication:

Chapter 2
A part of the work presented in Chapter 2 has been submitted for publication in *New Phytologist* as *Plant trait variation and change across the tundra biome* by Myers-Smith, I.H. (supervisor), Thomas, H.J.D., and Bjorkman, A.D. (supervisor).

**Author contributions:** All authors contributed equally to the writing of this manuscript.

Chapter 3
The work presented in Chapter 3 has been previously submitted for publication in *Science* as *Global plant trait relationships extend to the climatic extremes of the tundra biome* by Thomas, H.J.D, Bjorkman, A.D. (supervisor), Myers-Smith, I.H. (supervisor), Elmendorf, S.E., and 101 additional authors.

**Author contributions:** HT, IMS and AB conceived the study. HT performed statistical analysis with additional input from AB and IMS. HT wrote the manuscript with input from IMS, AB and contributions from all authors. AB compiled the TTT database with assistance from IMS and HT. IMS, SE and AB led the sTundra working group.
Chapter 4

The work presented in Chapter 4 has been accepted for publication in *Global Ecology and Biogeography* as *Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome* by Thomas, H.J.D., Myers-Smith, I.H. (supervisor), Bjorkman, A.D. (supervisor), Elmendorf, S.E., and 85 additional authors.

**Author contributions:** HT and IMS conceived the study. HT performed statistical analysis with additional input from IMS and AB. HT wrote the manuscript with input from IMS and AB and contributions from all authors. AB compiled the TTT database with assistance from IMS and HT. IMS, SE and AB led the sTundra working group.

Any additional author contributions are acknowledged in the relevant chapters or appendices.
Abstract

The tundra is currently warming twice as rapidly as the rest of planet Earth, which is thought to be leading to widespread vegetation change. Understanding the drivers, patterns, and impacts of vegetation change will be critical to predicting the future state of tundra ecosystems and estimating potential feedbacks to the global climate system. In this thesis, I used plant traits – the characteristics of individuals and species – to investigate the fundamental structure of tundra plant communities and to link vegetation change to decomposition across the tundra biome.

Plant traits are increasingly used to predict how communities will respond to environmental change. However, existing global trait relationships have largely been formulated using data from tropical and temperature environments. It is thus unknown whether these trait relationships extend to the cold extremes of the tundra biome. Furthermore, it is unclear whether approaches that simplify trait variation, such as the categorization of species into functional groups, capture variation across multiple traits. Using the Tundra Trait Team database – the largest tundra trait database ever compiled – I found that tundra plants revealed remarkable consistency in the range of resource acquisition traits, but not size traits, compared to global trait distributions, and that global trait relationships were maintained in the tundra biome. However, trait variation was largely expressed at the level of individual species, and thus the use of functional groups to describe trait variation may obscure important patterns and mechanisms of vegetation change.

Secondly, plant traits are related to several key ecosystem functions, and thus offer an approach to predicting the impacts of vegetation change. Notably, understanding the links between vegetation change and decomposition is a critical research priority as high latitude ecosystems contain more than 50% of global soil carbon, and have historically formed a long-term carbon sink due to low decomposition rates and frozen soils. However, it is unclear to what extent vegetation change, and thus changes to the quality and quantity of litter inputs, drives decomposition compared to environmental controls. I used two common substrates (tea), buried at 248 sites, to quantify the relative importance of temperature, moisture and litter quality on litter decomposition across the tundra biome. I found strong linear relationships between decomposition, soil temperature and soil moisture, but found that litter quality had the
greatest effect on decomposition, outweighing the effects of environment across the tundra biome.

Finally, I investigated whether tundra plant communities are undergoing directional shifts in litter quality as a result of climate warming. Given the importance of litter quality for decomposition, a shift towards more or less decomposable plant litter could act as a feedback to climate change by altering decomposition rates and litter carbon storage. I combined a litter decomposition experiment with tundra plant trait data and three decades of biome-wide vegetation monitoring to quantify change in community decomposability over space, over time and with warming. I found that community decomposability increased with temperature and soil moisture over biogeographic gradients. However, I found no significant change in decomposability over time, primarily due to low species turnover, which drives the majority of trait differences among sites.

Together, my thesis findings indicate that the incorporation of plant trait data into ecological analyses can improve our understanding of tundra vegetation change. Firstly, trait-based approaches capture variation in plant responses to environmental change, and enable prediction of vegetation change and ecosystem function at large scales and under future growing conditions. Secondly, my findings offer insight into the potential direction, rate and magnitude of vegetation change, indicating that despite rapid shifts in some traits, the majority of community-level trait change will be dependent upon the slower processes of migration and species turnover. Finally, my findings demonstrate that the impact of warming on both tundra vegetation change and ecosystem processes will be strongly mediated by soil moisture and trait differences among vegetation communities.

Overall, my thesis demonstrates that the use of plant traits can improve climate change predictions for the tundra biome, and informs the fundamental rules that determine plant community structure and change at the global scale.
Lay Summary

Climate change will transform plant communities across the planet. Perhaps nowhere is this more true than in the tundra biome - the cold Arctic and alpine regions beyond the treeline - where temperatures are increasing at twice the global average. As the tundra warms, the characteristics of tundra plants are changing, in turn altering key processes such as carbon storage that could have knock-on impacts for the Earth’s climate.

One way to understand how plant communities are changing is to look at the characteristics of individual plant species: their height, leaf size, stem thickness etc. These characteristics, known as ‘plant traits’, provide a wealth of information about how a plant might respond to change, and how it might affect the surrounding environment. For example, a tall, woody shrub may be able to outcompete neighbouring species for light and nutrients, capturing carbon in leaves and stems. Woody shrubs also decompose slowly, locking up this carbon in the soil.

Plant traits are strongly linked to climate, helping us to predict how climate change might alter plant communities. For example, plants tend to be taller in warmer and wetter regions of the tundra, and so plants may grow taller as the climate warms. However, plants are limited by trade-offs in how they access and allocate resources, and by different strategies of growth and survival. These trade-offs can be captured by measuring plant traits. It appears that trade-offs among plant traits are similar across the planet and break down into two key strategies: plant size (large versus small) and resource economics (living fast and dying young versus growing old and being conservative). These trade-offs allow us to understand how plant communities might respond to warming, but have yet to be tested in the tundra.

In the first part of this thesis, I tested fundamental patterns of trait variation across the tundra biome. I found that plants in the tundra have different characteristics to the rest of the planet – but only in terms of their smaller size. In terms of accessing resources, tundra plants are surprisingly similar to those in warmer regions, and have developed a wide range of economic strategies to cope with extreme climatic conditions. I also found that the greatest differences in plant traits occur among species (e.g. between a poppy or a birch shrub), and surprisingly not among functional groups (e.g. between a herb or a shrub) or within species (e.g. between a
tall or a small birch shrub). These findings strongly suggest that fundamental rules that underpin differences between plant species are generalizable across the broad spectrum of life on Earth.

In the second part of this thesis I examined whether tundra vegetation change will alter decomposition – the breakdown of organic matter in the soil. Decomposition is typically very slow in the tundra due to frozen soils and low temperatures, while leaf litter inputs are themselves relatively tough to break down. As a result, high latitude regions have locked up large amounts of carbon over millennia, and contain twice as much carbon as the Earth’s atmosphere. As the tundra warms and plant communities change, decomposition may increase, releasing this carbon to the atmosphere. However, it is not known whether decomposition rates will be more influenced by the direct impact of warming, or by the indirect impact of changing plant litter inputs.

I buried approximately 5,000 samples of two types of tea bags, representing rapidly and slowly decomposing leaf litter, at 250 sites across the tundra biome. Using this dataset, I examined the effect of environment versus tea type on decomposition. I found a strong linear relationship between temperature and decomposition, indicating that warming will increase decomposition in the tundra biome. However, I also found that differences between the two tea types had a seven-times larger effect on decomposition than temperature alone, indicating that vegetation change could have a profound impact on decomposition and carbon storage in the tundra biome.

In the final part of this thesis I examined whether vegetation change has altered how easily plant communities decompose. The rate at which plant litter breaks down can be predicted using plant traits. Based on this information, I modelled the ‘decomposability’ of plant communities across the tundra biome, and how this has changed over the last 30 years. I found that plant communities in warmer areas were more decomposable than those in colder areas. However, on average plant community decomposability has remained stable over the past 30 years, despite significant vegetation change. This finding suggests that, at least in the short term, changes to decomposition in the tundra biome will primarily be driven directly by warming, rather than by changes to the decomposability of plant communities.

Together, this thesis demonstrates that plant traits can be used to predict how climate change will transform plant communities and key functions such as carbon storage in the tundra biome, with consequences for global climate and entire planet.
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1. Introduction

1.1. Overview

The tundra is experiencing some of the most rapid rates of ecological change of any biome on the planet. Annual mean temperatures have increased by 2.06°C since 1978, approximately twice the global average rate (Callaghan et al., 2011; IPCC, 2013). Warming has been accompanied by increases in growing season length (Park et al., 2016), thawing of permafrost (Schuur et al., 2009), and melting of sea ice (Hinzman et al., 2013). Environmental change is thought to be driving widespread vegetation changes across the tundra biome (IPCC, 2014), including increased productivity (Beck and Goetz, 2011; Guay et al., 2014), shifts in the abundance (Elmendorf et al., 2012) and distribution (Steinbauer et al., 2018) of species, and changes to the traits of individuals (Hudson et al., 2011) and communities (Bjorkman et al., Nature in revision). Understanding and predicting vegetation change in the tundra, and resulting feedbacks to ecosystem function, is thus a pressing research need and forms the central focus of this thesis.

In this thesis, I use plant traits – the characteristics of individuals and species – to refine our understanding of vegetation change in the tundra biome, and to directly link vegetation change to ecosystem function. I focus on three primary questions that seek to establish quantitative links between warming, the changing characteristics of vegetation communities, and ecosystem function.

1) Can we use plant traits to refine our understanding of vegetation change in the tundra?

Predicting vegetation and trait change relies on understanding the existing constraints on trait expression in the tundra. To date, trait data has been largely unavailable for the tundra, and so it has not been possible to test trait variation in this biome. Furthermore, much of our existing understanding of tundra vegetation change is at the level of the functional group, such as an increase in shrubs (Myers-Smith et al., 2011a) or graminoids (Elmendorf et al., 2012). However, variation within functional groups could obscure key mechanisms of vegetation
change, particularly if assumptions regarding the nature of trait variation do not apply in the tundra biome.

2) **To what extent do plant traits affect key ecosystem functions?**
Vegetation change is likely to result in feedbacks to ecosystem function (Myers-Smith et al., 2011a; Pearson et al., 2013), including albedo (Chapin et al., 2005), productivity (Forkel et al., 2016), carbon storage (Mack et al., 2004) and decomposition (Cornwell et al., 2008). However, the relative importance of vegetation and trait change compared to warming and wider environmental change is unclear.

3) **Will trait change produce directional shifts in ecosystem function?**
Many hypothesised feedbacks between vegetation change and ecosystem function remain untested at tundra biome-wide scales (Sturm, 2005; Cornelissen et al., 2007). To do so requires experimental testing of the relationship between plant traits and key ecosystem functions, and quantification of trait change within tundra communities.

### 1.2. Structure of this thesis

In this thesis, I aim to enhance our understanding of the underlying structure and sources of trait variation in the tundra biome, and more widely to inform our understanding of trait variation at the global scale. Based on these plant trait relationships, I further aim to directly link tundra vegetation change to decomposition, a key ecosystem function that will determine the carbon balance of tundra ecosystems. Together, I offer an approach to using plant traits to predict functional change in tundra ecosystems undergoing rapid climate change.

The work presented in this thesis is divided into four key sections (Figure 1.7). The first (Chapter 2) provides a summary of the existing literature and research needs with regards to i) environmental and ecological change, ii) trait variation and change, and iii) decomposition in the tundra biome. The second (Chapters 3 & 4) examines trait variation within the tundra biome, and thus how plant traits inform an understanding of vegetation change. The third (Chapters 5 & 6) examines the potential implications of vegetation change on decomposition across the tundra biome. The final section
(Chapter 7) synthesises research results and draws out several key themes for discussion. All results chapters (Chapters 3-6) are written as stand-alone research papers and are either published, under review or prepared for submission at peer-reviewed journals. Due to the synthetic nature of the research presented, all chapters have involved substantial collaboration, with the contribution of all of authors summarised at the start of each chapter.

![Diagram](image)

**Figure 1.1** From traits to function: structure of this thesis. 1) Trait variation, comprising two result chapters (purple circles), 2) Decomposition change, comprising two results chapters (orange circles), and 3) Synthesis, comprising introduction and discussion chapters (blue circles). In addition, work undertaken as part of this PhD has contributed to two research projects that inform the trait change results presented in this thesis (white circles).

Finally, the work undertaken as part of this PhD has contributed to two substantial research efforts that inform the results of this thesis. ‘Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change’ summarises ecological changes at my focal field site on Qikiqtaruk-Herschel Island in
the Yukon Territory, Canada. ‘Changes in plant functional traits across a warming tundra biome’ synthesises trait change in the tundra across biogeographic gradients and over time. Abstracts to these two manuscripts are outlined in Chapter S1.

**Chapter 2: Background: Ecological change in the tundra**
In this chapter, I summarise the key literature underpinning this thesis in relation to three themes: 1) on-going environmental and ecological change, 2) trait variation and change, and 3) drivers of decomposition in the tundra.

**Chapter 3: Global plant trait relationships extend to the cold extremes of the tundra biome**
In this chapter, I test whether the relationships and variation among key plant traits observed at the global scale extend to the cold extremes of the tundra biome. The majority of variation in key plant traits is thought to be explained by two dimensions (Díaz et al., 2016), corresponding to strategies of plant size and resource acquisition. Trait variation is also assumed to primarily result from differences among species (Siefert et al., 2015), and to be independent of scale (Shipley et al., 2016). I test these assumptions in the tundra biome, where extreme cold conditions, large species’ ranges and previously low representation in global trait databases may challenge these foundational principles of trait-based ecology. Using the Tundra Trait Team database (Bjorkman et al., GEB in revision; Figure 1.2), I specifically test 1) constraints to tundra trait space within the global context, and whether such constraints alter trait relationships established at the global scale, 2) the contribution of within-species trait variation to total trait variation across the tundra, and 3) whether sources of trait variation vary with geographical scale.

**Chapter 4: Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome**
In this chapter, I test whether commonly used plant functional groups capture differences in trait variation among tundra species. Plant functional groups are widely used in community ecology and Earth system modelling to describe trait variation within and across plant communities, but rest on the assumption that functional groups explain a large proportion of trait variation among species (Harrison et al., 2010). I use the Tundra Trait Team database to 1) examine the variation in six widely collected tundra plant traits explained by four traditional functional groups, 2) to
explore whether the explanatory power of functional groups is dependent upon the traits used in analysis, and 3) compare the explanatory power and species composition of traditional functional groups to alternative classifications generated using post-hoc clustering of species-level traits.

Chapter 5: Litter quality outweighs environmental drivers of litter decomposition across the tundra biome
In this chapter, I quantify the effect and relative importance of temperature, moisture and litter quality on litter decomposition across the tundra biome. Anthropogenic warming is predicted to increase decomposition in the tundra (Crowther et al., 2016), but there is considerable uncertainty regarding the strength, direction and relative importance of drivers of decomposition (Sierra et al., 2015), in part arising from a lack of coordinated field studies (Bonan et al., 2013). Using two common substrates across 248 sites I test 1) the relationships between soil temperature, soil moisture and decomposition across the tundra biome, and 2) the relative importance of environmental drivers and litter quality on decomposition.

Chapter 6: Tundra vegetation change does not alter community litter decomposability
In this chapter, I quantify the decomposability of tundra plant communities based on their traits. Despite strong evidence that litter quality is a key driver of decomposition, the impact of vegetation change on litter decomposition in the tundra biome is unclear. I combine a multi-site litter decomposition experiment, the Tundra Trait Team database, and three decades of vegetation community monitoring to test 1) the relationships between the decomposability of tundra plant communities and temperature across biogeographic gradients, 2) the change in decomposability over 30 years of monitoring.

Chapter 7: Synthesis: Traits as predictors of ecosystem change and function
In this chapter, I synthesise the key findings of this thesis. I discuss three key themes arising from my results, 1) the use of plant traits as predictors of ecosystem function and change, across scales, under warming scenarios, and in novel environments, 2) the rates and mechanisms of trait change, and 3) the importance of indirect impacts of climate change, notably soil moisture and vegetation change. I conclude by outlining key future research directions arising from the findings of this thesis.
1.3. Research sites and data sources

The research contributing to thesis is collated from three main sources (Figure 1.2):

1) Data synthesis using existing global and biome-wide datasets
2) Collaboration with multiple researchers to create new, biome-wide datasets
3) Original data collection in the Canadian Arctic at two focal research sites

1.1.1 Existing Datasets

1.1.1.1 TRY
The TRY database is a global archive of over six million plant trait records, covering almost 150,000 plant taxa (Kattge et al., 2011). I used trait data for tundra species (Bjorkman et al., GEB in revision) to investigate trait variation and relationships in the tundra biome. I also used trait data for the six most commonly collected tundra plant traits (plant height, specific leaf area, leaf dry matter content, leaf area, leaf nitrogen, seed mass) for global species to compare trait variation in the tundra with global patterns.

1.1.1.2 ITEX (The International Tundra Experiment)
The International Tundra Experiment (ITEX) is a network of researchers conducting experimental warming and long-term ecological monitoring at sites across the tundra biome (Henry and Molau, 1997). I used long-term vegetation data from ambient ITEX and associated monitoring plots (Elmendorf et al., 2012) to examine changes in vegetation composition and abundance over space and over three decades of monitoring. The ITEX dataset includes long-term monitoring plots on Qikqtaruk-Herschel Island, to which I contributed two additional years of data.

1.1.1.3 Meeting of Litters
The Meeting of Litters experiment measured the decomposition of plant litter collected from 33 experiments across 18 tundra sites. It provides species-specific mass loss for a range of tundra vascular plant species (Cornelissen et al., 2007). I used two-year litter mass loss data from ambient experimental plots to characterise the decomposability of tundra species based on their leaf and stem traits.
1.1.4 Climate databases: CHESLA, WorldClim and CRU

I used three climate databases to link vegetation, trait and decomposition trends to climatic variables (temperature and precipitation). CHESLA (Climatologies at high resolution for the earth’s land surface areas; Karger et al., 2017) provides high resolution (0.01 degree) time series climate data from 1979-2013. WorldClim provides approximately 0.01 degree resolution climate data and long-term climate averages (1960-present; Hijmans et al., 2005). CRU (Climatic Research Unit) data provides 0.5 degree resolution climate time series data (Harris et al., 2014).
Chapter 1. Introduction

1.1.1.5 ESA Soil moisture

I used soil moisture data from the European Space Agency Climate Change Initiative (ESA CCI) dataset to link decomposition to soil moisture (Dorigo et al., 2017). This dataset provides 0.25 degree resolution combined satellite-measured soil temperature from 1978 to 2016.

1.1.2 NewDatasets

1.1.2.1 Tundra Trait Team (TTT)

The Tundra Trait Team (TTT) database contains 81,537 measurements of 18 plant traits collected at multiple sites across the tundra biome (Bjorkman et al., GEB in revision). Work undertaken as part of this thesis has contributed to creation and publication of the TTT dataset, including trait collection, data compilation and cleaning. All data are available in the following data paper:

Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand S, Thomas, H.J.D. et al, Tundra Trait Team: A database of plant traits spanning the tundra biome. GEB In revision. (Chapter S1)

1.1.2.2 Tundra Teabag Experiment

I established the ‘Tundra Teabag Experiment1’ to create a biome-wide dataset of decomposition in the tundra, following the Tea Bag Index (Keuskamp et al., 2013). The Tea Bag Index uses tea bags as a common substrate to provide a simple and standardised method of measuring decomposition across sites. The tundra teabag experiment dataset contains 4,680 individual decomposition samples, spanning 248 sites across 11 countries. Data will be made available upon publication, and are submitted to the global Tea Bag Index initiative.

1.1.2.3 Site specific climate data

I collated a dataset of climatic variables (air temperature, soil temperature, soil moisture) for all sites within the Tundra Teabag Experiment. Data were submitted directly by contributors or compiled from publicly available meteorological data for experimental sites.

1 tundratea.wordpress.com
1.1.3 Field data collection

I conducted field research at two focal research sites, Kluane Lake and Qikiqtaruk-Herschel Island, from 2015-2017. Research sites are located across a 1,000km latitudinal gradient in the Yukon Territory Canada (Figure 1.3), and incorporate both alpine and Arctic tundra.

![Figure 1.3 Location of Kluane Lake (top left) and Qikiqtaruk Herschel Island (top right) field sites.](image)

1.1.3.1 Kluane Lake

The Kluane Lake region is located in the southwest of the Yukon Territory, Canada (61.3° N, 138.8° W). This subarctic region experiences extreme seasonal temperature variations, with average winter temperatures reaching -20°C and summer averages of up to 16°C. Field sites are located in the surrounding alpine tundra from approximately 1,200 – 2,000 metres above sea level. There is evidence for expansion and upslope advance of tall shrubs in the region (Myers-Smith, 2007; Myers-Smith and Hik, 2018), as well as wider ecological impacts of glacial retreat (Shugar et al., 2017).
1.1.3.2 Qikiqtaruk-Herschel Island

Qikiqtaruk - Herschel Island is located on the Arctic Coast of the Yukon Territory (69.6°N, 138.9°W) at the northern extent of tall shrubs and in a zone of ice-rich permafrost. The wider western Arctic region is experiencing widespread shrub expansion (Tape et al., 2006; Myers-Smith et al., 2011b; Lantz et al., 2013; Moffat et al., 2016) and has undergone prominent greening according to different satellite records (Fraser et al. 2011, Guay et al. 2014, Ju and Masek 2016). The ecological monitoring program on Qikiqtaruk was established in 1999 and combines multi-parameter monitoring using international protocols with the collaborative efforts of territorial park rangers, Yukon government researchers, and academic scientists. Outputs of the monitoring programme, to which this thesis has contributed, indicate 1) advances in spring phenology, 2) a doubling of average plant canopy height per decade and 3) a doubling of shrub and graminoid abundance per decade (Myers-Smith et al., in revision; Chapter S1). The integrated ecological changes thus inform the patterns, drivers and impacts of vegetation change investigated by this thesis.


Chapter 1. Introduction


Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W.,
2. Background: Ecological change in the tundra biome

The tundra biome is experiencing some of the most rapid environmental change of any biome on Earth (Serreze and Barry, 2011; IPCC, 2014). Rapid climate warming is altering vegetation communities, which in turn may create critical feedbacks to the global climate system (Pearson et al., 2013). This chapter summarises the key literature surrounding on-going environmental and ecological change in the tundra, with a particular focus on 1) plant trait variation and change, and 2) decomposition in tundra ecosystems.

2.1 The tundra biome

The tundra biome encompasses the vegetated regions above treeline at high latitudes and high altitudes (Bliss et al., 1981, Figure 2.1). While a number of more specific definition exist, including division into Arctic and alpine tundra (Virtanen et al., 2016), this thesis adopts a broader definition of tundra throughout, in line with previous biome-wide assessments of tundra vegetation change (Walker et al., 2006; Elmendorf et al., 2012b, 2012a; Oberbauer et al., 2013; Elmendorf et al., 2015; Myers-Smith et al., 2015a; Prevéy et al., 2017; Bjorkman et al., Nature in revision).

Tundra plant communities are typically small in stature and slow growing (Callaghan and Emanuelsson, 1985; Molau, 1993). Recruitment and colonisation of new species is assumed to be low in the absence of disturbance (Gough, 2006; Lantz et al., 2010), with many species reproducing clonally (Douhovnikoff et al., 2010). Vascular plant diversity is also low compared to the majority of the world’s biomes and many species are widely-distributed across large geographical gradients and a variety of environments (Henry and Molau, 1997; Callaghan et al., 2004).

2.2 Environmental and ecological change in the tundra

The tundra is currently warming at approximately 0.07°C per year, with temperatures projected to increase by 2-9°C by the end of the century (IPCC, 2014). Warming trends are highly variable across geographical regions and over time (Cohen et al.,
2012), with the strongest warming occurring since the 1970s and during winter (Hinzman et al., 2005). Warming is associated with wider environmental changes, including a lengthening of the snow-free season by 9.1 days per decade (Chapin et al., 2005), declines in summer sea ice (Stroeve et al., 2007), and increased permafrost temperature (Romanovsky et al., 2010) and thaw depth (Lawrence and Slater, 2005). Many of these changes constitute positive feedbacks to climate change, contributing to an ‘Arctic amplification’ of warming (Serreze and Barry, 2011).

Figure 2.1 Map of the northern hemisphere tundra biome. Arctic and alpine tundra is represented by dark blue. Subarctic regions, which share similar plant communities and climatic characteristics with the tundra biome, are represented by light blue. Permanent ice is represented by grey. Map based on Kottek et al. (2006).

2.2.1 Vegetation change
Long term vegetation monitoring at sites across the tundra indicate a general trend towards increasing in plant cover and biomass and resultant decreases in bare
ground (Elmendorf et al., 2012b). Site observations are supported by satellite observations of a long-term greening trend in the Arctic, attributed to an increase in photosynthetic biomass (Jia et al., 2009; Forbes et al., 2010; Beck and Goetz, 2011; Bhatt et al., 2013; Ju and Masek, 2016), though with a high level of heterogeneity across sensory platforms (Guay et al., 2014) and sites (Bhatt et al., 2013; Epstein et al., 2013; Gamon et al., 2013).

Tundra plant communities are also undergoing changes in species composition and abundance. Shrub and graminoid cover is increasing across the majority of tundra sites (Myers-Smith et al., 2011a; Elmendorf et al., 2012b; Venn et al., 2014), while mosses and lichen cover is decreasing (Joly et al., 2009; Elmendorf et al., 2012b; Lang et al., 2012). There is evidence for an accelerating ‘thermophilisation’ of tundra communities, that is, the immigration and increased abundance of warm-loving species (Elmendorf et al., 2015; Steinbauer et al., 2018). Of particular note is an increase in shrubs at many tundra sites (Sturm et al., 2001b; Myers-Smith et al., 2011a, 2015a), which has been observed in long-term ecological monitoring (Elmendorf et al., 2012b), repeat photography (Sturm et al., 2001b; Myers-Smith et al., 2011b; Tape et al., 2012; Tremblay et al., 2012), dendroecological analysis (Hallinger et al., 2010; Myers-Smith et al., 2015b, 2015a), and indigenous knowledge (Thorpe et al., 2002). There is also evidence for poleward and altitudinal expansion of shrubline, at least at some sites (Myers-Smith, 2007; Hallinger et al., 2010; Myers-Smith and Hik, 2018). As a result, woody cover has been predicted to increase by 52% by 2050 (Pearson et al., 2013), with shrubs contributing to over 70% of tundra net primary productivity by 2100 (Mekonnen et al., 2018).

In addition to changing composition, tundra plant communities are also undergoing shifts in physical and phenological characteristics. This trait change is occurring both at the community level (Bjorkman et al., Nature in revision), and via plastic responses to environmental change (Myers-Smith et al., in revision). Many species are growing taller (Walker et al., 2006; Myers-Smith et al., 2011b), with larger leaves (Hudson et al., 2011), greater secondary growth (Campioli et al., 2012), and more frequent reproduction (Klady et al., 2011; Buizer et al., 2012). Leaf emergence and flowering times are also advancing at some but not all sites (Høye et al., 2007; Iler et al., 2013; Kerby and Post, 2013; Oberbauer et al., 2013; Bjorkman et al., 2015; Post et al., 2016), and have found to be particularly climate sensitive at colder versus warmer
Chapter 2. Background

sites (Prevéy et al., 2017). Changing plant phenology is thought to correspond with an advance in satellite-observed green-up in the tundra by approximately 1.6 to 4.7 days per decade (Myneni et al., 1997; Zeng et al., 2011; Park et al., 2016).

2.2.2 Drivers of change
The direct influence of warming is likely a primary driver of observed vegetation change in the tundra. Long-term monitoring, space-for-time substitution and experimental warming indicate similar relationships, though rates of change differ between monitoring and experiments when compared to space-for-time substitutions that do not incorporate ecological lags (Elmendorf et al., 2015). Paleoecological evidence indicates that similar ecological characteristics, such as a higher abundance of shrubs, are associated with warmer periods of the Holocene (Bigelow, 2003; Klemm et al., 2013). Tundra greening trends coincide with recent warming and exhibit a spatial correlation between aboveground biomass and summer warmth (Raynolds et al., 2006; Epstein et al., 2008; Blok et al., 2011; Walker et al., 2012). However, satellite-observed greening trends do not always correspond with in situ vegetation change (Pattison et al., 2015).

Vegetation change is also likely driven, at least in part, by wider ecological changes associated with warming. Firstly, soil moisture is a limiting factor for growth in much of the tundra, and has been found to modify the warming sensitivity of community composition change (Elmendorf et al., 2012b), shrub growth (Myers-Smith et al., 2015a), and trait change (Bjorkman et al., Nature in revision). Secondly, warming can increase nutrient availability by stimulating higher decomposition rates (Weintraub and Schimel, 2003, 2005) and increasing permafrost thaw (Keuper et al., 2012). Nutrient availability has been demonstrated to exert a strong effect on growth, traits and composition of tundra plant communities (Baddeley et al., 1994; Sistla et al., 2013; DeMarco et al., 2014), to the extent that fertilised plots often exhibit single-species dominance over time (Deslippe and Simard, 2011; DeMarco et al., 2014; Zamin et al., 2014). Thirdly, herbivore intensity strongly controls plant community characteristics (Tape et al., 2010; Plante et al., 2014; Ravolainen et al., 2014), and can decouple relationships between temperature and growth (Post and Pedersen, 2008; Olofsson et al., 2009; Väisänen et al., 2014). Lastly, increased potential growing season length (Park et al., 2016), primarily as a result of earlier snowmelt (Post et al., 2009; Liu et al., 2018), corresponds with tundra greening trends (Bunn et
al., 2005; Bunn and Goetz, 2006; Buitenwerf et al., 2015). However, while longer growing seasons are implicated in several site-specific changes, both above and below ground (Rundqvist et al., 2011; Weijers et al., 2013; Blume-Werry et al., 2016), the extent to which it may drive large-scale change is largely unknown.

Finally, observed ecological changes exhibit high unexplained heterogeneity in vegetation responses at sites around the Arctic (Elmendorf et al. 2012b, Oberbauer et al. 2013, Guay et al. 2014, Myers-Smith et al. 2015a, Prevéy et al. 2017). For example, some sites have demonstrated remarkably little change despite long-term warming (Hudson and Henry, 2010). There is also evidence for decreased growing season length and delayed phenology at some sites as a result of higher snowfall (Wipf and Rixen 2010, Bjorkman et al. 2015, Legault and Cusa 2015). Such heterogeneity likely arises from the interaction of site-level drivers, including soil moisture (Ackerman et al. 2017), topography (Tape et al. 2012, Ropars and Boudreau 2012), disturbance (Lantz et al. 2009, 2010), herbivory (Kaarlejärvi et al., 2017), and plant-plant interactions (Bret-Harte et al. 2004, Dormann et al. 2004), which will require multiple lines of evidence to determine underlying mechanisms of change (Myers-Smith et al., in revision; Hobbie et al., 2017).

2.2.3 Research Needs
Tundra vegetation change represents one of the clearest and most rapid ecosystem responses to anthropogenic climate change (IPCC, 2014). However, predicting and modelling tundra vegetation change remains a major challenge due to the complex nature of change drivers, a limited understanding of the constraints to vegetation and trait change in future environments, and the uncertainty surrounding feedbacks between warming, vegetation change and ecosystem function. This thesis aims to inform these research needs, with a particular focus on using plant traits to constrain and inform predictions of vegetation change, and to directly link vegetation change to decomposition.
2.3 Plant trait variation and change across the tundra biome

The following section, ‘Plant trait variation and change across the tundra biome’, is under review as a ‘Tansley Insight Review’ at New Phytologist.

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Trait-based ecology asserts that the properties and functioning of any ecosystem can be related to the phenotypic traits of its resident species (McGill et al., 2006). This ‘traits manifesto’ (Reich, 2014) - the promise that understanding plant traits enables us to understand and quantify community change - has seen a dramatic rise in popularity in recent years. However, progress is hampered by fundamental unknowns regarding the nature of trait variation and physiological trade-offs (Siefert et al., 2015; Díaz et al., 2016; Shipley et al., 2016), by issues of prediction across scales (Messier et al., 2010, 2017; Albert et al., 2011; Asner et al., 2017), and by uneven data coverage among traits, species, and ecosystems (Bjorkman et al., GEB in revision; Bardgett et al., 2014; Jetz et al., 2016). For trait-based ecology to reach its full potential, trait-function relationships must be tested across the world’s biomes, including in our planet’s most extreme environments.

The temperature-limited plant communities found above treeline in Arctic and alpine tundra regions have thus far been largely overlooked in global trait-based analyses. Addressing this ‘trait gap’ is especially critical as tundra ecosystems represent some of the most rapidly changing places on the planet. Despite rapid ecological change, the tundra has featured in less than 3% of plant trait research1 in the last decade and

comprises less than 10% of data in TRY, the largest available database of plant traits (Kattge et al., 2011). However, new trait databases (Bjorkman et al., GEB in revision) and large-scale syntheses (Bjorkman et al., Nature in revision; Prevéy et al., 2017; Steinbauer et al., 2018) are now providing critical new insight into ecological change and resultant feedbacks to ecosystem process in the northern and high elevation regions of the planet.

### 2.3.1 The global context of tundra trait variation

The tundra provides an ideal ‘natural laboratory’ in which to test many fundamental questions of trait-based ecology. Low species richness enables trait coverage for the majority of tundra species (Bjorkman et al., GEB in revision; Jetz et al., 2016), while extreme environmental conditions and large species ranges may challenge our current understanding of environmental filtering (Cornwell et al., 2006), trait-trait relationships (Díaz et al., 2016), and sources of trait variation (Siefert et al., 2015). Tundra trait distributions are thought to be largely determined by climatic conditions (Wielgolaski, 1980) and are associated with small plant size and conservative economic strategies (Callaghan and Emanuelsson, 1985; Molau, 1993). However, short growing seasons also drive high relative growth rates (Chapin, 1987) and high leaf nitrogen concentrations (Körner, 1989). Consequently, it is unclear whether environmental constraints in the tundra filter trait distributions within multivariate trait space, particularly for traits associated with resource economics (Figure 2.2), and thus whether tundra plants exhibit unique trait relationships resulting from adaptation to extreme environmental conditions.

Large geographical ranges of tundra plant species (Henry and Molau, 1997) and convergence in trait expression in the tundra could also challenge the assumption that the majority of trait variation occurs among species or functional groups (Díaz et al., 2016; Shipley et al., 2016; Figure 2.2). This assumption is key because much of our existing understanding of vegetation change in the tundra is at the functional group level (Myers-Smith et al., 2011a; Elmendorf et al., 2012b). However, traditional tundra functional groups do not explain the majority of trait variation in some commonly measured traits (Dorrepaal et al., 2005; Körner et al., 2016), while intraspecific trait variation has been demonstrated to mediate community assembly (Kichenin et al., 2013) and warming responses (Baruah et al., 2017). Genetic differentiation and local adaptation in leaf and phenological traits is also evident in
several widespread tundra species (Bjorkman et al., 2017; Parker et al., 2017). High within-species variation may reduce the ability for species or functional group approaches to improve our understanding of plant community responses to environmental change (Clark, 2016; Laughlin et al., 2017; Saccone et al., 2017; Anderegg et al., 2018). However, if fully accounted for, the incorporation of all sources of trait variation could improve ecological prediction (Siefert, 2012) and climate change projections for the tundra biome (Bjorkman et al., Nature in revision).

**Figure 2.2** Hypothesized location of tundra trait space within global trait space, and possible sources of trait variation. Global trait space is conceptualized as a ‘galactic plane’ defined by two major axes of trait variation, corresponding to strategies of plant size and resource economics (Díaz et al., 2016). Tundra trait space could be constrained along both size and economic dimensions (1), along only the size dimension (2), or exhibit no strong constraints (3). Trait variation could be primarily expressed among species (a), or could exhibit high within-species variation, with larger overlap between species-level or functional group-level traits (b).

### 2.3.2 Trait change in the tundra biome: what we know

Predicting the consequences of climate change for tundra plant traits requires a mechanistic understanding of the drivers of trait variation across scales. Much of what we currently know about the causes of trait variation globally relies on
correlational relationships between traits and environmental variables (e.g., temperature) over space (Reich and Oleksyn, 2004; Wright et al., 2004; Moles et al., 2009; Read et al., 2014; Asner et al., 2016). Space-for-time substitution can thus inform projections of trait shifts over time as the environment changes. In the tundra, many community-level traits, including maximum height, specific leaf area (SLA) and leaf dry matter content (LDMC), vary significantly with temperature over large spatial scales. However, water availability frequently influences the strength (SLA, LDMC) and even the direction (leaf nitrogen, leaf area) of these temperature-trait relationships (Bjorkman et al., Nature in revision).

Strong temperature-trait relationships across space suggest that shifts in many traits are likely as a consequence of climate warming. However, spatial gradients do not necessarily align with change over time, particularly where barriers to migration or other time lags may limit community response to change (Elmendorf et al., 2015, Figure 2.3). Increases in community or individual plant height have been widely documented at individual tundra sites (Hudson et al., 2011; Myers-Smith et al., 2011a; Baruah et al., 2017), linked to experimental warming (Elmendorf et al., 2012a; Hollister et al., 2015), higher summer temperatures (Macias-Fauria et al., 2012), increasing nutrient availability (Zamin and Grogan, 2012), and altered snow depth (Wahren et al., 2005). Warming and earlier snowmelt are also associated with larger leaves, greater reproductive effort, and in some cases with earlier plant phenology (Arft et al., 1999; Choler, 2005; Hollister et al., 2005; Hudson et al., 2011; Klady et al., 2011). However, a synthesis of trait change across more than 100 tundra sites indicates that only community canopy height has changed consistently over the past three decades (Bjorkman et al., Nature in revision). This increase in height was due to the immigration of taller species into existing communities, and was correlated with changes in temperature over the same period.
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2.3.3 The links between traits and ecosystem functions

A major challenge for tundra ecologists is understanding how observed and predicted vegetation changes are likely to influence ecosystem functioning. Mechanistic links between functional traits and ecosystem function offer opportunities to understand the impacts of vegetation change and to quantify climate change feedbacks in the tundra (Figure 2.4). Phenological and reproductive traits determine trophic interactions, and thus have potentially far-reaching impacts within tundra ecosystems (Cleland et al., 2012; Oberbauer et al., 2013; Prevéy et al., 2017). Surface albedo and energy balance are associated with morphological traits, including canopy height and leaf area (Sturm, 2005; Blok et al., 2010; Myers-Smith and Hik, 2013). For

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**Figure 2.3** Response of six key plant traits to warming across biogeographic gradients (community-weighted mean (CWM), and intraspecific), warming experiments, among years (temperature sensitivity), and over time. Green arrows represent temperature-trait relationship in wet sites; orange arrows represent temperature-trait relationship in dry sites. For intraspecific temperature-trait relationships, “s” indicates summer temperature and “w” indicates winter temperature. Temperature-trait relationships, sensitivity, and change over time are derived from Bjorkman et al., Nature in revision (functional traits), and Oberbauer et al., 2013; Prevéy et al., 2017; (phenology). Responses to experimental warming are derived from Baruah et al., 2017; Chapin and Shaver 1996; Graglia et al., 1997; Hudson et al. 2011; Natali et al. 2012 (functional traits), and Arft et al., 1999; (phenology).
example, the lower albedo of shrub canopies may enhance warming (Chapin et al., 2005; Sturm, 2005; Loranty et al., 2014), particularly in spring when stems protrude from the snowpack (Bonfils et al., 2012; Ménard et al., 2014). Taller and denser canopies also trap snow in winter, increasing soil temperatures by 3-10˚C (Chapin et al., 2005; Sturm, 2005), but increase shade in summer, protecting permafrost soils (Blok et al., 2010; Nauta et al., 2014).

Trait change could form an important feedback to global biogeochemical cycling through alterations to the high latitude carbon pool, which comprises over 50% of global soil carbon (Hugelius et al., 2013). Leaf traits exert strong controls over litter decomposition in the tundra, outweighing among-site differences (Sundqvist et al., 2011), experimental warming (Hobbie, 1996), snow depth (Baptist et al., 2010; Blok et al., 2016), and nutrient addition (Aerts et al., 2006). Litter quality also affects decomposition of older carbon by stimulating microbial communities (Kuzyakov et al., 2000; Mack et al., 2004; Wild et al., 2014), and determines rates of biogeochemical cycling (Cornelissen and Makoto, 2014; Reich, 2014). Trait change may thus decrease (Cornelissen et al., 2007) or increase litter decomposition, nutrient cycling and carbon storage (Wookey et al., 2009; Buckeridge et al., 2010; Hobbie, 2015), though the size and direction of this effect remains unknown.

Finally, ecosystem carbon balance depends on trade-offs between decomposition and carbon uptake in biomass (Sistla et al., 2013; Lafleur and Humphreys, 2018). Relationships between warming and traits associated with high productivity (Bjorkman et al., Nature in revision; Elmendorf et al., 2015; Steinbauer et al., 2018), longer growing seasons (Oberbauer et al., 2013), increased plant size (Hudson et al., 2011) and woodiness (Hobbie, 1996; Myers-Smith et al., 2011a; Pearson et al., 2013) suggest that carbon storage in plant biomass will increase (Weintraub and Schimel, 2005). However, increased carbon uptake above ground may be offset by below-ground losses (Parker et al., 2015; Sistla et al., 2013 but see Lafleur and Humphreys, 2018). Quantifying ecosystem carbon balance thus requires a vastly improved understanding of below-ground traits such as root biomass (Zhu et al., 2016) and mycorrhizal association (Cornelissen et al., 2001; Soudzilovskaia et al., 2015), which remain largely unknown in tundra ecosystems (Iversen et al., 2015).
Figure 2.4 Trait change links to ecosystem functions such as surface albedo, energy balance, soil temperature, biogeochemical cycling and carbon storage. Changes in these key ecosystem functions could create feedbacks to the global climate system. Currently the direction and magnitude of many of these feedbacks remain uncertain. Trait data and analyses have the potential to fill in the gaps in ecological data syntheses and Earth System models to improve the quantification of the ecological feedbacks of tundra ecosystem change.

The majority of the evidence for tundra vegetation and trait change thus far comes from above ground and a small number of particularly well-monitored locations (Figure 2.5). Substantial variation in vegetation change at landscape and regional scales (Bjorkman et al., Nature in revision; Elmendorf et al., 2012a, 2012b; Guay et al., 2014) suggests that data collection beyond the most intensively monitored sites is a future research priority. Furthermore, with up to 90% of tundra biomass located below ground, we require new data collection to quantify trait change in below-ground traits across the tundra biome (Iversen et al., 2015). Additional priorities include quantifying the diversity of trait responses above and below ground, across the landscape and across trophic levels, and linking this directly change to key ecosystem functions (Bjorkman et al., Nature in revision; Bardgett et al., 2013, 2014; Gauthier et al., 2013).
Figure 2.5 Map of currently available georeferenced trait data for tundra ecosystems above 48°N. Observations represent a combination of data from the Tundra Trait Team (tundratraitteam.github.io; 82,203 observations) and TRY (www.try-db.org; 22,066 observations) trait databases. TRY trait data were filtered to include only likely tundra (Arctic or alpine) habitats. We first extracted all points above 65°N (Arctic tundra), then those points between 60 and 65°N that occurred above 1000 m in elevation, then those points between 55 and 60°N that occurred above 1500 m in elevation, and finally points south of 55°N that occurred above 2500 m in elevation. Circle colours represent trait type (belowground, structural, leaf, chemical). Circle size represents the relative number of observations in each location.

2.3.4 Conclusion and research needs
Taken together, recent evidence indicates that ecological change in the tundra biome can be confidently attributed to climate warming across the tundra biome (Elmendorf et al., 2012b; IPCC, 2014; Elmendorf et al., 2015; Myers-Smith et al., 2015a; Prevéy et al., 2017), yet the mechanisms and trajectories of community and trait change are
complex (Bjorkman et al., Nature in revision). Trait-based ecology can inform our understanding of tundra functional change in ways that vegetation monitoring and remote sensing alone cannot (Jetz et al., 2016). Tundra plant trait analyses indicate that plastic traits such as plant height are increasing rapidly (Elmendorf et al., 2012b), yet others such as leaf traits have not undergone change at the community-level (Bjorkman et al., Nature in revision). The substantially different rates of change among traits can inform our predictions of which functional changes will be particularly rapid with future warming. Functions associated with plant height, such as albedo, are likely to change more rapidly than feedbacks involving changes in litter decomposition and soil nutrient processing (Bjorkman et al., Nature in revision). Incorporating current and future tundra trait research into Earth system models (Wullschleger et al., 2014; Fisher et al., 2018) will thus allow plant functional traits to fulfil their promise of predicting community responses and feedbacks of tundra ecosystems to on-going global change.

2.4 Decomposition in tundra ecosystems

High latitude regions contain over 50% of global organic soil carbon (Hugelius et al., 2013), more than double current atmospheric carbon stocks (Schuur et al., 2009). However, rapid warming in the tundra could release large amounts of carbon to the atmosphere through decomposition (Schuur et al., 2015; Crowther et al., 2016), transforming the tundra from a carbon sink to a carbon source (Oechel et al., 1993). Warming temperatures are predicted to cause a 30-70% decline in permafrost extent by the end of the 21st century (Xue et al., 2016), accompanied by deeper active layer depths, and altered precipitation and snowmelt regimes (IPCC, 2013). Meanwhile, widespread vegetation change may alter photosynthetic carbon uptake (Lafleur and Humphreys, 2018) and modify litter inputs to tundra soils (Mack et al., 2004; Cornelissen et al., 2007; Sistla et al., 2013). Understanding the drivers of decomposition in the tundra, and how these may be affected by environmental change, is thus a critical research need.
2.4.1 Drivers of decomposition
Decomposition involves the physical and chemical breakdown of organic matter into its chemical constituents (Aerts, 2006). Decomposition is commonly considered to be controlled by three primary factors: climate, substrate quality, and decomposer community, which operate in a hierarchy of decreasing importance across spatial and temporal scales (Couteaux et al., 1995, Figure 2.6). Climatic factors, notably temperature and moisture, explain approximately 70% of variation in decomposition at global scales (Liski et al., 2003; Davidson and Janssens, 2006; Keuskamp et al., 2013), and are commonly considered the key drivers of decomposition in the tundra (Hobbie, 1996; Aerts, 2006). Substrate quality, incorporating the chemical and physical characteristics of plant litter or organic soils, is traditionally considered most influential at the site scale (Hobbie, 1996). However, there is evidence that substrate quality may outweigh the influence of climate at the biome or global scale (Cornwell et al., 2008). Soil decomposer community exerts a clear influence on decomposition (García-Palacios et al., 2013), but is considered highly site specific (Bradford et al., 2014) and can change rapidly over short time scales (Schmidt et al., 2007).

2.4.2 Climate

2.4.2.1 Temperature
Within the tundra biome, temperature is commonly considered to be the major control over decomposition (Hobbie, 1996; Aerts, 2006). Cold conditions in the tundra mean that decomposition is typically slow (Liski et al., 2003; Aerts, 2006), and may be negligible in winter due to low temperatures and absence of liquid water (Bokhorst et al., 2010, Douglas & Tedrow 1959). However, warming increases both the rate of decomposition (Aerts, 2006; Davidson and Janssens, 2006), and increases available substrates as permafrost thaws and active layer depth increases (Schuur et al., 2009, 2015; Natali et al., 2015; Salmon et al., 2016). As such, decomposition in the tundra is thought to be particularly sensitive to warming due to temperature limitation (Davidson and Janssens, 2006) and crossing of critical thresholds such as the freezing point of water (Sierra et al., 2015).
2.4.2.2 Moisture

Decomposition in the tundra is potentially strongly influenced by soil moisture (Blok et al., 2016, Hicks Pries et al., 2013), particularly in the early stages of decomposition due to leaching of soluble compounds (Trofymow et al., 2006). Soil moisture is also a key control over microbial activity (Thakur et al., 2018) and thaw depth (Hicks Pries et al., 2013). Consequently, warming may only increase decomposition rates where sufficient moisture is available (Butenschoen et al., 2011). For example, passive warming experiments commonly reduce surface soil moisture, resulting in an overall decreasing in decomposition, despite warming (Robinson et al., 1995, 1997; Sjögersten and Wookey, 2004; Rinnan et al., 2008). Interactions between temperature and soil moisture have also produced counterintuitive results such as increasing decomposition with altitude (Walker et al., in revision; Withington and Sanford, 2007).
Despite these observed relationships, the role and importance of soil moisture in the tundra remains unclear. Relationships between decomposition rate and soil moisture are highly inconsistent across biogeochemical models (Sierra et al., 2015), which variously assume linear, saturating or optimal relationships with temperature and soil moisture (Sierra, 2015). Uncertainty is exacerbated by high variability in soil moisture over space and time (Wookey, 2002), a lack of coordinated field data from tundra sites (Bonan et al., 2013), and difficulty in predicting future changes in soil moisture (Seneviratne et al., 2010).

2.4.2.3 Snow depth and freeze-thaw dynamics
Snow dynamics directly influence decomposition in the tundra by modifying soil temperature and moisture, and indirectly via controls over the composition of vegetation communities (Baptist et al., 2010). Deeper, earlier developing and longer lasting snow is widely associated with higher soil temperatures (Edwards et al., 2007; Natali et al., 2012), a deeper active layer (Nowinski et al., 2010), larger microbial nutrient pools (Buckeridge & Grogan, 2008), and higher decomposition rates (Blok et al, 2016, Saccone et al, 2013, McLaren & Turkington, 2010, Blok et al, 2016, though see Walker et al, 1999). Deep snow packs, such as those forming under shrub canopies, can maintain soil temperatures above freezing over winter, facilitating year-round microbial activity (Sturm et al., 2001a; Buckeridge and Grogan, 2008, 2010). However, winter decomposition under snow may instead be driven by leaching (Bokhorst et al., 2010), melt timing (Thomas and Venn, in prep), physical processes such as freeze-thaw action (Bokhorst et al., 2013, Zhu, 2012), or variation in microbial community among melt zones (Garcia-Palacios et al, 2013).

2.4.3 Vegetation community

2.4.3.1 Litter quality and quantity
Litter quality exerts strong within-site controls over decomposition in the tundra (Aerts, 2006), and is likely a major factor determining decomposition at the biome scale (Cornwell et al., 2008). Decomposition rates vary according to the volume and the physical and chemical properties of litter inputs (Cornelissen, 1996; Aerts et al., 2012). For example, faster litter decomposition is associated with higher specific leaf area (Cornelissen et al., 1999), higher leaf nitrogen (Cornwell et al., 2008) and lower leaf lignin (Meentemeyer, 1978). At the site scale, litter quality commonly explains
greater differences in decomposition than environmental factors (Baptist et al., 2010; Carbognani et al., 2014; Demarco et al., 2014; Blok et al., 2016), though with several notable exceptions (Butenschoen et al., 2011; Saccone et al., 2013).

Tundra vegetation change may significantly alter decomposition if it results in a major shift in litter quantity and quality. Litter inputs are generally greater following shrub expansion (Dorrepaal et al., 2007), while litter quantity and quality has been found to increase in long-term warming and nutrient addition experiments (Mack et al., 2004; DeMarco et al., 2014; Paradis et al., 2014). Litter quality appears to be highly specific to functional groups (Cornelissen et al., 2007; Buckeridge et al., 2009) and species (Dorrepaal, 2007), and can very substantially among communities (Cahoon et al., 2012). The temperature sensitivity decomposition, and thus the impact of warming, is also dependent on litter quality, with recalcitrant litters exhibiting greater temperature sensitivity compared to labile litters (Conant et al., 2008; Craine et al., 2010; Suseela et al., 2013). Finally, changes in litter quality may mediate the decomposition of old soil carbon via priming effects or by altering decomposer community composition (Moorhead and Sinsabaugh, 2006; Wang et al., 2015; Christiansen et al., 2018). For example, addition of fresh carbon and nitrogen has been shown to double the decomposition of deeper soil carbon (Mack et al., 2004; Wild et al., 2014; Phillips et al., 2018). Climate induced shifts in litter quality could thus profoundly alter decomposition in the tundra (Wookey et al., 2009), though the direction and magnitude of this potential change remains unknown.

2.4.3.2 Microclimate
Vegetation community characteristics change can further affect decomposition via their effects on microclimate (McLaren and Turkington, 2010, Myers Smith & Blok, 2010), though these are likely to be of smaller magnitude than litter quality effects (DeMarco et al., 2014). Snow trapping under shrub canopies, and a higher albedo, particularly in spring, may contribute to higher rates of decomposition and permafrost thaw (Sturm et al., 2001a; Sturm, 2005; Pomeroy et al., 2006). Conversely, shrubs may contribute to the protection of permafrost due to canopy shading (Blok et al., 2010; Myers-Smith and Hik, 2013), so reducing decomposition in summer.
2.4.4 Decomposer community

Soil organisms are responsible for much of the physical and chemical breakdown of organic matter, and thus the size and composition of the microbial community is an important control over decomposition rates (Aerts, 2006). Exclusion of soil fauna on average decreases decomposition rates by 28% across biomes (García-Palacios et al., 2013), while litter decomposition commonly demonstrates a ‘home field advantage’, occurring approximately 8% faster at home sites (Ayres et al., 2009; Veen et al., 2015).

The role of decomposers is strongly mediated by decomposer identity (Bradford et al., 2002; Chapman et al., 2013), diversity (Gessner et al., 2010; Handa et al., 2014) and biomass (Bryant et al., 1998). Decomposer communities are sensitive to both temperature (Sistla and Schimel, 2013; Sistla et al., 2014) and moisture (Rinnan et al., 2008), which influence the biomass and relative abundance of different decomposer groups (Robinson, 2002; Christiansen et al., 2017). Decomposer communities also demonstrate strong associations with certain vegetation types (Wallenstein et al., 2007). For example, the growth of fungal hyphae networks under shrubs is thought to be an important pathway by which soil carbon is made available to microbial degradation (Parker et al., 2015).

Rapid change and turnover in decomposer, and particularly microbial communities (Schmidt et al., 2007), means that they are likely to respond rapidly to climate change, and thus could be one of the key drivers of decomposition change in the short term (Xue et al., 2016). However, changes to decomposer community structure and activity do not necessarily influence decomposition rates. For example, Bokhorst et al (2013) found that decreased snow depth reduced winter decomposer abundance by 99% and bulk soil respiration by 47%, but found no significant response in litter decomposition rates. The role of decomposer communities thus remains a significant ‘black box’ for understanding decomposition change (Kardol et al., 2015).

2.4.5 Implications of decomposition change

Increased decomposition in the tundra over the coming century is predicted to greatly modify biogeochemical cycling (Wookey et al., 2009). Faster decomposition may increase plant-available nitrogen inputs (Hobbie, 1996), though decomposition
change does not always significantly alter nutrient availability (Blok et al., 2016, Baptist et al., 2010, Aerts et al., 2008, Rinnan et al., 2008). Decomposition also comprises approximately 70% of the global carbon flux from soils worldwide (Althuizen et al., 2018), globally releasing approximately 98 PgC per year (Bond-Lamberty and Thomson, 2010). Carbon losses from high latitude regions are likely to be greater than any other part of the planet (Crowther et al., 2016; Van Gestel et al., 2018), releasing up to 37–174 Pg of carbon by 2100 (Schuur et al., 2015). As such, tundra decomposition may form a significant positive feedback to climate change (Davidson and Janssens, 2006; Koven et al., 2011).

2.4.6 Research Needs
Despite the rate and potential impact of change in the tundra, the environmental drivers of decomposition are not yet well quantified (Bradford et al., 2014; Walz et al., 2017). Firstly, the magnitude and direction of change in carbon stores at high latitudes remains unclear due to large variability in model predictions (Sierra et al., 2015), low data availability (Crowther et al., 2018; Van Gestel et al., 2018), and uncertainty regarding the relative importance of different controls on decomposition (Aerts, 2006; Hicks Pries et al., 2013). Secondly, the impact of vegetation change on decomposition in the tundra remains unquantified, despite potentially large feedbacks to climate change (Cornelissen et al., 2007). This thesis informs these two critical research needs by examining drivers of litter decomposition at the biome scale, and by quantifying the decomposability of tundra plant communities across spatial gradients and over time.


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3. Global plant trait relationships extend to the climatic extremes of the tundra biome

The following chapter, ‘Global plant trait relationships extend to the climatic extremes of the tundra biome’, has been prepared for submission to Proceedings of the National Academy of Sciences of the United States of America.


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## Chapter 3. Plant trait variation across the tundra biome

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3.1 Abstract

Global variation in key traits determining plant fitness is thought to be explained by just two dimensions: plant size and resource economics. However, previous global trait analyses do not incorporate the tundra biome. We tested whether relationships among six fundamental traits extend to the cold extremes of life on Earth using the largest database of tundra plant traits yet compiled. Tundra plants demonstrated remarkable consistency in resource economic traits, but not size traits, compared to global distributions, and exhibited the same two dimensions of trait variation. Three quarters of trait variation occurred among species, mirroring global estimates, except at local scales. Plant trait relationships are thus generalizable to the edge of global trait-space, informing prediction of plant community change in a warming world.

3.2 Introduction

Despite the vast diversity of life on Earth, the characteristics of vascular plants are limited by trade-offs in leaf (Wright et al., 2004), wood (Chave et al., 2009a), seed (Westoby et al., 1992) and root (Iversen et al., 2015) traits. Relationships among plant traits enable the diverse characteristics of global plant species to be described by just two dimensions (Diaz et al., 2016), approximating strategies of resource economics (acquisitive vs. conservative) and plant size (large and woody vs. small and non-woody). Trait relationships can thus be used to predict community assembly (Cornwell et al., 2006; McGill et al., 2006; Messier et al., 2010) and ecosystem functions (Lavorel and Garnier, 2002; Suding et al., 2008; Freschet et al., 2012) across biogeographic gradients (Bjorkman et al., Nature in revision) and in response to environmental change (Lavorel and Garnier, 2002; Moran et al., 2016). However, our current understanding of trait relationships has been formulated using datasets that are dominated by tropical and temperate data, which comprise over 90% of global trait observations (Kattge et al., 2011; Fig. 3.1). It is thus unknown whether trait relationships are generalizable to temperature-limited biomes such as the tundra, where environmental conditions could strongly filter trait expression and promote rare or unique ecological strategies.

Current understanding of global trait relationships is also based on the assumption that the majority of trait variation occurs among species (Shipley et al., 2016). Large
within-species trait variation could obscure or invalidate trait relationships (Laughlin et al., 2017; Anderegg et al., 2018), restricting their potential for ecological prediction across scales and among biomes. Within-species variation accounts for approximately 25% of trait variation at the global scale (Siefert et al., 2015), but has been hypothesised to be greater for species that span large biogeographical gradients (Siefert et al., 2015), or in extreme environments (Fajardo and Piper, 2011) and at small geographical scales (Albert et al., 2011; Messier et al., 2017) where species richness is low. The tundra biome thus provides an optimal location to challenge our understanding of trait variation within plant communities due to a small species pool (Jetz et al., 2016), large species ranges (Bjorkman et al., Nature in revision), and extreme environmental conditions (Pearson et al., 2013).

In this study, we test whether our existing understanding of plant trait relationships extends to the tundra biome. We established the largest database of Arctic and alpine tundra plant traits ever compiled by combining 20,991 records from the TRY database (14) with 30,616 records from the Tundra Trait Team (TTT) (Bjorkman et al., GEB in revision), representing 89% of the tundra species pool. We selected six globally well-sampled plant traits: adult plant height, leaf area, seed mass, leaf mass per area (LMA), leaf nitrogen, and leaf dry matter content (LDMC) (Table S2.1). These traits underpin the two known dimensions of global trait space (Díaz et al., 2016), and link to key ecosystem functions including primary productivity (Reich, 2014), carbon storage (Manning et al., 2015), and nutrient cycling (Lavorel and Garnier, 2002). We tested three hypotheses: 1) Tundra species will exhibit the same two dimensions of plant form and function, yet will be constrained relative to global trait space. 2) Within-species trait variation among tundra species will be greater than the global average of 25% (Siefert et al., 2015). 3) Within-species trait variation will contribute to a greater proportion of total trait variation at small geographical scales relative to large scales.

### 3.3 Methods

To examine constraints to trait expression in the tundra biome, we visualised the multidimensional trait space occupied by vascular plant species in the global TRY trait dataset, defined by principal component analysis (PCA), and identified the position of tundra species within global trait space. We repeated the PCA using only tundra species to compare trait relationships in the tundra to global patterns. To
Chapter 3. Plant trait variation across the tundra biome

To examine sources of trait variation, we quantified the proportion of variation explained by functional group (deciduous shrubs, evergreen shrubs, graminoids, forbs) and species identity using generalized linear mixed-effects models. We tested whether sources of trait variation were dependent upon spatial scale by performing variance partitioning at every individual trait collection site in the dataset, and iteratively adding nearest sites. Using this approach, we examined sources of trait variation continuously across geographical scales from the plot-level to the tundra biome.

Figure 3.1: Tundra trait data within geographical and climate space. (a) Map of trait observation sites for six plant traits, indicating global trait observations in TRY (grey points), tundra species observations in TRY (orange points) and TTT data (purple points). (b) Location of trait collection sites in climate space for all available plant species (grey) and tundra species (blue). Major biomes are mapped onto climate space (T - Tundra; B - Boreal Forest; TG - Temperate Grassland; TeF - Temperate Deciduous Forest; TeRF - Temperate Rain Forest; TrF - Tropical Deciduous Forest; TrRF - Tropical Rain Forest; Sa - Savanna; D – Desert). (c) Number of trait observations (upper panel) and species (lower panel) for all available plant species (grey) and tundra species (blue), by latitude. Dotted curves indicate global distributions with the inclusion of TTT collected data.
3.4 Results

Tundra species occupied a constrained subset of global trait space for size-related traits but not resource economic traits (Fig. 3.2, Fig. S2.1). The lower plant height of tundra species compared to global species corresponded with smaller leaf area and seed mass (Fig. 3.2a, axis 1, Fig. S2.1), as would be predicted from global trait relationships (Díaz et al., 2016). In contrast, traits associated with resource economics occupied almost the full global range (Fig. 3.2a, axis 2), with both highly acquisitive species such as chickweed (*Stellaria media*), and highly conservative species such as crowberry (*Empetrum nigrum*) present at tundra sites. This broad range of resource economic trait values occurred independently of the bioclimatic range of tundra species, extending to the cold limits of plant life on Earth (Fig. S2.1). Given low vascular plant diversity, particularly in Arctic tundra, this variation in plant leaf resource economics is remarkably high, and suggests that plants have developed a wide range of ecological strategies to cope with extreme conditions and limiting resources.

Plant trait relationships among tundra species were consistent with global patterns (Fig. 3.2b), despite partially constrained trait expression and lower biodiversity in the tundra biome. The two dimensions of global trait space (plant size and resource economics) aligned with trait relationships among tundra species (Fig. S2.2), and together explained 64.5% of trait variation in the tundra. However, the relative importance of PCA axes was reversed (Fig. S2.3), suggesting that tundra plant strategies are primarily differentiated by resource economics. Trait co-variation was also maintained in the tundra despite an absence of trees (Pearson et al., 2013), which comprise half of global trait space (Díaz et al., 2016) and have been a focus of many previous studies of plant trait relationships (Wright et al., 2004; Chave et al., 2009b). Our findings thus indicate that plants are subject to globally consistent trade-offs in trait expression (Freschet et al., 2010; Reich, 2014; Díaz et al., 2016) despite dramatically different environmental constraints across biomes.
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Figure 3.2: Global trait relationships are maintained in the tundra biome despite constrained size, but not resource economic, traits among tundra species. (a) Global trait-space defined by six plant traits for 1,358 plant species in the global dataset (grey points) and 219 tundra species (blue points). (b) Distribution of trait space for tundra species only. Points are coloured by temperature category, corresponding to the summer temperature of the coldest observation site for each species (Cold < 5°C, Mid < 10°C, Warm > 10°C, Fig. S2.1). Arrows indicate the direction and weighting of trait vectors.

Differences among species explained the majority of trait variation in the tundra biome, accounting for an average of 76.8% of variation across the six traits examined (Fig 3.3a) and reinforcing one of the key principles of trait-based ecology (Shipley et al., 2016). The contribution of within-species variation to total trait variation (23.2%) was surprisingly close to global estimates (25%; Siefert et al., 2015) despite harsh environmental conditions and large species ranges in the tundra (Fig 3.3b). However, within-species variation varied substantially by trait, accounting for as much as 55% of trait variation for leaf nitrogen, in line with previous studies (Messier et al., 2010; Kattge et al., 2011; Siefert et al., 2015). Functional group categorisation explained relatively little variation for single traits (25.6%) (Thomas et al., in press). Size-related traits demonstrated greater biogeographic variation than resource economic traits, even though variation was constrained along the size-related axis relative to global trait space (Fig. 3.2a). Overall, our findings indicate that species-level variation comprises the majority of the global spectrum of plant form
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and function (Díaz et al., 2016; Shipley et al., 2016), underlining the importance of species richness and turnover in determining plant community characteristics, trait diversity, and linkages to ecosystem function.

![Figure 3.3](image)

**Figure 3.3**: Sources of trait variation for six plant traits in the tundra biome. (a) Relative proportion of trait variation explained by functional group (deciduous shrubs, evergreen shrubs, graminoids, forbs; yellow), species (red) and within species (blue). (b) Total trait variation, represented by the coefficient of variation (ratio of the standard deviation to the mean), and component sources of trait variation.

The contribution of within-species trait variation was largely consistent across spatial scales (Fig 3.4 a-d), but comprised a greater proportion of total variation at local scales (< 10 km²), approximately the size of current high-resolution cells in gridded climate datasets. Sites with low sampled species richness also exhibited high within-species variation (< 10 species; Fig 3.4 e-h), suggesting that spatial patterns are at least in part driven by small species pools at local scales. Although both theoretical models (Albert et al., 2011) and empirical studies (Siefert et al., 2015) have suggested that within-species trait variation should increase at small scales, our study demonstrates this clear scaling relationship from the plot to the biome scale.
Figure 3.4: Among-species trait variation (red) accounts for the majority of total trait variation across the tundra, but the importance of within-species trait variation (blue) increases at small scales and at low species richness. Sources of trait variation across geographical scale (a-d) and species richness (e-h) for plant height, leaf area, LMA and leaf nitrogen (see also Figs. S2.5-7). Coloured lines indicate linear break point model fit with one break point (dashed line). Grey boxes indicate if differences between among- and within-species variation are not significant ($P > 0.05$).
3.5 Discussion and conclusions

Our findings indicate that the relationships between plant traits found at the global scale are generalizable even at the climatic edge of global trait-space, and are not primarily driven by differences in growth form and evolutionary history between biomes (Westoby and Wright, 2006). Our findings thus reinforce claims that relationships between widely measured plant traits are indicative of fundamental trade-offs in plant life strategy, including resource acquisition, survival, competition and reproduction (McGill et al., 2006; Freschet et al., 2010; Reich, 2014; Díaz et al., 2016). However, to be truly indicative of whole-plant life strategy, conceptualisations of trait space should incorporate unrepresented traits that capture critical links to ecosystem function, including chemical, physiological and below-ground traits (Iversen et al., 2015).

We find considerable support for environmental filtering in the tundra, with tundra plant species occupying half the global range of size-related traits (Fig 3.2, Fig S2.1, Fig. S2.3). However, we reveal remarkable variation in resource economic traits within the tundra biome relative to global trait space (Díaz et al., 2016). This difference suggests that the two major axes of global trait variation are differentially affected by environmental conditions, and will respond differently to environmental change. In the tundra, where growth is highly temperature-limited (Hudson et al., 2011; Pearson et al., 2013), climate change will likely shift trait distributions towards increased plant height, leaf area and seed mass, as has already been observed at some sites (Hudson et al., 2011), and for plant height at the biome scale (Bjorkman et al., Nature in revision). However, since the majority of trait variation occurs among species, community trait change may require immigration of species from warmer sites. The broad range of resource economic traits found within and across tundra plant communities could additionally enhance resilience in the face of climate change.

More broadly, our findings inform recent calls to increase the collection of additional trait data in current and novel climate conditions (Bjorkman et al., GEB in revision), to improve technology to remotely sense plant trait information (Jetz et al., 2016), and to incorporate trait variation into Earth system modelling (Wullschleger et al., 2014). Our findings indicate that within-species trait variation is strongly trait
dependent, and comprises an important component of trait variation at the local scale, at which many critical ecological processes occur (Suding et al., 2008). Quantifying variation across spatial and temporal scales has been shown to constrain trait-based vegetation models (Lavorel and Garnier, 2002; Reich, 2014) and improve prediction of the response of key ecosystem processes to environmental change (Suding et al., 2008; Wullschleger et al., 2014). However, trait-based modelling approaches must better incorporate hierarchical trait variation, and require precisely geo-referenced trait databases that link trait records to environmental variables.

Overall, our findings demonstrate that relationships and trade-offs among fundamental plant traits are generalizable across lineages and among biomes, even at cold extremes of the planet. As climate change alters environmental conditions around the world, and most notably in the tundra, quantifying the constraints on trait expression offers a clearer picture of how plant communities and feedbacks to ecosystem function will change with warming. Together, these insights provide a significant step forward for trait-based ecology, and offer fundamental insight into the rules that underpin evolution, community assembly, and ecosystem response to environmental change across the spectrum of plant life on Earth.
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4. Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome

The following chapter, ‘Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome’, is in press at *Global Ecology and Biogeography*.


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4.1 Abstract

Plant functional groups are widely used in community ecology and Earth system modelling to describe trait variation within and across plant communities. However, this approach rests on the assumption that functional groups explain a large proportion of trait variation among species. We test whether four commonly used plant functional groups represent variation in six ecologically important plant traits. We compiled a database of six plant traits (plant height, leaf area, specific leaf area, leaf dry matter content, leaf nitrogen, seed mass) for 295 tundra vascular plant species. We examined the variation in species-level trait expression explained by four traditional functional groups (evergreen shrubs, deciduous shrubs, graminoids, forbs), and whether variation explained was dependent upon the traits included in analysis. We further compared the explanatory power and species composition of functional groups to alternative classifications generated using post-hoc clustering of species-level traits. Traditional functional groups explained significant differences in trait expression, particularly among traits associated with resource economics, which were consistent across sites and at the biome scale. However, functional groups explained 19% of overall trait variation and poorly represented differences in traits associated with plant size. Post-hoc classification of species did not correspond well with traditional functional groups, and explained twice as much variation in species-level trait expression. Our findings suggest that traditional functional groups only coarsely represent variation in well-measured traits within tundra plant communities, and better explain resource economic traits than size-related traits. We therefore recommend caution when using functional group approaches to predict tundra ecosystem change, or ecosystem functions relating to plant size, such as albedo or carbon storage. We argue that alternative classifications or direct use of specific plant traits could provide new insight for ecological prediction and modelling.

4.2 Introduction

Many ecosystems around the world are responding rapidly to global change drivers, including warming (IPCC, 2013), changing precipitation patterns (Weltzin et al., 2003), increased nutrient availability (Galloway et al., 2008), elevated atmospheric CO₂ (Cramer et al., 2001), and altered herbivory regimes (Díaz et al., 2007). Perhaps nowhere will ecosystem response to climate change be greater than in the tundra, which is warming at twice the global average rate (Serreze & Barry, 2011; IPCC,
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2013) and undergoing rapid vegetation change (Myers-Smith et al., 2011; Elmendorf et al., 2012b). Predicting how plant communities will respond to environmental change, and the resulting impact on ecosystem structure and function, has been described as the 'holy grail' of ecology (Lavorel & Garnier, 2002). However, the responses of different species and environments are often highly complex, representing a major challenge for the prediction of community response to environment change (McGill et al., 2006; Diaz et al., 2016).

One approach to reducing complexity in ecological communities is to classify species with similar characteristics into plant functional groups or plant functional types (Harrison et al., 2010). Species are commonly grouped based on a priori classification by growth form (e.g. forb, shrub), life history (e.g. evergreen, deciduous), or other morphological characteristics (Wright et al., 2006; Wullschleger et al., 2014). In the tundra, vascular plant species are most commonly categorized into four functional groups: evergreen shrubs, deciduous shrubs, graminoids and forbs. This grouping structure is rooted in Chapin et al.’s (1996) demonstration that clustering of 37 species based on 21 plant traits aligned with growth-form based groupings. The use of functional groups is thus inherently a trait-based approach, based on the hypothesis that plant species within functional groups possess similar traits and act in ecologically similar ways (Lavorel & Garnier, 2002; McGill et al., 2006). This hypothesis has so far only been tested at the site scale (Chapin et al., 1996) or for individual traits (Dorrepaal et al., 2005; Körner et al., 2016), yet continues to underpin a wide range of studies examining tundra plant community responses to environmental change (Fig. 4.1).

There is evidence that functional groups display distinct differences in their response to environmental change in the tundra. Experimental warming and fertilisation are associated with increases in cover and biomass of deciduous shrubs and graminoids, often at the expense of other functional groups (Dormann & Woodin, 2002; Elmendorf et al., 2012a). In turn, the relative abundance of different functional groups influences multiple ecosystem properties, including biomass accumulation, light interception, soil moisture and soil nutrients (McLaren & Turkington, 2010, 2011). Functional groups also integrate multiple plant traits and may therefore better explain ecosystem function and community change compared to single trait-based approaches (Soudzilovskaia et al., 2013; Laughlin & Messier, 2015). By extension, plant functional groups may integrate information from traits that are difficult to
collect, including root structure or mycorrhizal association, that may be critical to explaining vegetation change (Cornelissen et al., 2001; Soudzilovskaia et al., 2015).

Despite their prevalence in ecological analysis, functional groups have often displayed low explanatory power and inconsistent responses among experiments (Dorrepaal, 2007; Bret-Harte et al., 2008). In a meta-analysis of 36 environmental manipulation experiments in the tundra, Dormann & Woodin (2002) found that plant functional groups did not predict community response, except in the case of fertilization and warming treatments. Even among these treatment types, differences in functional group response have not always been clear in the literature (Fig. 4.1). Functional groups have also shown highly conflicting responses across studies; for example, evergreen shrubs have shown positive, neutral, and negative responses to warming (Hollister et al., 2005; Elmendorf et al., 2012b; Zamin et al., 2014). Finally, functional groups have shown inconsistent responses among and within experiments, in different years (Cornelissen & Makoto, 2014), time-scales (Saccone & Virtanen, 2016), environmental conditions (Dorrepaal, 2007), and spatial scales (Mörsdorf et al., 2015).

Low explanatory power may arise from high trait variation within functional groups, such that group differences are not significant, particularly among small species pools (Cornelissen et al., 2004). For example, Körner et al. (2016) found that tissue carbon and nitrogen did not vary by functional group in European alpine plants, while Iversen et al. (2017) reported greater variation in fine-root carbon-to-nitrogen ratios within groups than among groups in biomes spanning the globe. Many studies have instead found that tundra species respond highly individualistically to change (Lavorel & Garnier, 2002; Hollister et al., 2005; Hudson et al., 2011), and that functional group responses instead reflect strong species-specific responses, often of dominant species (Shaver et al., 2001; Bret-Harte et al., 2008; Little et al., 2015). An alternative hypothesis is, therefore, that traditional functional groups do not represent key dimensions of trait variation among species, and thus may obscure certain aspects of ecosystem function and change. Given that much of our current understanding of tundra vegetation change is based on functional group responses (McLaren & Turkington, 2010; Myers-Smith et al., 2011; Elmendorf et al., 2012b), testing this hypothesis is critical to understanding the mechanisms and future patterns of tundra vegetation change.
Figure 4.1 Studies employing an ‘evergreen shrub - deciduous shrub - graminoid - forb’ functional group classification (or close variant) to examine the response of tundra communities to environmental change over the past two decades. Studies were identified based on a literature search on Web of Science using the search terms ‘tundra’ and ‘plant functional group’ or ‘plant functional type’. For a list of studies see Table S4.1. Studies are grouped by whether they found clear differences in functional group response (Yes: clear differences were found between some (but not necessarily all) functional groups; Not clear: differences between groups were inconsistent among sites or over time; No: No significant differences in functional group response). Studies vary in duration from 2-30 years and incorporate a range of bioclimatic contexts and experimental types. For full meta-analyses of functional group response see Dormann & Woodin (2002) and Dorrepaal (2007).
4.2.1 Research Questions

1. How well do functional groups represent species trait variation?

In this study, we test whether traditional functional groups explain differences in six plant functional traits among Arctic and alpine tundra species, and whether explanatory power is sensitive to: i) differences in species composition among sites or ii) the use of different plant traits in analyses. We examine six traits, plant height (PH), seed mass (SM), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen (LN), that are the most commonly collected plant traits in the tundra biome (Bjorkman et al., GEB in revision) and considered to be cornerstones of plant ecological strategy (Díaz et al., 2016). We hypothesize that plant functional groups will exhibit distinct trait distributions, and that traits associated with plant economics (SLA, LDMC, LN) will be better explained by traditional functional groups than traits associated with plant size (PH, SM, LA), reflecting consistent functional group responses in resource addition experiments (fertilization and warming), but not in other experimental types (Dormann & Woodin, 2002).

2. Does functional group composition align with post-hoc trait-based clustering of species?

We compare the species composition and explanatory power of traditional functional groups with two statistically derived, trait-based clustering approaches, which represent optimal grouping of species within multivariate trait-space. Given that traditional functional groups were formulated using trait-based clustering, albeit with a smaller species pool, we hypothesize that post-hoc classification will produce similar species groupings to traditional functional groups. This approach directly addresses calls to compare traditional functional groups with other trait-based classifications (Dorrepaal, 2007; Hudson et al., 2011; Boulangeat et al., 2012), and provides the first trait-based assessment of traditional functional groups at the tundra biome scale.
4.3 Methods

4.3.1 Tundra biome definition
In line with previous biome-scale assessments of tundra vegetation community change, we considered tundra biome as the vegetated regions above treeline, both at high latitude and high altitude (Bliss et al., 1981; Elmendorf et al., 2012b). Tundra plant communities include many widely distributed common species, and functional groups are considered to be consistent across the large geographical gradients and a variety of environments (Henry and Molau, 1997).

4.3.2 Dataset
We established a database of tundra plant traits by combining 18,613 plant trait records from the TRY database (Kattge et al., 2011; Chapter S3) with 37,435 records from Tundra Trait Team (TTT) contributors (Bjorkman et al., GEB in revision), forming the largest database of tundra plant traits compiled to date. We considered all species present at International Tundra Experiment (ITEX) and associated plots as tundra species (Henry and Molau, 1997; Elmendorf et al., 2012b; Bjorkman et al., Nature in revision). We included all available trait records for tundra species, but excluded records from manipulated locations such as experiments or botanical gardens. Of the 449 species in the ITEX dataset, 386 (86%) had trait data available. Species lacking trait data were generally rare or uncommon species unique to single sites, and on average represented <3% of total plant cover across all sites.

We combined taxonomic synonyms following The Plant List (www.theplantlist.org) to ensure consistent taxonomy across all studies. Since sampling problems inevitably arise from compiling trait data from a large number of disparate studies (Jetz et al., 2016), we removed duplicate entries, obviously erroneous values (e.g. values <0), and observations more than four standard deviations from each species mean (Bjorkman et al. GEB in revision). For seed mass, which is prone to measurement error due to the small masses involved and large variation within individuals (Pérez-Harguindeguy et al., 2013), we manually checked values more than three standard deviations from each species' mean and removed values that had clear measurement or transcription error.
4.3.3 Trait selection

We selected six plant traits for analyses: plant height (maximum measured height), seed mass (dry mass), leaf area per leaf (fresh leaf area), specific leaf area (ratio of fresh leaf area to dry leaf mass), leaf dry matter content (ratio of leaf dry mass to fresh leaf mass), and leaf nitrogen (nitrogen per unit leaf dry mass). A total of 295 species had data available for all six traits. A review of the ecological associations of each trait can be found in Diaz et al. (2016). We additionally tested two traits with low data availability, stem density (ratio of stem dry mass to fresh stem volume) and leaf lifespan. These traits align with key characteristics of functional groups, but are rarely measured among tundra species (Table S4.2). We log-transformed trait values to account for log-normal distributions, standardised between 0 and 1 using variance scaling, and aggregated traits at the species level to allow multivariate comparison among species and different units of measurement. Within-species variation cannot be captured using this approach, but is assumed not to contribute to a large proportion of trait variation at the biome scale (Siefert et al., 2015). However, we also re-ran analysis using the 25th and 75th percentile of species-level trait data, representing the lowest and highest quarter of trait values for each species, to test whether results were altered by within-species variation in the dataset as a whole.

4.3.4 Trait variation explained by functional groups

We assigned species to four functional groups – evergreen shrubs, deciduous shrubs, graminoids, and forbs – based on previous classification of ITEX species (Elmendorf et al., 2012b). We also examined two more detailed functional group classifications: i) a six-group classification separating graminoids into grasses, sedges and rushes, and a ii) seven-group classification further separating shrubs into dwarf and tall shrubs and by leaf habit. To examine the distribution of individual traits within and among functional groups, we plotted the distribution of species-level mean traits for each of the six plant traits studied and tested significance of distributions using pairwise Wilcoxon signed-rank tests. To visualise multivariate trait distributions and examine the weighting of different traits, we performed principal component analysis (PCA) on multivariate trait distributions using the ‘prcomp’ function in the R ‘stats’ package, and plotted the first two component axes. We conducted PERMANOVA analysis to test the significance of, and variance explained by, functional groups to estimate how well traditional functional groups represent trait characteristics. We used Euclidian distance with 999 permutations for the
combination of all six traits using the ‘adonis’ function in the R package ‘vegan’ (Oksanen et al., 2010).

We performed all analyses at the biome scale using all trait data, encompassing 1,333 unique georeferenced locations and non-georeferenced trait data for tundra species. To examine if functional group significance was affected by species composition, we also conducted analyses at three unique geographical locations: Abisko (Northern Sweden, 68°N, 18°E, 98 species available) representing European subarctic tundra, Davos (the Swiss Alps, 47°N, 10°E, 67 species available) representing European alpine tundra, and Qikiqtaruk-Herschel Island (Northern Canada, 69°N, -139°E, 16 species available) representing North American arctic tundra. We chose these sites to represent variation in geography and species richness across the tundra. We also repeated all analyses using a subset of only georeferenced trait data collected north of 60°N to examine if findings were influenced by environmental variation across collection locations.

To examine if the variation explained by functional groups was dependent on the traits included in analysis, we repeated PERMANOVA analysis for every possible multivariate combination of traits. This enabled us to test whether particular trait combinations were well differentiated by functional groups. We also differentiated between size-related and economic traits, reflecting the two major dimensions of trait variation among global plant species (Díaz et al., 2016). Since some traits were available for more species than others, resulting in unequal sample sizes among different trait combinations, we randomly selected 295 species (the minimum number of species for which all six traits were available) for each trait combination and calculated the mean variance explained over 999 replications for each combination.

4.3.5 Comparison with post-hoc classifications

We compared the species composition and explanatory power of functional groups to post-hoc species classifications created using statistical clustering of species-level plant traits. We grouped species using two contrasting clustering approaches, k-means clustering (k-means) and hierarchical agglomerative clustering (HCA). K-means clustering employs a top-down approach, assigning species to groups based on multivariate distance from group means (Ding and He, 2004). Hierarchical agglomerative clustering employs a bottom-up approach, iteratively combining
groups with similar traits (Lukasová, 1979). We performed clustering using the R package ‘vegan’ and selected a four-cluster solution for both methods to correspond with the number of functional groups. When testing alternative six- and seven-functional group classifications we selected six-cluster and seven-cluster solutions, respectively. For HCA clustering, we used Euclidian distance and Ward’s criterion to measure linkage. We compared differences in species composition between post-hoc trait-based classifications and traditional functional groups by calculating the maximum possible number of consistently categorised species among grouping methods. We also estimated the relative abundance of consistently grouped species within the ITEX database (Elmendorf et al. 2012b, www.polardata.ca/pdcsearch/PDCSearchDOI.jsp?doi_id=10786) using the most recent year for all plots and aggregating at the site level.

Finally, we repeated PERMANOVA analysis for post-hoc trait-based classifications and examined the variance explained by groups for all traits, for only size-related traits and for only economic traits. This enabled us to i) test the variation remaining unexplained when using post-hoc classification of species, and thus ii) test the explanatory power of traditional functional groups compared to optimal four-group clustering of species, acknowledging that it is unlikely that all trait variation will be explained, and iii) examine whether post-hoc trait-based classifications could differentiate between axes of trait variation.

All analyses were conducted in R version 3.3.2 (R Core Team, 2017). Data are submitted to the TRY database (http://www.try-db.org) and publicly available in the Polar Data Catalogue (http://www.polardata.ca/) and NERC Polar Data Centre (http://www.bas.ac.uk/data/uk-pdc/). Code is available at github.com/hjdthomas/Tundra_functional_groups.
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4.4 Results

4.4.1 Trait variation explained by traditional functional groups

We found large overlap between the trait distributions of functional groups for the majority of traits examined, such that trait distributions were often not significantly different among functional groups (Fig. 4.2, Fig. S4.1). The significance of functional group distributions was strongly trait dependent, for example with significant differences among all groups for specific leaf area, but no significant differences between any groups for seed mass. Among functional groups, evergreen shrubs exhibited the most distinct differences in trait expression compared to other tundra plants, primarily driven by economic traits (Fig 4.2, Fig 4.3). In contrast, deciduous shrubs and graminoids exhibited largely overlapping trait distributions for many individual traits and in multivariate trait-space.

![Figure 4.2](image_url)

**Figure 4.2** Smoothed distribution of species-level traits represented by the four traditional tundra plant functional groups. Distributions are based on species-level mean traits for the 295 tundra species for which data are available for all six plant traits of interest. Trait values are presented on the x axis in untransformed units on a log scale. Significance of distributions is indicated by symbols (pairwise Wilcoxon rank sum test; * = P < 0.05; ** = P < 0.01, *** = P <0.001). Pairs of traits that are significantly different from each other, but not different from other functional groups, are indicated by black bars connecting the centre of those two distributions.
Figure 4.3 Distribution of tundra species in trait space. Inset plots indicate PCA multivariate distribution of six plant traits for three tundra sites, (a) Qikiqtaruk, (b) Abisko (c) Davos, and for (d) the whole tundra biome. Trait space was defined based on plant height (PH), seed mass (SM), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen content (LN). Individual species are represented by points and functional groups by point colour (blue = evergreen shrub,
Functional groups explained 18.5% of multivariate trait expression among species across all six traits (four cluster PERMANOVA, $R^2 = 0.185$, $p < 0.001$), and were significant both for the tundra biome and at the site level. The direction of trait weightings indicated that economic traits (SLA, LDMC, LN; greater association with PCA axis 1) and size-related traits (PH, SM, LA; greater association with PCA axis 2) comprised distinct axes of trait variation, with functional groups primarily differentiated along the first PCA axis. The relative position of functional groups was consistent among sites, regardless of species composition or geographical location (Fig. 4.3).

The explanatory power of functional groups was strongly dependent on the traits included in the analysis. Trait combinations including only economic traits (SLA, LN, LDMC) were better explained by functional groups than size-related traits (PH, SM, LA), regardless of the number of traits included in analysis (Fig. 4.4a). This was largely driven by LDMC, since combinations containing this trait were best explained by functional groups (Fig. 4.4b). In contrast, trait combinations containing PH or SM were comparatively poorly explained by functional groups (Fig. 4.4c). Inclusion of leaf lifespan and stem density traits reduced data availability by over 80% (Table S4.2) but improved the explanatory power of groups from 19% to 55% and 41% respectively. This improvement was driven by economic differences, and primarily differentiated shrubs (wood density) or evergreen shrubs (leaf lifespan) from other groups (Fig S4.4).
Figure 4.4 Trait variation explained by functional groups for all possible trait combinations. Functional groups best explained combinations of (a) only economic traits, or (b) those containing leaf dry matter content (LDMC), and worst explained combinations of only size-related traits or (c) those containing plant height or seed mass. Points indicate the mean variance explained (PERMANOVA $R^2$) by functional groups and coloured to visualise the importance of different trait combinations.
4.4.2 Comparison of post-hoc trait-based classifications with functional groups

Post-hoc trait-based classification of species did not correspond well with traditional functional group composition. The four groups identified by post-hoc classification were consistently located within trait-space across clustering methods, and were differentiated by the two axes of trait variation, though more strongly by size-related traits (Fig. 4.5). Post-hoc classifications thus represented i) tall species with large leaves and seeds (high PH, SM and LA), ii) mid-sized species with economically acquisitive strategies (low LDMC, high SLA and LN), iii) small species with economically acquisitive strategies, and iv) small species with economically conservative strategies.

Table 4.1 Top: Similarity in species composition between traditional functional groups and post-hoc trait-based classifications ($k$-means = k-means clustering; HCA = hierarchical agglomerative clustering), calculated as the proportion of consistently classified species out of all species. Bottom: Relative abundance of consistently classified species within tundra (ITEX) vegetation communities, calculated as the proportion of the summed abundance of consistently classified species out of the summed abundance of all species for which trait data are available across all ITEX plots.

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Functional groups vs. $k$-means</th>
<th>Functional groups vs. HCA</th>
<th>K-means vs. HCA</th>
<th>All Methods</th>
</tr>
</thead>
<tbody>
<tr>
<td>All groups</td>
<td>42%</td>
<td>43%</td>
<td>74%</td>
<td>35%</td>
</tr>
<tr>
<td>Evergreen shrubs</td>
<td>89%</td>
<td>94%</td>
<td>94%</td>
<td>89%</td>
</tr>
<tr>
<td>Deciduous shrubs</td>
<td>0%</td>
<td>13%</td>
<td>87%</td>
<td>0%</td>
</tr>
<tr>
<td>Graminoids</td>
<td>52%</td>
<td>51%</td>
<td>78%</td>
<td>42%</td>
</tr>
<tr>
<td>Forbs</td>
<td>37%</td>
<td>37%</td>
<td>69%</td>
<td>30%</td>
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<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Similarity between group species composition</th>
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<tbody>
<tr>
<td>Evergreen shrubs</td>
<td>99%</td>
</tr>
<tr>
<td>Deciduous shrubs</td>
<td>0%</td>
</tr>
<tr>
<td>Graminoids</td>
<td>74%</td>
</tr>
<tr>
<td>Forbs</td>
<td>24%</td>
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<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Relative abundance of consistent species</th>
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<tbody>
<tr>
<td>Evergreen shrubs</td>
<td>99%</td>
</tr>
<tr>
<td>Deciduous shrubs</td>
<td>0%</td>
</tr>
<tr>
<td>Graminoids</td>
<td>62%</td>
</tr>
<tr>
<td>Forbs</td>
<td>22%</td>
</tr>
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</table>
42% of species were consistently classified between traditional functional groups and k-mean clustering, and 43% between traditional functional groups and HCA clustering (Fig. 4.5f, Table 4.1). In contrast, 74% of species were consistently classified between post-hoc clustering methods. Evergreen shrubs, approximately half of graminoids and one third of forbs were largely assigned to consistent groups across the three clustering methods (Fig. 4.5f). Deciduous shrubs showed very low correspondence between traditional functional groups and post-hoc classifications due to large trait overlap with both graminoids and forbs, but showed high correspondence between clustering methods (Table 4.1, Table S4.3).

Abundant species were more likely to be consistently classified across grouping methods (Fig. S4.2a), and the relative abundance of consistently classified species within tundra plant communities (51%) was greater than would be expected if all species had equal abundance (35%). Although abundant species had more available trait observations, and thus may have more representative species-mean traits, the number of trait observations did not significantly affect whether a species was consistently classified (Fig S4.2b). Species that were consistently categorized across grouping methods occupied a distinct region of trait-space ($P < 0.001$) and were mostly large (taller, larger leaves or larger seeds) with extreme economic traits (i.e. highly conservative or highly acquisitive species, Fig. S4.2d). Inconsistently classified species had traits closer to the centre of the overall distribution of tundra species within functional trait space, suggesting that the traits of these species may be poorly represented by traditional functional groups.
Figure 4.5 Comparison of group structure, trait variation explained, and group composition between traditional functional groups and post-hoc classifications. (a-c): PCA visualization of species clusters as defined by (a) traditional functional groups, (b) k-means clustering, and (c) hierarchical-agglomerative clustering (HCA). Species are indicated by points and group distribution by ellipses. Colours indicate groups (dark blue = evergreen shrub, green = deciduous shrub, yellow = graminoid, purple = forb). Post-hoc classifications are matched with functional groups based on maximum species correspondence between grouping methods, such that each post-hoc classification corresponds with a traditional functional group. Post-hoc groups approximately represent i) tall species with large leaves and seeds (purple), ii) mid-sized species with economically acquisitive strategies (yellow), iii) small species with economically acquisitive strategies (green), and iv) small species with economically conservative strategies (blue). (d-f): Trait variation explained by (d) traditional functional groups, (e) k-means, and (f) HCA for multivariate combinations of all six plant traits (white), size-related traits only (red), and economic traits only (light blue). (g): Comparison of group composition across clustering methods. The stacked bars
represent individual species and are ordered by traditional functional group (species order remains consistent across columns). The colour of each stacked bar represents the group to which species were assigned by each classification method (classification can change across columns). For example, a species categorised as a graminoid by traditional functional groups can be categorised in the group most corresponding to forbs by post-hoc classifications.

Post-hoc classifications explained 45% (k-means, $R^2 = 0.448$, $p < 0.001$) and 37% (HCA, $R^2 = 0.366$, $p < 0.001$) of trait variation among tundra species, compared to 19% for traditional functional groups (Fig. 4.5, d-f). Despite derivation using all six plant traits, post-hoc classifications explained greater variation in size-related traits than traditional functional groups for both clustering methods (functional groups: $R^2 = 0.080$, $p < 0.001$; k-means: $R^2 = 0.474$, $p < 0.001$; HCA: $R^2 = 0.406$, $p < 0.001$), while k-means sampling also slightly better explained variation in economic traits (functional groups: $R^2 = 0.339$, $p < 0.001$, k-means: $R^2 = 0.343$, $p < 0.001$; HCA: $R^2 = 0.266$, $p < 0.001$, Fig. 4.5 d-f). Our results demonstrate that unexplained trait variation does not solely arise due to aggregation of species into a small number of groups, and that functional groups have less than half the explanatory power of optimal species classification for the six most commonly collected tundra plant traits.

### 4.5 Discussion

#### 4.5.1 Trait variation is poorly explained by traditional functional groups

To be meaningful for ecological analyses, plant functional groups should accurately and consistently represent differences in species characteristics that underpin their environmental preferences and responses (Chapin et al., 1996). In this study, we find that traditional plant functional groups represent 19% of variation in the six most commonly measured plant traits among tundra species. Furthermore, the species composition of functional groups did not align well with post-hoc trait-based classification of species. Together, our findings indicate that traditional functional groups poorly represent species-level variation in the six plant traits considered by this study, and highlight potential limitations of functional group approaches to predicting community responses to environmental change in the tundra.
Our findings support a previous trait-based criticism of traditional functional groups in European alpine species (Körner et al., 2016), and may explain low explanatory power and contradictory responses of functional groups in previous tundra studies (Dormann & Woodin 2002; Dorrepaal 2007, Fig. 4.1). Although it is possible that the tundra is unusual in the global context due to small plant growth-forms and harsh environmental conditions, our study is in line with findings that functional groups poorly describe trait variation in tropical forests (Wright et al., 2013), temperate grasslands (Wright et al., 2006; Fry et al., 2014; Forrestel et al., 2017), and among certain traits at the global scale (Wright et al., 2005; Kattge et al., 2011; Reichstein et al., 2014; Iversen et al., 2017).

Our findings for the six most commonly measured traits in part contradict Chapin et al.'s (1996) finding that growth-form based functional groups can be reproduced from trait information. This discrepancy could arise from the greater number of species and individual trait records represented in our study, which may increase variability within functional groups and species, or the greater number of traits included in Chapin et al. (1996). Trait variation may also be better represented by alternative classifications such as those distinguishing between tall and dwarf shrubs, or between grasses and sedges. Although alternative six-group and seven-group classifications schemes did slightly increase the explanatory power of functional groups (from 18.5% to 21.4% and 24.9% respectively, Fig S4.3), the overall variance explained remained low and substantially less than post-hoc classifications (53.6% and 56.8% respectively).

Low explanatory power of functional groups could also arise from the choice of traits included in analysis. The traits investigated in this study are considered critical determinants of ecological processes (Pérez-Harguindeguy et al., 2013; Díaz et al., 2016), and represent both available tundra trait data and the focus of trait-based research in tundra ecosystems (Bjorkman et al. GEB in revision). Nevertheless, we found that the explanatory power of functional groups was highly trait-specific (Fig. 4.4), and thus functional groups may represent differences among plant traits not investigated here that are nonetheless critical to ecosystem function in the tundra (Figure 4.6). For example, inclusion of stem density increased the explanatory power of traditional functional groups to over 50% (Fig. S4.4), but reduced species representation by 80% (n = 53) and did not improve representation of size-related traits.
Figure 4.6 Functional groups and post-hoc trait-based classifications capture different characteristics of tundra plant communities. Solid circles enclose characteristics represented by functional groups, post-hoc classifications, and by both approaches, according to the findings of this study. The dotted circle encloses the data gaps for traits that are not well represented in tundra trait databases or trait-based analysis yet are suggested to be important in the literature (Eckstein et al., 1999; Chave et al., 2009; Cleland et al., 2012; Bardgett et al., 2014).

4.5.2 Functional groups align with economic traits
Among tundra species, traditional functional groups better represented variation in economic traits (SLA, LDMC, LN) than size-related traits (PH, SM, LA). Indeed,
functional groups explained roughly equal variation in economic traits to *post-hoc* clustering (33.5% compared to 34.3% for k-means clustering). As such, ecosystem functions related to resource economics such as photosynthetic rate or nutrient cycling may be well represented using functional group approaches (Lavorel and Garnier, 2002). This difference may also explain why studies focusing on community responses to resource addition (Dormann and Woodin, 2002; Elmendorf et al., 2012a; Zamin et al., 2014) or litter quality (Dorrepaal et al., 2005; Cornelissen et al., 2007; Carbognani et al., 2014) find the clearest differences between functional groups.

Low representation of size-related traits may arise due to convergence of growth forms in the tundra; all functional groups contain both comparatively large (e.g., the tall deciduous shrub *Salix glauca* or forb *Chamaenerion angustifolium*) and comparatively small (e.g., the dwarf deciduous shrub *Salix polaris* or forb *Saxifraga bryoides*) species. As a result, functional groups may poorly represent ecosystem functions or properties relating to size-related traits, such as albedo, carbon storage, seed dispersal or competitive ability (Lavorel and Garnier, 2002; Westoby et al., 2002; Loranty et al., 2011). Such properties are implicated as key drivers of community-level vegetation change in the tundra (Kaarlejärvi et al., 2017; Mekonnen et al., 2018). Functional group classifications that explicitly recognize morphological characteristics, such as distinguishing between tall and dwarf shrubs (Elmendorf et al., 2012b; Vowles et al., 2017), may better characterize differences in trait expression, though we found limited evidence for this (Fig. S4.3). As such, *post-hoc* classification of species or direct use of trait data may identify differences among size-related traits, and associated drivers of community change and ecosystem function, that are obscured by variation within traditional functional groups (Matesanz et al., 2009).

**4.5.3 Trait-based approaches as an alternative to functional groups**

Our findings contribute to growing support for the use of trait-based approaches as an alternative to functional groups within ecological research and earth system modelling. Trait-based approaches include *post-hoc* grouping of species according to common traits (Suding et al., 2008), common responses to environmental conditions (Cornwell and Ackerly, 2010), or common effects on ecosystem processes (Cornwell et al., 2008; Laughlin, 2011), as well as direct use of trait data in analysis (McGill et
al., 2006). In this study post-hoc classifications explained more than twice as much trait variation as functional groups, and were distinguished along two global axes of trait variation (Diaz et al., 2016), representing large versus small species, and economically ‘fast’ versus ‘slow’ species (Reich, 2014; Diaz et al., 2016). Post-hoc classifications thus better captured the multi-dimensionality of trait variation compared to traditional groupings (Maire et al., 2015), and produced relatively robust species groupings across the two clustering methods.

Post-hoc approaches have nevertheless been criticized on the basis of inconsistencies across methodologies and ecological communities (Dyer et al., 2001; Fry et al., 2014), and could be biased towards representing rarer species with more extreme traits. In this study, functional groups better represented differences among more abundant species (Table 4.1), and thus may capture community-level characteristics even if representation of differences among individual species is low. Species that were consistently categorized (Table S4.4) possessed similar traits including a larger structure (tall with large leaves and seeds) and either highly conservative or acquisitive resource economic traits. However, some species that were inconsistently classified, notably deciduous shrubs such as Betula nana and graminoids such as Agrostis spp., have dominated vegetation responses at many tundra sites (Bret-Harte et al., 2001; Venn et al., 2014), suggesting that traditional functional groups may obscure some important trait characteristics associated with vegetation change (Saccone et al., 2017).

4.5.4 Underpinning assumptions
The findings of this study are based on several key assumptions. First, we assume that the species for which trait data are available are representative of all tundra species. Species lacking trait data are often rare (low abundance) or endemic (occur at few sites). The data gap for these missing species could represent unusual trait combinations not easily captured by trait-based classification (Sandel et al., 2015). We also do not examine mosses and lichens, which play an important role in ecosystem function in the tundra (Turetsky et al., 2010). Nevertheless, the species included in this study reflect the vast majority of tundra plant biomass and include the species known to be most rapidly responding to climate change (Elmendorf et al., 2012b).
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Second, we assume that plant traits are meaningful predictors of species response to environmental dynamics or effect on ecosystem function. In this study, we do not examine whether traits or alternative trait-based classifications better predict community dynamics than functional groups. Traditional functional groups may better predict certain ecological dynamics than trait-based approaches as they integrate multiple measured and unmeasured traits across plant organs, ecological strategy, and life cycle (Grime et al., 1997). Nevertheless, there is widespread evidence to support trait-based approaches to modelling ecosystem dynamics (Suding et al., 2008; Violle & Jiang, 2009; Cornwell & Ackerly, 2010; Soudzilovskaia et al., 2013, but see Clark, 2016). Single traits, such as plant height, have also predicted vegetation responses to change that are obscured within traditional functional groups (Elmendorf et al., 2012b). Continuing to assess the extent to which trait-based approaches can meaningfully describe and predict ecosystem processes therefore remains an essential research focus (McGill et al., 2006). Differentiating community responses or ecosystem processes using post-hoc trait-based classifications would provide a direct test of this question, and could offer valuable insight into the relative importance of different traits for prediction and modelling.

Third, we assume that the majority of trait variation occurs among species. Should large trait variation occur within species this could invalidate species-level clustering (Violle et al., 2012; Shipley et al., 2016). The species considered in this study have large geographical ranges, encompassing both Arctic and alpine tundra, and nontundra locations. However, our findings are robust when using individual trait-data (Fig S4.1), across site-specific species assemblages (Fig. 4.3), for the 25th and 75th percentile of species-level trait data (Fig. S4.5), and for only trait collection locations north of 60°N (Fig. S4.6-9). Furthermore, most studies have found within-species variation to be small compared to among-species variation (Kattge et al., 2011; Siefert et al., 2015; Anderegg et al., 2018), including in the tundra (Chapter 3). Nevertheless, within-species trait variation may be an important driver of community change, particularly at small spatial scales, and may explain highly individualistic species responses to change (Hollister et al., 2005). Thus, we advocate that studies should recognize and account for the extent of trait variation within communities.
Finally, attempts to classify species into functional groups may be impossible if trait expression or species response is dependent upon environmental and ecological context (Dorrepaal, 2007; Laughlin and Messier, 2015). Group classifications and even growth strategies may change depending on resource availability (Bret-Harte et al., 2001), such that division into discrete classifications may obscure the variability inherent to natural environments (Westoby and Wright, 2006). Although differences between functional groups were statistically significant in this study, the majority of trait variation was not explained by classifications, whether using traditional functional groups (81% of variance unexplained) or post-hoc classification (55% of variance unexplained). We therefore join those who advocate that ecological analyses should continue to move towards incorporating explicitly trait-based approaches, focusing on traits themselves as the fundamental units of analysis (McGill et al., 2006; Westoby and Wright, 2006; Violle and Jiang, 2009; Weiher et al., 2011; Laughlin, 2014).

### 4.5.5 Future priorities

Our findings suggest that new trait data collection campaigns should focus on traits that distinguish among ecological strategies and responses to changing growing conditions. While existing trait records have been informed by standardised protocols and contemporary research priorities (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013), these have tended to focus on easily measurable leaf traits. Future trait collection campaigns should therefore focus on ecologically important traits for which we have few records, including chemical and physiological traits (Eckstein et al., 1999), and whole-plant measurements, incorporating stem (Chave et al., 2009) and belowground (Iversen et al., 2015) characteristics (Fig 4.6). Finally, phenological traits such as leaf out or flowering time are rarely integrated into wider trait-based approaches, yet may be critical to predicting ecological responses, particularly in a warming tundra (Cleland et al., 2012).
4.6 Conclusions

In this study, we demonstrate that traditional plant functional groups poorly represent differences in the six most commonly-measured plant traits among tundra vascular plant species. Although functional groups were statistically distinct and consistent among sites, they explained only 19% of overall trait variation and primarily differentiated between resource economic traits rather than size-related traits. Post-hoc trait-based classification of species did not align with functional group classification, but produced robust alternative groupings that aligned with two global axes of trait variation. Together, our findings indicate that traditional functional groups may not characterize trait variation within tundra vegetation communities, particularly among size-related traits. We therefore argue that: i) traditional functional groups should be used with caution when testing ecological responses or ecosystem functions associated with size-related traits; ii) functional group approaches require sufficient species and trait measurements to capture variation within groups, within species, and among traits; and iii) the use of alternative classifications based on trait expression, or direct use of underlying trait data, could provide new insights for predicting vegetation change and ecosystem processes in response to global drivers of environmental change.


Dorrepaal, E., 2007. Are plant growth-form-based classifications useful in predicting northern


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diversity from space. Nature Plants 2, 1–5.
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Ecology and Evolution 21, 261–268.


Chapter 5. Drivers of tundra litter decomposition

5. Litter quality outweighs environmental drivers of litter decomposition across the tundra biome

The following chapter, ‘Litter quality outweighs environmental drivers of litter decomposition across the tundra biome’, has been prepared for submission as a Letter to *Nature*.

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Author contributions: HT and IMS conceived the study. JS devised and helped to adapt the Tea Bag Index for tundra settings. Data were collected by all authors except AD, DB and JS. HT compiled the tundra teabag dataset. HT and AB performed statistical analysis. HT wrote the manuscript with input from IMS, AB and contributions from all authors.
Chapter 5. Drivers of tundra litter decomposition

5.1 Abstract

High latitudes store over 50% of global soil carbon in cold and frozen ground (Hugelius et al., 2013), more than double current atmospheric stocks (Schuur et al., 2009). Anthropogenic warming is predicted to reduce tundra carbon stores by thawing frozen soils and altering decomposition rates (Crowther et al., 2016), either by stimulating decomposition directly (Aerts, 2006) or by changing plant litter inputs (Cornelissen et al., 2007). However, there is considerable uncertainty regarding the strength, direction and relative importance of the drivers of decomposition in the tundra (Sierra et al., 2015), partly due to a lack of coordinated field studies in this remote environment (Bonan et al., 2013). Here, we use two uniform substrates, green and rooibos tea, buried at 248 circum-Arctic and alpine sites to quantify the effect of temperature, moisture and litter quality on decomposition across the tundra biome. We found a strong linear relationship between decomposition and soil temperature across all sites. Decomposition increased with soil moisture even where soils were almost fully saturated. Litter quality had a seven times greater effect on summer mass loss than soil temperature alone, and was the strongest driver of litter decomposition across the tundra biome. Our results indicate that warming will directly increase decomposition across all high latitude environments, and that the indirect effects of climate change, particularly vegetation change, could have a profound impact on the carbon balance of the tundra biome.
5.2 Introduction

The decomposition of terrestrial carbon pools is a vital component of the global carbon cycle (Schuur et al., 2009). Climate warming may increase decomposition (Davidson and Janssens, 2006), accelerating carbon outputs (Crowther et al., 2016). Quantifying changes in decomposition will thus be critical for identifying major climate feedbacks. Perhaps nowhere is this more pertinent than in high latitude ecosystems, which contain over 50% of global soil carbon (Tamocai et al., 2009; Hugelius et al., 2013). Decomposition in the tundra is currently constrained by cold temperatures, frozen soils, and recalcitrant litter, encouraging the build-up of organic matter in soils (Aerts, 2006). However, tundra ecosystems are warming at twice the rate of the rest of the planet, with annual temperatures in the Arctic predicted to increase by 2-9°C by the end of the century (IPCC, 2014). As a result, decomposition is expected to accelerate in the tundra over the coming century (McGuire et al., 2009), releasing up to 37–174 Pg of carbon by 2100 (Schuur et al., 2015).

Despite the rate and potential impact of climate change on decomposition in the tundra, the environmental drivers of decomposition are not yet well quantified in this biome (Hicks Pries et al., 2013; Walz et al., 2017). Temperature and soil moisture are commonly considered the primary drivers of decomposition (Aerts, 2006), and together explain approximately 70% of variation in decomposition rates at global scales (Liski et al., 2003; Davidson and Janssens, 2006; Keuskamp et al., 2013). However, biogeochemical models exhibit large differences in both the shape and slope of the relationships between decomposition, temperature and soil moisture, particularly at climatic extremes (Sierra et al., 2015; Fig 5.1). This disagreement is in part driven by a lack of available real-world data from high-latitude regions (Bonan et al., 2013; Van Gestel et al., 2018), and contributes to the large uncertainty surrounding predictions of global soil carbon losses (Crowther et al., 2016; Van Gestel et al., 2018).
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Figure 5.1: Conceptual relationship between decomposition rate and (a) temperature, and (b) moisture across nineteen different biogeochemical model functions outlined in Sierra et al. (2015). Decomposition is modelled as an exponential (exp; red, six models) or sigmoidal (sig; blue, four models) relationship with temperature. Decomposition is modelled as a saturating (sat; blue, four models), optimal (opt; purple, three models), linear (lin; orange, one model) or sigmoidal (sig; red, one model) relationship with moisture. The blue shaded area indicates the temperature and moisture range of sites included in this study.

Decomposition is also highly dependent on substrate quality, and thus the structural and chemical traits of plant communities (Hobbie, 1996). Plant traits may be the dominant control on litter decomposition worldwide, outweighing environmental drivers even across biomes (Cornwell et al., 2008). Tundra plant communities are undergoing widespread changes, notably an expansion of woody shrubs (Myers-Smith et al., 2011), that could dramatically alter litter characteristics (Cornelissen et al., 2007). Site-scale experiments commonly indicate that litter quality explains greater variation in litter decomposition than environment variables. (Hobbie, 1996; Baptist et al., 2010; Carbognani et al., 2014; Demarco et al., 2014; Blok et al., 2016). However, the effect of litter quality on decomposition in the tundra has not yet been tested at large scales, primarily due to the challenge of controlling for litter quality across multiple experiment sites. Understanding the influence of litter quality on decomposition at large scales and in relation to environmental variation will therefore be critical to improving predictions of decomposition change in the tundra.

In this study, we quantify the drivers of litter decomposition across the circum-Arctic
and alpine tundra using a standardised method and common litter substrates – the Tea Bag Index (Keuskamp et al., 2013). This protocol uses two commercially available tea types of differing decomposability (rooibos and green tea), providing a highly replicable method for measuring early-stage decomposition across sites. Decomposability of the two tea types is also representative of leaf litters for tundra species (Fig S5.1) and thus provides an appropriate analogue of the potential impact of vegetation community change in tundra ecosystems.

### 5.3 Methods

We buried 4,680 tea bags at 5cm depth at 248 sites across the tundra biome (Fig 5.2; Table S5.1). Mean annual temperatures ranged from -10.2°C to 12.7°C, with summer temperatures up to 24.9°C at the warmest site. We recovered tea after three (summer), nine (winter) or twelve months (year) and calculated three metrics of decomposition: 1) percent mass loss, indicating the proportion of initial mass decomposed, 2) decomposition rate \(k\), indicating the rate at which labile material is lost and thus short-term turnover, and 3) stabilisation factor \(S\), indicating the proportion of labile material remaining when initial decomposition has stabilised, and thus long-term carbon storage potential.

We examined the relationship between the three decomposition metrics, three locally-measured environmental variables (air temperature, soil temperature and soil moisture), and three gridded climate variables: Climatologies at High Resolution for the Earth’s Land Surface (CHELSA) air temperature, CHELSA precipitation, and European Space Agency (ESA) soil moisture data. We used Bayesian hierarchical models with tea type, environmental variable and days of burial as fixed effects, and grid cell, site and plot as hierarchical random effects. This approach allowed us to account for multiple levels of variation and the different scales at which environmental variables were measured. We ran separate models for each environmental variable, and also examined the interaction and relative importance of temperature and moisture (measured and gridded variables) using the same model structure but including an interaction term between temperature and moisture. To allow comparison across variables, we standardised all data using mean zero, unit variance scaling. We examined within-site relationships using the same model structure and standardising decomposition and environmental variables within grid cells. Finally, we modelled decomposition across the tundra by extrapolating relationships using CHELSA and ESA soil moisture data from 1979 to 2013.
Figure 5.2. Modelled summer decomposition (percent mass loss) of green tea for tundra and sub-Arctic regions based on long-term average summer air temperature (Climatologies at high resolution for the Earth's land surface; CHELSA) and soil moisture (European Space Agency data; ESA) from 1979-2013. Field collection regions from Arctic and alpine tundra locations are illustrated by green circles, grouped by geographic region (Table S5.1; excludes Australian alpine region). Circle size indicates the number of tea bag replicates within each geographic region.

5.4 Results

Summer mass loss increased linearly with soil temperature (Fig 5.3) across all tundra sites by 1.81% ± 0.30% per ºC for labile green tea and 0.94% ± 0.29% per ºC for recalcitrant rooibos tea. In contrast to the relationships assumed in the majority of biogeochemical models (Sierra et al., 2015), we did not see an exponential increase in decomposition with temperature across the temperatures experienced in the tundra biome (Liski et al., 2003; Sjögersten and Wookey, 2004). Relationships were consistent across incubation periods (Figs S5.2-S3) and decomposition variables (Figs S5.4-S5), with higher temperatures associated with a faster decomposition rate.
and lower stabilisation factor across litter types. Mass loss also increased with soil temperature within grid cells (Fig S5.6), and not only across large biogeographic gradients of the tundra. However, we observed considerable within-site variation in decomposition, emphasising the importance of site-specific factors (Bradford et al., 2014) such as microbial community (Wardle et al., 2004; García-Palacios et al., 2013) and soil chemistry (Knorr et al., 2005).

Figure 5.3. Relationships between decomposition (summer mass loss), measured environmental variables (a-c), and gridded climate data (d-f). Points indicate individual tea bag replicates across all sites. Lines indicate hierarchical Bayesian model fit with 95% credible intervals. Colours indicate tea type (red = rooibos tea, green = green tea). See also Table S5.2.

Summer mass loss slightly increased with site-measured soil moisture across tundra sites (green tea: 0.08% ± 0.07% per °C, rooibos tea 0.01% ± 0.06% per °C, not significant; Fig 5.3c), and notably did not decrease at high moisture values, even where soils reached nearly 100% saturation. Relationships for winter and year-long incubations were weaker than those for summer-only incubations (Figs S5.2-3), potentially due to freezing of soil water which inhibits decomposition. Mass loss also demonstrated a positive but non-significant relationship with soil moisture within grid cells (Fig S5.6). When accounting for the interaction between temperature and moisture, soil moisture increased the intercept, but not the slope, of the temperature-
decomposition relationship (Fig S5.7), with decomposition greater in wetter sites regardless of soil temperature. Soil moisture had a marginally lower effect on decomposition than temperature across all tundra sites (Fig 5.4), but effect sizes were surprisingly similar given strong temperature limitations in the tundra biome.

We found strong relationships between decomposition and all gridded climate variables across the tundra (Fig 5.3 d-f; all relationships significant). The interaction between gridded temperature and moisture variables was comparable to site-measured variables, with greater mass loss in wetter sites (Fig S5.7). Extrapolating relationships across tundra and subarctic regions revealed strong spatial variation in decomposition along biogeographic gradients, suggesting high sensitivity to future warming (Fig 5.2). This ability to map decomposition across large scales using standardised data could act as a powerful tool for predicting future carbon loss if combined with existing carbon inventories (Hugelius et al., 2013) and climate change projections (IPCC, 2014). For example, central European Arctic and eastern Canadian Arctic regions that currently experience some of the lowest rates of decomposition across the tundra are projected to be highly vulnerable to future soil carbon loss (Crowther et al., 2016).

Litter quality was the strongest driver of decomposition across the tundra biome (Fig 5.4 a - c), with a seven times greater effect on summer mass loss than soil temperature and eleven times greater effect than soil moisture. This strong effect of litter quality was maintained regardless of environmental context or incubation length (Fig 5.4 d - f). Although litter quality may have a smaller effect on decomposition over longer time periods (Trofymow et al., 2002; Hollister et al., 2005; Harmon et al., 2009), which cannot be accounted for in this study, mass loss of these two tea types did not converge after two years (Fig S5.8). Our results align with a large number of site-specific studies that find decomposition is more strongly influenced by litter quality than climatic variability (Hobbie, 1996; Baptist et al., 2010; Carbognani et al., 2014; Demarco et al., 2014; Blok et al., 2016). However, our study is the first to demonstrate the importance of litter quality versus temperature and soil moisture as drivers of decomposition across the large biogeographic scales and extreme environmental conditions of the tundra biome.
Figure 5.4. Litter quality had a stronger effect on litter decomposition than environmental variables. Standardised effect sizes of environmental variables and litter substrate for summer incubations, year incubations and winter incubations (a-c). Data were insufficient to calculate the effect of days of burial (days within each incubation period) or temperature-moisture interaction for winter incubations. Distribution of mass loss values for the two litter substrates (rooibos tea – red; green tea – green) for summer incubations, year incubations and winter incubations (d-f).
5.5 Discussion and conclusions

Our findings demonstrate that decomposition in the tundra is sensitive to both increases in temperature and climate-induced changes to litter quality. We found positive linear relationships between decomposition, soil temperature and soil moisture, with the greatest decomposition occurring in warmer and wetter sites (Fig 5.3, Fig S5.7). Based on these relationships, we estimate that predicted Arctic warming of 2-9°C over the 21st century could produce up to a doubling of summer litter mass loss at the coldest tundra sites. However, potential changes are highly contingent upon site-specific factors, including moisture availability, substrate quality and decomposer community (García-Palacios et al., 2013; Bradford et al., 2014). Although we focus on short-term decomposition processes, increases to early-stage decomposition due to warming or more labile litter inputs could accelerate biogeochemical cycling (Buckeridge et al., 2009) and stimulate the loss of older organic carbon (Mack et al., 2004; Cornelissen et al., 2007) through nitrogen mining (Moorhead and Sinsabaugh, 2006) or priming of microbial communities (Sistla et al., 2013).

Contrary to our expectations, we observed neither an exponential increase in decomposition with temperature, nor a decrease in decomposition at the highest moisture values (Fig 5.3). The temperature and soil moisture relationships assumed in many biogeochemical models (Sierra et al., 2015; Fig 5.1), with exponentially greater decomposition rates at warmer temperatures and saturating or optimal relationships across variation in soil moisture, could thus overestimate decomposition at warmer tundra sites, but underestimate decomposition in colder or wetter sites. This discrepancy may arise from important interactions in field settings. For example, higher temperatures dry surface soils and could counteract the direct effect of warming due to insufficient available moisture to support decomposer communities (Thakur et al., 2018), as has been observed in warming manipulation experiments (Rinnan et al., 2008). Higher soil moisture may also increase mass loss due to leaching (Bokhorst et al., 2010). Accounting for such interactions in biogeochemical models will thus be critical to predicting the impacts of warming of decomposition (Liski et al., 2003; Hicks Pries et al., 2013; Thakur et al., 2018) and resulting impacts on the carbon cycle (Crowther et al., 2016).

Our findings provide strong biome-level evidence that changes to plant communities, and thus the plant traits that determine litter quality, could have a larger impact on
litter decomposition than the direct impacts of warming in the tundra, even at large scales (Fig 5.4; Baptist et al., 2009; Gavazov, 2010; Blok et al., 2016). The two tea types in this study have highly contrasting chemical characteristics (Keuskamp et al., 2013), but are representative of litter decomposition for the range of species in tundra communities (Fig S5.1). The tundra is currently experiencing rapid vegetation change (Elmendorf et al., 2012), notably an increase in shrub and graminoid species and a decrease in bryophytes and lichens (Joly et al., 2009; Myers-Smith et al., 2011; Elmendorf et al., 2012). Warming may also alter leaf trait characteristics within species (Hudson et al., 2011). Vegetation change could thus mitigate or accelerate the effects of warming on litter decomposition in the tundra (Cornelissen et al., 2007), though the direction and magnitude of this effect is unknown. Thus, a critical direction for future research will be to quantify the direction, rate and magnitude at which decomposition-related trait change could occur across tundra ecosystems.

Finally, changing decomposition rates will have profound implications for the global carbon cycle as the climate warms. Plant litter decomposition makes up 70% of the global carbon flux from soils (Althuizen et al., 2018), and so warming-induced acceleration of litter decomposition could greatly increase carbon losses in the tundra. High-latitude ecosystems have also historically acted as long-term carbon sinks (Schuur et al., 2009) and contain a substantial proportion global soil carbon stocks (Tamocai et al., 2009; Hugelius et al., 2013). As the tundra warms, these high latitude regions are predicted to experience the greatest carbon losses in the coming century (Crowther et al., 2016), though such predictions are highly sensitive to data availability (Van Gestel et al., 2018). Our findings provide well-resolved statistical relationships from standardised field observations that can be used to parameterise Earth system models and refine this critical feedback to the global carbon cycle. Ultimately, our findings demonstrate that climate change will highly likely increase decomposition across the tundra biome, with profound repercussions for the carbon balance of this globally important carbon sink.


Chapter 5. Drivers of tundra litter decomposition


Chapter 5. Drivers of tundra litter decomposition


Chapter 6. Vegetation change does not alter litter decomposability

6. Tundra vegetation change does not alter community litter decomposability

The following chapter, ‘Tundra vegetation change does not alter community litter decomposability, has been prepared for submission as a Letter to Ecology Letters.

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Author contributions: The sTUNDRA working group conceived the study. JHCC conducted the original ‘Meeting of Litters’ study. HT collected additional decomposition data with help from IMS. AB compiled the TTT database. The ITEX group provided vegetation monitoring data. HT and AB conducted statistical analysis. FS provided additional statistical support. HT wrote the manuscript with input from IMS and contributions from all authors.
6.1 Abstract

The impact of warming on the carbon balance of tundra ecosystems is a critical unknown for predicting global climate change feedbacks. Plant litter represents the primary carbon input to tundra soils, yet it is unclear whether ongoing vegetation changes are altering litter decomposability. Here we combine 1) a multi-site litter decomposition experiment, 2) the largest database of tundra plant traits, and 3) three decades of vegetation monitoring to quantify the decomposability of plant communities across the tundra biome. We find that litter decomposability increases with temperature and soil moisture over biogeographic gradients, but find no significant change in community-level decomposability over three decades of vegetation monitoring. Our results suggest that tundra vegetation change has so far had no net impact on litter decomposability, but that in the long-term vegetation change could produce a positive feedback to climate change.

6.2 Introduction

The tundra biome is a globally important store of organic soil and litter carbon (Schuur et al., 2015). The combination of low temperatures, permafrost soils and low quality plant litter has meant that the tundra has historically acted as a global carbon sink (Oechel et al., 1993; Schuur et al., 2009), with over 50% of terrestrial soil carbon found at high latitudes (Hugelius et al., 2013). However, high latitude ecosystems are experiencing rapid warming (IPCC, 2013), with soil carbon stores vulnerable to release to the atmosphere via decomposition (Davidson and Janssens, 2006; Schuur et al., 2015), potentially transforming the tundra from a carbon sink to a carbon source (Koven et al., 2011). Enhanced decomposition may be at least partially offset by increased carbon storage in biomass (Schuur et al., 2009; Sistla et al., 2013; Lafleur and Humphreys, 2018) and plant litter (Cornelissen et al., 2007) as warming increases productivity and alters the structure and composition of vegetation communities (Myers-Smith et al., 2011; Elmendorf et al., 2012a, 2012b; Pearson et al., 2013). Understanding the balance between decomposition and carbon storage in plant biomass is thus critical to predict the future carbon balance of tundra ecosystems.
Chapter 6. Vegetation change does not alter litter decomposability

Warming-induced vegetation change has been hypothesised to produce a negative feedback to climate change by decreasing the decomposability of tundra plant community litter (Cornelissen et al., 2007). This hypothesis has not yet been directly tested, despite litter decomposition comprising approximately 70% of the global carbon flux from soils worldwide (Althuizen et al., 2018). There is a growing evidence that litter quality is a key driver of decomposition rates, both at the global scale (Cornwell et al., 2008) and in the tundra (Hobbie, 1996; Shaw and Harte, 2009; Chapter 5). Litter quality commonly explains greater variation in decomposition than environmental factors in manipulation experiments (Baptist et al. 2010; Carbognani et al. 2014; Blok et al. 2016 but see Cornelissen et al. 2007), and exhibits a stronger control over litter mass loss than soil temperature or moisture across the tundra biome (Chapter 5). Litter quality also mediates the decomposition of old soil carbon via priming or changes to microbial communities (Moorhead and Sinsabaugh, 2006; Wang et al., 2015; Christiansen et al., 2017; Blok et al., 2018). For example, addition of fresh carbon and nitrogen has been shown to double the decomposition of deeper soil carbon (Mack et al., 2004; Wild et al., 2014; Phillips et al., 2018). A shift in litter quality could thus profoundly alter decomposition, nutrient cycling and carbon storage in tundra ecosystems, yet the potential direction and magnitude of net litter quality change in a warming tundra is currently unknown.

Tundra plant communities are currently undergoing rapid change, including increased abundance of shrubs and graminoids, a decline in bare ground, and often a decline in lichen and bryophyte functional groups (Joly et al., 2009; Elmendorf et al., 2012b). In particular, shrub expansion has been observed across the tundra (Sturm et al., 2001; Tape et al., 2006; Myers-Smith et al., 2011), with woody cover predicted to increase by more than 50% by 2050 (Pearson et al., 2013). The lower decomposability of shrub litter compared to other species (Cornelissen et al. 2007), an increase in litter quantity (Mack et al., 2004; Elmendorf et al., 2012b), and greater proportion of recalcitrant woody biomass (Hobbie, 1996), have together been hypothesised to decrease the decomposability of tundra plant communities (Cornelissen et al. 2007). Should this be the case, on-going vegetation change towards a more shrub-dominated tundra could produce a negative feedback to warming through the storage of carbon in living biomass and plant litter.
At the same time, tundra plant communities are experiencing ‘thermophilisation’ – undergoing a shift towards species or traits associated with warmer thermal niches (Elmendorf et al., 2015; Steinbauer et al., 2018). Such a shift could increase the abundance of opportunistic, ‘fast’ species associated with rapid decomposition (Sundqvist et al., 2011; Freschet et al., 2012; Reich, 2014). Furthermore, many plant traits linked to decomposition, including specific leaf area (Cornwell et al., 2008; Sundqvist et al., 2011; Liu et al., 2018) and leaf nitrogen content (Cornwell et al., 2008; Freschet et al., 2012) exhibit strong positive biogeographic relationships with temperature (Bjorkman et al., Nature in revision; Hobbie, 2015). As such, thermophilisation of tundra plant communities could increase litter decomposability, speeding up biogeochemical cycling and potentially producing a positive feedback to warming. Understanding the direction of the vegetation-litter feedback is thus critical to quantifying and predicting decomposition change and rates of biogeochemical cycling.

In this study, we quantify for the first time the change in plant community decomposability in the tundra biome. We combine i) a litter decomposition experiment, ii) the largest available database of tundra plant traits, and iii) three decades of vegetation monitoring to estimate community-level decomposability of tundra plant communities over space, over time, and with warming. We hypothesise 1) that the decomposition potential (decomposability) of litter inputs to soils from tundra plant communities will increase with temperature across biogeographic gradients, and therefore 2) that litter inputs to soils from tundra plant communities have become more decomposable over time as a result of climate warming.

## 6.3 Methods

### 6.3.1 Litter decomposition

We quantified two-year decomposition of fresh leaf litter for 63 tundra plant species, representing six plant functional groups (12 deciduous shrubs, 6 evergreen shrubs, 16 graminoids, 24 forbs, 4 mosses and 1 lichen). We also decomposed fresh stem litter for an additional six shrub species (5 deciduous, 1 evergreen). We combined data from a previously published experiment (Cornelissen et al., 2007) with a new litter bed experiment replicating the original study’s methods. Fresh leaf litter was collected from 33 sites in 1996-2001 (Cornelissen et al., 2007); fresh leaf and stem litter was collected from three sites in the Yukon, Canada in 2015 (Fig 6.1; Table S6.1). Litter
collection followed a standardised protocol based on Quested et al. (2003) and air dried in the dark. Approximately 500mg of litter was weighed into nylon bags with a 1mm mesh size, with a 0.3 mm mesh size used for very fine-leaved species. Two subsamples per species per collection site were used in (Cornelissen et al., 2007) and 10 per species per plant organ per collection site in the litter bed added by this study. Mesh size or initial litter amount had no significant effect on percentage mass loss (Cornelissen et al., 2007).

**Figure 6.1:** Methods used to estimate the community-weighted decomposability of tundra plant communities. Data were collated from three separate datasets i) the ‘meeting of litters’ experiment (Cornelissen et al., 2007), with additional experimental data, providing standardised litter decomposition for 63 tundra species (red and yellow points), ii) the ‘tundra trait team’ database, providing 79,509 trait observations for 703 tundra species (grey points; Bjorkman et al. GEB in revision), and iii) the International Tundra Experiment (ITEX), providing up to 26 years of ambient vegetation monitoring across 1,781 tundra plots (Henry and Molau, 1997; Elmendorf et al., 2012b).
We decomposed litter at three sites: Abisko, northern Sweden, (alt. 380 m a.s.l., 68.35 °N, 18.82 °E, 2001-2003), Latnjajaure, northern Sweden (alt. 980 m a.s.l., 68.36 °N, 18.49 °E, 2001-2003) and Kluane Lake, Canada (alt 690 m a.s.l, 61.03 °N, -138.41 °E, 2015-2017; Fig 6.1). Litter beds followed a standardised design across all experiments, composed of a wooden frame sunk 30mm into the soil. Litter bags were laid out flat in the litter bed without overlap and covered with an incubation medium of local species. The litter medium was held in place using mesh netting and protected against mammals using chicken-wire. We retrieved all litter bags after two years, which were cleaned and dried at 70°C for 48 hours. We calculated two-year mass loss as the ratio of final to initial litter mass.

6.3.2 Community decomposition data
We compiled community composition data for 117 sites (defined as plots in a single contiguous vegetation type) within 38 regions (defined as a CRU2 grid cell) based on previous syntheses of tundra vegetation change (Bjorkman et al., Nature in revision; Elmendorf et al., 2012b). Repeat plot-level surveys of species composition and cover were conducted at each site between 1989 and 2015 over a minimum duration of 5 and up to 21 years, for a total of 1,781 unique plots and 5,507 plot-year combinations. Vegetation monitoring sites were located in Arctic or alpine tundra, ranged in latitude from 40° N (Colorado Rockies, USA), to 80° N (Ellesmere Island, Canada), and were circumpolar in distribution (Fig 6.1).

We extracted summer (warmest quarter) temperature estimates for each of the vegetation survey sites from both the WorldClim3 (for long-term averages; http://www.worldclim.org/) and CRU2 (for temporal trends; http://www.cru.uea.ac.uk/) gridded climate datasets. WorldClim temperatures were corrected for elevation based on the difference between the recorded elevation of a site and the mean elevation of the WorldClim grid cell according to a correction factor of -0.005 °C per meter increase in elevation (Bjorkman et al., Nature in revision). The average long-term (1960-present) temperature trend across all sites was 0.26 (range -0.06 to 0.49) and 0.43 (range -0.15 to 1.32) °C/decade for summer and winter temperature, respectively. We included a categorical soil moisture variable, measured in the field at each site, representing dry, moist and wet tundra, according to the methods described in Elmendorf et al. (2012b).
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6.3.3 Trait data
We used plant functional traits to model the relationship between live-plant characteristics and litter decomposability in order to estimate the decomposability of tundra species not included in experimental litter beds. Leaf traits have been demonstrated to correlate with litter quality and decomposition across a range of previous studies in multiple biomes (Cornwell et al., 2008; Fortunel et al., 2009; Hattenschwiler et al., 2011). We compiled trait data for species in the community composition dataset from the ‘Tundra Trait Team’ database (Bjorkman et al., GEB in revision), the largest currently available database of tundra plant traits. We selected twelve traits that we hypothesised could relate to litter decomposition based on previous analyses and had sufficient traits for tundra species: specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen, leaf carbon, leaf phosphorous, leaf carbon:nitrogen ratio, leaf area, leaf dry mass, leaf fresh mass, leaf δ15 nitrogen, leaf lifespan, and stem specific density (SSD). In total, 79,509 trait observations were available, for a median of 3,858 observations per trait (1,290 – C:N ratio to 17,610 – SLA) and 389 species per trait (57 – SSD to 621 – leaf area) per trait. We extracted WorldClim climate variables for all trait observations with latitude/longitude values recorded (74,372 records in total). Because most trait observations did not include elevation information, temperature estimates for individual trait observations were not corrected for elevation.

6.3.4 Data analysis

Decomposition
We examined the sources of variation in leaf and stem litter decomposition to account for potential explanatory variables in our predictive models. We partitioned sources of variation using a generalised linear mixed-effects model with species, litter bed location and litter collection site as random effects using the R package ‘nlme’. We conducted variance component analysis on this model using the R package ‘varcomp’ with variance scaling. We examined differences in mass loss across latitude, and mean summer and winter temperatures of litter collection sites using linear mixed effects models with latitude / temperature as a fixed effect and species as a random effect with random slopes. To account for differences in the temperature ranges across species, we standardised temperature variables within each species using mean zero, unit variance scaling.
Decomposition - trait relationships

We tested the relationships between plant traits and two-year mass loss for all traits hypothesised to influence decomposability (Figs S6.1-2), both for individual traits and for trait combinations, using linear mixed effects models with decomposition site as a fixed effect and species and collection site as random effects. We did not test trait combinations of correlated traits (Pearson’s correlation coefficient > 0.6). We used species-mean traits as predictor variables as we found no significant effect of litter collection site on mass loss, and litter collection site information was too variable to estimate site-specific traits. We selected models for each plant organ (leaves and stems) based on comparison of estimated marginal $R^2$ and AIC scores across models (Tables S6.2-4).

Leaves: $Mass\ loss \sim LDMC + Leaf\ nitrogen + \sqrt{Leaf\ Area}$

Stems: $Mass\ loss \sim LDMC$

The traits selected represent different leaf properties, capturing both structural (LDMC and leaf area) and chemical (leaf nitrogen) characteristics, and have been identified as key drivers of litter decomposition in previous studies (Cornwell et al., 2008). We did not test some traits found to correlate strongly with litter decomposition, most notably leaf lignin (Melillo et al., 1982), as these traits were available for too few tundra species to be included in this study.

Trait estimates across monitoring plots

We calculated the community-weighted decomposability – the decomposability of each species, weighted by the abundance of that species – of all ambient vegetation plots in the International Tundra Experiment (ITEX; Henry & Molau 1997) and associated sites (Elmendorf et al., 2012b). Following Bjorkman et al. (Nature in revision), we used a Bayesian approach to calculate trait means for every species (s) using an intercept-only model (such that the intercept per species ($\alpha_s$) is equivalent to the mean trait value of the species) and variation per species ($\sigma_s$) with a lognormal error distribution (beta for LDMC as bounded between 0 and 1).

$traitobs_i \sim logNormal(\alpha_s, \sigma_s)$
Where species were measured multiple times in different locations, we additionally included dataset-by-location as a random effect. For species with more than four unique trait observations, we used non-informative priors (intercept estimated from the data). For species with fewer than four unique trait observations, we used a normal prior with mean and variance estimated from all species in the dataset. For species with no trait observations, we used a normal prior based on the genus, or if unavailable, family mean and variance. We sampled the mean and standard deviation of the posterior distribution 1,000 times in order to capture uncertainty and within-species variation.

To account for within-species trait variation, we estimated the species-specific trait-climate relationships for all species for which traits had been measured in at least four unique locations and spanned a temperature range of at least 10% of the entire (mean summer) temperature range (2.6°C). We estimated the relationship between each trait and temperature using a Bayesian hierarchical model, with temperature as the predictor variable and species (s) and dataset-by-location (d) as random effects:

\[
\begin{align*}
\text{trait}_{obs_i} & \sim \log\text{Normal}(\alpha_{s,d}, \sigma_s) \\
\alpha_{s,d} & \sim \text{Normal}(\alpha_s + \beta_s \cdot \text{temperature}_d, \sigma_1) \\
\beta_s & \sim \text{Normal}(B, \sigma_2) \\
\alpha_s & \sim \text{Normal}(A, \sigma_3)
\end{align*}
\]

where A and B are the intercept and slope hyperparameters (the parameters of the prior distribution), respectively. For LDMC we used a beta error distribution as trait values are bounded between 0 and 1. Temperature values were mean-centred within each species and we used non-informative priors for all coefficients. We estimated the trait value per species in every plot by combining the trait mean per species with estimated within-species variation, based on the slope of the species-specific temperature-trait relationship and temperature anomaly per plot. Where species-specific temperature-trait relationships could not be calculated, we used the mean temperature-trait relationship across all species.

**Community-weighted decomposability**

We calculated the community-weighted decomposability of all ITEX plots by combining trait estimates with decomposition models for leaf and stem litter. In this
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way, we treat litter decomposability as a ‘derived trait’, calculated from measured plant trait observations. To account for the influence of stem decomposition on plot-level decomposability, we partitioned species-level decomposability of woody (shrub) species into contributions from leaf and stem litter. We assumed that stem litter comprised 10% of annual litter inputs of shrub species, estimated based on litter collection across six 1 x 1m plots from alpine and Arctic tundra (H.J.D. Thomas, unpublished data). We also tested the sensitivity of models to the proportion of stem litter inputs, from 0% to 50%. We multiplied the decomposability of each species by the relative abundance of that species, across all iterations, to calculate the plot-level community distribution, and took the mean and standard deviation of this distribution to carry uncertainty through to community-weighted mean estimates.

Community decomposability over biographic gradients
We examined the change in community-weighted decomposability with summer temperature, categorical soil moisture, and the interaction between temperature and moisture over space using a hierarchical Bayesian modelling approach. This accounts for 1) the nestedness of sites within regions, and 2) site-level moisture variation versus regional level (WorldClim cell) temperature variation. We used the most recent year of plot-level data to estimate spatial relationships, to a total of 117 sites (s) nested within 73 regions (r):

$$cwmp \sim Normal(\alpha_s + \alpha_r, sd_p)$$

$$\alpha_s \sim Normal(\gamma_1 \cdot moisture_s + \gamma_2 \cdot moisture_s \cdot temperature_s, \sigma_1)$$

$$\alpha_r \sim Normal(\gamma_0 + \gamma_3 \cdot temperature_r, \sigma_2)$$

where cwmp is the estimated community-weighted mean (CWM) decomposability value per plot (p) and sd_p is the standard deviation of the posterior distribution. When there was only one site within a region, as was set to 0.

Change in decomposability over time
We examined change in community-weighted decomposability over time across repeated vegetation survey plots. We used a hierarchical Bayesian approach to estimate change at the region (CRU grid cell) level (r), with site (s) and plot (p) as a nested random effects where sites or plots were permanent and repeated.

$$cwmd_{decomp,p,y} \sim Normal(\alpha_p + \alpha_s + \alpha_{r,y}, decomp_{sd,p,y})$$
For non-permanent plots and for sites that were the only site within a region, the parameters $\alpha_p$ and $\alpha_s$ were set to 0. Region-level slopes were used to fit an average trend of community decomposability values over time:

$$
\alpha_{r,y} \sim \text{Normal}(a_r + \beta_r \cdot \text{year}_r, \sigma)
$$

$$
\beta_r \sim \text{Normal}(B, \sigma_1)
$$

$$
\alpha_r \sim \text{Normal}(A, \sigma_2)
$$

where $A$ and $B$ are the intercept and slope hyperparameters, respectively.

We also compared change in decomposability to the rate of temperature change over the same time interval (minus a lag of four years) and soil moisture at every site to determine whether change in decomposability was related to temperature change,

$$
\beta_r \sim \text{Normal}(\gamma_0 + \gamma_1 \cdot \text{temp}_r + \gamma_2 \cdot \text{moisture}_r + \gamma_3 \cdot \text{temp}_r \cdot \text{moisture}_r, \sigma)
$$

where $\beta_r$ is the rate of trait change per site (Fig 6.5). A four-year lag was chosen because this interval has been shown to best explain vegetation change in tundra (Elmendorf et al., 2015) and alpine (Gottfried et al., 2012) plant communities.

Finally, we examined whether species that have increased in abundance over time had higher or lower decomposability than species that have decreased or remained stable over time. We identified ‘winners’ (common tundra species that have increased in abundance by over 1% across all vegetation monitoring plots) and ‘losers’ (species that have decreased in abundance by over 1% across all vegetation monitoring plots) based on the results presented in Bjorkman et al. (Nature in revision). We estimated the decomposability of species in each category based on the trait-decomposability relationships presented above, and using species-mean traits. We examined differences in decomposability among categories using two-tailed t-tests.

All analysis was conducted in R version 3.3.2 (R Core Team, 2017). Data are available through Bjorkman et al., (GEB, in revision). Code is available at github.com/hjdthomas/tundra_litter_decomposability.
6.4 Results

6.4.1 Sources of variation in litter decomposition
We found consistent patterns in decomposition across experimental decomposition sites and among species, which correlated with plant trait expression. Species identity explained the majority of variation in two-year mass loss of leaf litter (60.9%, Fig 6.2a), with species and functional group rankings consistent across litter bed experiments (Fig 6.2b). Forbs demonstrated the greatest mass loss (68.4% mean mass loss), followed by lichens (62.5%), graminoids (55.0%), deciduous shrubs (40.5%), evergreen shrubs (37.7%), and mosses (4.5%). On average, stem litter lost 35.4% less mass than leaf litter of the same species, though differences were smaller or non-significant for the most recalcitrant shrub species (Fig 6.2c). Litter origin site explained only 5.8% of variation in leaf litter decomposition, and exhibited no significant relationship across species (Fig 6.2d, Fig S6.3). Leaf decomposition exhibited significant relationships with five plant traits: LDMC, leaf nitrogen, leaf area, leaf dry mass and leaf fresh mass, and a marginally significant relationship with leaf carbon (Fig 6.2e, Fig S6.1). Stem decomposition only exhibited a significant relationship with leaf dry matter content (Fig S6.2, Fig S6.4). In combination, the best predictors of decomposition were leaf dry matter content, leaf nitrogen and leaf area for leaf litter (40.2% of variation, Table S6.2), and leaf dry matter content for stem litter (26.5% of variation, Table S6.3).

6.4.2 Community decomposability over biographic gradients
The decomposability of tundra plant communities increased with mean summer temperature over space, and was strongly mediated by soil moisture. Community decomposability increased by 2.78% ± 1.49% °C⁻¹ across wet sites, but showed no significant change across dry sites (-0.35% ± 1.49% °C⁻¹; Fig 6.3a). Community decomposability demonstrated large variation within sites, particularly where gradients in moisture were present, in some cases exceeding biogeographical trends.
Figure 6.2: Litter decomposition was primarily explained by species identity, and demonstrated significant relationships with plant traits. a) Proportion of leaf decomposition variation explained by species identity, decomposition site and litter origin site. b) Two-year leaf mass loss of tundra plant species across six functional groups. Colours indicate litter bed location (red = Abisko, orange = Kluane, blue = Latnjajure). c) Two-year mass loss of leaf (green) and stem (brown) litter for six shrub species at the Kluane litter bed site. d) Relationship between two-year mass loss and litter origin for all tundra species collected from at least two sites. e) Standardised effect sizes of leaf decomposition-trait relationships for 11 plant traits. Symbols indicate trait significance (** = \( P < 0.01 \), ** = \( P < 0.01 \), = \( P < 0.1 \)) with significant traits coloured red.

6.4.3 Change in decomposability over time and with warming

Despite the strong biogeographic relationship between plant community decomposability and temperature (Fig 6.3a), we observed no significant change in community-weighted mean decomposability of tundra plant communities over the last three decades (decomposability-time slopes: -0.06% ± 0.11% °C⁻¹ (wet); 0.04% ± 0.04% °C⁻¹ (dry); Fig 6.3b). Soil moisture significantly altered the intercept of decomposability-time relationships, with consistently higher decomposability at wetter sites, but had no effect on the slope of the relationship. The rate of warming at a given site had no significant effect on decomposability change (Fig. 6.3c), with site-specific relationships evenly distributed around zero and no overall trend across sites.
Chapter 6. Vegetation change does not alter litter decomposability

Figure 6.3: Tundra plant community decomposability increases with summer temperature over spatial gradients, except at dry sites, but shows no change over time or with warming. Relationship between community-weighted decomposability and a) summer temperature and b) year of observation. c) Relationship between change in community-weighted decomposability (slope of decomposability-time relationship) and site-specific warming trend (slope of temperature-time relationship). All relationships are categorised by moisture class. Points represent community decomposability estimates and errors indicate the 95% credible interval of relationships. See also Table S6.5.
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6.5 Discussion

6.5.1 Litter decomposability as a long-term positive feedback to warming

In this study, we test the hypothesis that warming-induced vegetation change could produce a global negative feedback to climate change by decreasing the decomposability of tundra litter inputs to soils (Cornelissen et al., 2007). We find that the decomposability of tundra plant communities increases with temperature over biogeographic gradients, but observe no significant change in decomposability over three decades of vegetation monitoring, despite warming and vegetation change. Consequently, it is unlikely that the impacts of vegetation change on litter quality will greatly alter rates of decomposition and nutrient cycling in the short term, despite the importance of litter quality as a driver of decomposition rates (Aerts, 2006; Cornwell et al., 2008; Chapter 5). This lack of change reduces the potential for large-scale carbon storage in plant biomass and litter, despite productivity increases high latitude ecosystems (Natali et al., 2012; Sistla et al., 2013). Rather, litter decomposition in the tundra will likely be more strongly affected by climate warming (Liski et al., 2003; Aerts, 2006), or the effect of vegetation change on microclimate (Blok et al., 2010; McLaren and Turkington, 2010) or decomposer community (Eskelinen et al., 2009; Parker et al., 2015; Xue et al., 2016).

If observed spatial gradients mirror temporal vegetation changes over longer timescales, our findings suggest that tundra litter decomposability will increase in response to warming as plant communities shift towards species and traits associated with warmer environments. Such as shift could increase litter turnover (McLaren et al., 2017), accelerate nutrient cycling (Buckeridge et al., 2010), and reduce the strength of the long-term carbon sink in tundra plant litter (Mack et al., 2004; De Deyn et al., 2008). Moreover, faster decomposition and higher quality litter inputs may stimulate the breakdown of existing carbon stocks within tundra soils through priming of microbial communities (Kuzyakov et al., 2000). Given the magnitude of high latitude carbon stocks (Hugelius et al., 2013; Schuur et al., 2015) and high predicted rates of carbon loss over the 21st century (Crowther et al., 2016), these changes could have globally significant impacts on carbon cycling, and act as a long-term positive feedback to climate change.
6.5.2 Stable decomposability despite vegetation change

The relative stability of community-level litter decomposability over the last 30 years is surprising given strong biogeographic gradients in decomposability, and rates of warming and vegetation change in the tundra. On average, summer temperatures have increased by 0.26°C since the 1960s across monitoring sites in this study, associated with increased abundance of shrubs (Myers-Smith et al., 2011, 2015; Elmendorf et al., 2012b), and numerous site-specific shifts in community composition (Myers-Smith et al., in revision; Forbes et al., 2010; Villarreal et al., 2012; Callaghan et al., 2013; Hobbie et al., 2017) and plant traits (Choler, 2005; Hollister et al., 2005; Hudson et al., 2011). However, our results indicate that changes to plant communities have so far not significantly altered the traits most relating to litter decomposability, aligning with evidence that community-level resource-economic traits have not changed in response to warming over the last three decades in the tundra (Bjorkman et al., Nature in revision).

A lack of change in community decomposability could arise from counteracting processes within plant communities. Species that significantly increased in abundance over the last three decades were primarily shrubs (8 of 11 species; Bjorkman et al., Nature in revision), and had lower decomposability than species that remained stable or decreased in abundance (Fig 6.4). This suggests that abundance changes alone, notably shrub expansion (Myers-Smith et al., 2011, 2015), might be expected to decrease the decomposability of tundra plant communities (Cornelissen et al., 2007). However, abundance change could be offset by responses to warming within species (Hudson et al., 2011) or by species turnover (Elmendorf et al., 2015). For example, leaf nitrogen demonstrates large within-species variation (Kattge et al., 2011; Chapter 3) and increases with temperature (Bjorkman et al., Nature in revision; Reich and Oleksyn, 2004). Species turnover over time will also likely result in the migration of species from warmer environments (Elmendorf et al., 2015; Steinbauer et al., 2018), which are associated with greater decomposability (Figure 6.3; Reich, 2014). As such, counteracting drivers of trait change within plant communities could produce no net effect on ecosystem function at the community level (Suding et al., 2008).
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Figure 6.4: Common tundra species that have increased in abundance over the last three decades have lower decomposability than rare species, or common species that have remained stable or decreased in abundance. Abundance changes for the 50 most common tundra species identified from Bjorkman et al. (Nature, in revision). Increasing abundance = increased by > 1% across monitoring plots, No change = increased by < 1% but decreased by < 1%, Decreasing abundance = decreased by > 1%). Abundance change was not calculated for rare species. Symbols represent statistical significance (*** = $P < 0.001$; . = $P < 0.1$).

Stable community decomposability could also arise from a lack of species turnover over time. The majority of plant community (Elmendorf et al., 2015) and trait change (Bjorkman et al., Nature in revision; Soudzilovskaia et al., 2013) over spatial gradients is driven by species turnover. In contrast, observed vegetation change in the tundra has so far been largely driven by changes in abundance (Bjorkman et al., Nature in revision; Klanderud, 2008). Recruitment and colonisation of new species is assumed to be low in the tundra in the absence of disturbance (Gough, 2006), while factors such as soil properties (Lafleur et al., 2010) or photoperiod (Keller and Körner, 2003) may limit the migration of species from warmer regions (Aitken et al., 2008). Given strong spatial gradients in decomposability, a lack of clear evidence for interspecific trait change (Bjorkman et al., Nature in revision; Kaarlejärvi et al., 2012), and the counteractive effects of shrub expansion (Fig 6.1, Fig 6.4), we therefore argue that
community decomposability change in the tundra will occur slowly, requiring migration and establishment of new species. More broadly, such counteracting processes underline the importance of species identity and community turnover, rather than changing abundance or trait expression alone, as drivers of ecosystem function change (Tilman et al., 1997; Symstad et al., 1998; Allan et al., 2011).

6.5.3 Soil moisture as a change multiplier
Soil moisture emerges as a critical determinant of plant community decomposability in this study. Dry sites exhibited no significant change in decomposability over space, while wet sites displayed strong biogeographic gradients with temperature. Soil moisture has also been found to be a critical determinant of change across a range of ecological processes, including productivity (Huemmrich et al., 2010), vegetation change (Elmendorf et al., 2012b), shrub growth sensitivity (Myers-Smith et al., 2015; Ackerman et al., 2017), trait-environment relationships (Bjorkman et al., Nature in revision), and decomposition rates (Hicks Pries et al., 2013; Natali et al., 2015; Chapter 5). We therefore emphasise the potential role of soil moisture as a change multiplier – whereby wet sites exhibit greater rates of decomposition, while simultaneously experiencing the greatest rates of vegetation and trait change. Water availability could also act as a limiting factor to decomposition if warming increases drying of the litter layer (Christiansen et al., 2017). It is thus imperative to improve predictions of soil moisture change in the tundra (Seneviratne et al., 2010; IPCC, 2013), and that the role of soil moisture is incorporated into Earth system modelling (Lawrence et al., 2015), particularly at small scales (Todd-Brown et al., 2013) and at different depths (Hicks Pries et al., 2013).

6.5.4 Quantifying additional unknowns
Two key unknowns in this study are the contribution of woody matter and roots to community litter pools, and the role of non-vascular species. Greater shrub abundance will increase the proportion of woody inputs, which lost on average 35% less mass than leaves of the same species. However, the proportion of woody matter entering the litter pool is largely unknown, and may vary greatly among species (Hobbie, 1996; Freschet et al., 2013). In this study, we assume that 10% of annual shrub litter is composed of woody matter based on litter collection from six tundra plots. Altering this assumption changed the slope of temperature-decomposability relationships, particularly at dry sites, but did not significantly alter our findings (Fig
S6.5). However, if the proportion of woody species continues to increase as predicted (Pearson et al., 2013), quantifying woody matter inputs will be critical to understanding litter dynamics. Warming may also change root characteristics, which are critical for determining soil carbon sequestration (Clemmensen et al., 2013), particularly in the tundra where up to 90% of biomass is below ground (Iversen et al., 2015). Since the majority of trait data and litter decomposition studies focus on above ground inputs, understanding change in root decomposability is a key priority for future research.

Secondly, this study focuses on vascular plants, and does not include bryophyte cover in community decomposability estimates. Mosses play a critical role in the carbon balance of tundra ecosystems (Street et al., 2013), are highly recalcitrant (Fig 6.2, Hobbie 1996), and can retard the decomposition of other plant litter (Turetsky et al., 2012). Declines in moss abundance could thus alter community litter decomposability and increase the rates of carbon and nutrient cycling in tundra communities (Hobbie, 1996). However, evidence for moss abundance change is mixed (Elmendorf et al., 2012b; Lang et al., 2012), and data are currently insufficient to include mosses in the community decomposability approach taken by this study. Incorporating moss cover and traits into biome-wide syntheses of vegetation change could therefore further constrain decomposition predictions.

Finally, this study treats litter decomposability as a consistent ‘trait’, and thus estimates decomposability based entirely on plant community composition. This approach therefore cannot account for several key components of litter decomposition. Firstly, we cannot incorporate site-specific factors, including ‘home-field advantage’ of decomposer communities (Ayres et al., 2009; Veen et al., 2015), soil and nutrient characteristics (Mack et al., 2004; Street et al., 2017), or microclimate (Blok et al., 2010, 2016; McLaren and Turkington, 2010). Secondly, we cannot account for species diversity and interactions, and thus neither the effect of litter mixing (Gartner and Cardon, 2004) nor the functional diversity of plant or decomposer communities (Tilman et al., 1997; Díaz and Cabido, 2001; Scherer-Lorenzen, 2008). Thirdly, we cannot account for changes to decomposer communities that nevertheless may respond rapidly to warming (Xue et al., 2016) or vegetation change (Parker et al., 2015). Finally, the litterbag approach to measuring decomposition excludes soil macrofauna, and thus may significantly underestimate potential litter decomposition (Bradford et al., 2002). As such, although litter quality consistently emerges as a
critical determinant of litter decomposition across studies (Blok et al., 2016; Carbognani et al., 2014; Cornwell et al., 2008; Dorrepaal et al., 2007; Fierer et al., 2005; Chapter 5), it is critical to test decomposability predictions within site-specific contexts, especially where climate change could produce novel communities above or below ground.

6.6 Conclusions

The carbon balance of high latitude ecosystems will be strongly determined by the balance between decomposition and accumulation of carbon in plant biomass and litter (Cornelissen et al., 2007). In this study, we find that the litter decomposability of tundra plant communities increases with warming over biogeographic gradients, and has not changed over three decades of vegetation monitoring. A lack of change in decomposability is most likely due to slow species turnover in the tundra, and thus decomposability change will occur slowly, lagging behind warming. As a result, tundra vegetation change will not offset warming-driven carbon losses through increased carbon storage in plant litter, and in the long term could produce a global positive feedback to climate warming.


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Huemmrich, K.F., Gamon, J.A., Tweedie, C.E., Oberbauer, S.F., Kinoshita, G., Houston, S.,
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Chapter 6. Vegetation change does not alter litter decomposability

subarctic tundra. PLoS ONE 6, e27056.
7. Synthesis: Traits as predictors of ecosystem change and function

The overall objective of this thesis was to use plant traits to refine our understanding of vegetation change in the tundra biome, and to directly link vegetation change to ecosystem function. As the tundra continues to warm over the coming century (IPCC, 2014), it will be critical to predict the response of tundra vegetation communities beyond current analogues, and to quantify potential feedbacks to the global climate system. The findings of this thesis feed into these overarching research needs, firstly by refining trait-based approaches to understanding vegetation change (Díaz et al., 2016; Bjorkman et al., in revision), and secondly by using such trait-based approaches to link vegetation change to decomposition (Cornelissen et al., 2007; Cornwell et al., 2008).

In following section I synthesise the key findings of this thesis in relation to three major research themes, 1) the use of plant traits as predictors of ecosystem change and function, 2) the mechanisms, rates and relative importance of trait change in the tundra, and 3) the interactions between warming and other drivers of ecological change. I finish by highlighting key priorities for trait-based research in the tundra.

7.1 Summary of findings

7.1.1 Plant traits refine our understanding of vegetation change in the tundra

Trait-based approaches offer a potentially powerful framework through which to study ecological change and function, both in the tundra and worldwide (McGill et al., 2006; Reich, 2014; Shipley et al., 2016). However, trait-based ecology relies on several assumptions that are untested in extreme environments, including that relationships between plant traits are generalizable across biomes (Freschet et al., 2010), that the majority of trait variation occurs among species (Niinemets, 2015; Siefert et al., 2015; Shipley et al., 2016), and that trait variation is independent of scale (Messier et al., 2010, 2017). These assumptions are critical if traits are to be used to predict vegetation change, since they underpin the differences between major plant strategies, and the response of individuals, species and communities to environmental change.
Figure 7.1 Summary of thesis findings. Plant traits in the tundra vary along two key dimensions – plant size and resource economics, and primarily differ among species (Chapters 3 & 4). Warming is predicted to primarily alter traits related to plant size (Chapter 3), and this change has been demonstrated across tundra communities (Bjorkman et al., in revision). Plant traits are a key control over decomposition (Chapter 5), but vegetation change has so far had no net effect on litter decomposability in the tundra (Chapter 6).

I tested whether global trait relationships extended to the tundra biome, and how extreme environmental conditions in the tundra affected trait expression (Chapter 3). I found that tundra species exhibited the same two dimensions of plant form and function as global species (Díaz et al., 2016), and thus that they could be characterised according to two axes of variation – plant size and resource economics. I also found that these two dimensions were differentially affected by environmental conditions, with size related traits, but not resource economic traits, constrained compared to global distributions. These findings have two key implications. Firstly, the relationships between key plant traits, notably trade-offs along size and economic dimensions, are generalizable even to the coldest regions of the planet. These trait relationships thus likely represent fundamental constraints on plant life strategy that are largely independent of evolutionary history or geographical location (Wright et al., 2004; Flores et al., 2014; Díaz et al., 2016). Secondly, warming within the tundra
biome will likely increase traits associated with plant size, such as plant height or leaf area, but is less likely to lead to directional changes in resource economic traits at the community scale. This provides theoretical support for observations from warming experiments (Hudson et al., 2011), long-term monitoring at the site level (Elmendorf et al., 2012b), and recently of biome-scale community trait-change (Bjorkman et al., in revision).

I also examined the primary sources of trait variation within the tundra (Chapter 3), and whether traditional plant functional groups represented trait differences within plant communities (Chapter 4). I found that the majority of trait variation occurred among species, and that differences within species, or within functional groups accounted for 20-25% of overall trait variation. Although functional groups exhibited statistically distinct trait distributions, these were defined by resource economic traits and not size-related traits. This finding lends strong support to species-based approaches to assessing vegetation change, such as the use of species-mean traits to simplify variation within plant communities (Laughlin and Laughlin, 2013; Shipley et al., 2016). In contrast, functional group approaches may obscure some key patterns of vegetation change or subsequent impacts on ecosystem process (Saccone et al., 2017), particularly where related to plant size. Finally, I found that within-species trait variation is higher at small scales, and thus could play an important role in explaining the heterogeneity of vegetation responses to warming (Laughlin et al., 2012, 2017).

7.1.2 Plant traits strongly affect key ecosystem functions

Trait change in the tundra biome impacts a range of key ecosystem processes, including biomass accumulation (Forkel et al., 2016), carbon storage (Mack et al., 2004; Sistla et al., 2013), nutrient cycling (Lavorel and Garnier, 2002; Larsen et al., 2012), surface energy balance (Sturm, 2005; Blok et al., 2010; Loranty et al., 2014), and snow cover (Sturm et al., 2001; Myers-Smith and Hik, 2013; DeMarco et al., 2014a). In this thesis, I focussed on the potential feedback between community trait change and decomposition. Decomposition in the tundra is projected to increase with warming (Aerts, 2006), potentially releasing large quantities of carbon to the atmosphere (Schuur et al., 2015; Crowther et al., 2016). However, decomposition is also strongly dependent upon litter quality, and thus the traits of vegetation communities (Cornelissen et al., 2007; Cornwell et al., 2008). The relative importance of litter quality versus environmental controls on decomposition had not previously been tested at large scales in the tundra.
I quantified the key drivers of litter decomposition in the tundra using a standardised experiment across 248 circum-Arctic and alpine sites (Chapter 5). I found linear relationships between litter decomposition and soil temperature that were moderated by soil moisture. Temperature- and moisture-decomposition relationships did not align with the majority of modelled relationships contained within Earth system models (Sierra et al., 2015). My results suggest that existing Earth system models may overestimate carbon losses at the warmest tundra sites, but underestimate losses in wet sites. Despite strong relationships between decomposition and climatic variables, litter quality was the strongest driver of litter decomposition at the biome scale (Cornwell et al., 2008; Djukic et al., 2018). The importance of litter quality challenges previous assumptions that climate is the greatest determinant of decomposition in the tundra (Couteaux et al., 1995; Aerts, 2006), and suggests that changes in plant community composition could have profound impacts on decomposition and carbon loss in the tundra (Cornelissen et al., 2007; Baptist et al., 2010; Hobbie, 2015; McLaren et al., 2017).

7.1.3 Trait change has not yet produced a directional shift in litter decomposability

Litter decomposition makes up 70% of the global carbon flux from soils to the atmosphere (Althuizen et al., 2018), and is strongly dependent on litter quality (Cornwell et al., 2008; Chapter 5). Warming-induced changes to vegetation communities have thus been hypothesised to change decomposition and carbon storage in the tundra biome (Cornelissen et al., 2007). However, the direction, magnitude and rate of this feedback have not previously been quantified.

I examined the relationship between decomposition and key plant traits in 63 tundra species, creating a composite ‘decomposability’ trait for each species (Chapter 6). Based on this trait-decomposability relationship, I estimated the decomposability of all tundra species and created a community-weighted decomposability score for 1,781 long-term monitoring plots across the tundra. I then quantified change in decomposability over biogeographic gradients, over time, and with warming across the tundra biome.

I found that community litter decomposability increased with temperature over biogeographic gradients, particularly in wet sites. However, I found no net change in litter decomposability over time, or with warming. Although species that are increasing
in abundance, notably woody shrubs, have low decomposability compared to many other tundra species, this could be offset by species turnover or adaptation within species. My findings indicate that, despite widespread vegetation change at these long-term ecological sites, there has so far been no directional change in the traits relating to decomposability at the community scale.

A lack of change in community litter decomposability is perhaps unsurprising given that I do not find evidence for environmental filtering of economic traits in the tundra (Chapter 3), and that so far there is only evidence for a directional change in community canopy height at the biome scale (Bjorkman et al., in revision). This lack of change suggests that the direct impacts of warming and soil moisture change on decomposition will likely outweigh litter quality feedbacks (Baptist et al., 2010; DeMarco et al., 2014a), despite the importance of litter quality for decomposition (Blok et al., 2016; Carbognani et al., 2014; Chapter 5). However, long term trait change could produce a positive feedback to climate change as plant communities shift towards species and traits associated with rapid decomposition (Elmendorf et al., 2015; Steinbauer et al., 2018).

### 7.2 Plant traits as predictors of ecosystem change and function

Many existing approaches to understanding and predicting vegetation change in the tundra examine differences between plant functional groups (Figure 4.1, Table S4.1), or differences between individual species (Bret-Harte et al., 2001; Shaver et al., 2001; Deslippe and Simard, 2011; Klady et al., 2011; Little et al., 2015). These two approaches have provided a range of critical insights into the patterns and processes of tundra vegetation change, yet also have several key limitations. The functional group approach provides a broad, generalizable framework that can operate across scales (Dyer et al., 2001), yet risks obscuring key differences between species within groups, and thus key components of vegetation change (Dormann and Woodin, 2002; Saccone et al., 2017). The species approach offers a greater level of detail into patterns of vegetation change, yet also has limited power to explain mechanisms of change (Pennings et al., 2005), does not account for variation within species (Violle et al., 2012) or among populations (Gonzalo-Turpin and Hazard, 2009; Parker et al., 2017), and is less generalizable at large scales (Rumpf et al., 2014).
Trait-based approaches to understanding vegetation change offer an alternative framework, which assumes that it is the characteristics of individuals, rather than their species identity, that determines community change and ecosystem process (Lavorel and Garnier, 2002; McGill et al., 2006; Funk et al., 2017). In this thesis I test several key assumptions that underpin trait-based ecology (Shipley et al., 2016), and indicate that key axes and sources of trait variation are generalizable even in the cold extremes of the tundra biome. Differential environmental constraints on these two trait axes predict two further key findings - that traditional, growth-form based functional groups will be primarily explained by economic traits (Chapter 4), and that size related traits are more likely to demonstrate directional responses to warming (Bjorkman et al., in revision). Furthermore, in this thesis I demonstrate that plant traits are a dominant driver of litter decomposition in the tundra, and thus exert globally significant controls on ecosystem function (Chapter 5). Strong relationships between plant traits and decomposition rates level enable litter decomposability to be extrapolated over large scales and into the future (Freschet et al., 2012). Thus, the combined findings of this thesis strongly support the ‘traits manifesto’ (Reich, 2014): that plant traits act as predictors of ecosystem change and function.

7.2.1 Accounting for change and variation

The use of plant traits offers a flexible approach that can account for change and variability. Although the majority of trait variation occurs among species, differences within-species play a key role in community assembly and ecosystem functioning (Violle et al., 2012), and ultimately determine evolutionary change (Bolnick et al., 2011). Furthermore, tundra communities demonstrate intraspecific trait changes in response to warming, including an increase in canopy height, leaf size, shoot length and seed size (Walker et al., 2006; Hudson et al., 2011; Barrett et al., 2015; Baruah et al., 2017). For example, increased community canopy height on Qikiqtaruk – Herschel Island, Canada, has been driven by both an increased abundance of taller species, and height increases within species (Figure 7.2; Myers-Smith et al., in revision). Approaches that incorporate hierarchical trait change and variation can thus account for differences in both community composition (e.g. more Salix pulchra), and in individual characteristics (e.g. taller Salix pulchra) at different scales, among communities, and over time. However, the direct use of trait data in ecological analysis requires high quality and widespread data availability – something that was previously unavailable for the tundra (Kattge et al., 2011). Although new tundra trait
databases have now greatly improved trait coverage (Bjorkman et al., in revision), major trait gaps still remain, particularly for below ground traits (Bardgett et al., 2014; Iversen et al., 2015).

Figure 7.2. Increases in plant canopy height on Qikiqtaruk, - Herschel Island, Canada, are driven by both community change and interspecific responses. (a) Mean canopy height in twelve long-term monitoring plots in two vegetation communities, the ‘Komakuk type’ (blue) and the ‘Herschel type’ (orange). (b) Community mean canopy height (mean trait value multiplied by relative cover) of long-term monitoring plots, representing height changes due only to changing species abundance and turnover. Mean trait values are based upon height data collected on Qikiqtaruk - Herschel Island from 2014-2016. (c) Mean canopy height of *Salix pulchra* individuals within ‘Herschel type’ monitoring plots, representing height changes due only to intraspecific responses.

7.2.2 Insight into mechanism
Trait-based approaches have explained key components of ecological change that are obscured by species or functional group approaches (Pennings et al., 2005; Elmendorf et al., 2012b), and offer insight into patterns of change over time and with warming (Bjorkman et al., in revision; Hudson et al., 2011). Differences in trait response to change along principal trait axes or among species thus help to identify key underlying mechanisms of vegetation change. For example, there is strong evidence to suggest that taller species dominate plot-scale responses to warming or fertilisation, at the cost of smaller species such as forbs or bryophytes (Holliester et al., 2005; Walker et al., 2006; Klanderud, 2008). Indeed, shading is hypothesised to be one of the key mechanisms driving shrub dominance at many sites as the tundra warms (Mekonnen et al., 2018).
The findings of this thesis indicate that size-related traits, many of which have been demonstrated to strongly mediate community dynamics both in the tundra (Kaarlejärvi et al., 2017) and across global biomes (Kunstler et al., 2016), are likely to be most responsive to change, and thus that competition will be a major driver of vegetation change in the tundra (Brooker, 2006). Similarly, differences in resource acquisition traits such as mycorrhizal association (Deslippe and Simard, 2011) and rooting depth (McKane et al., 2002), or phenological traits, such as leaf out date (Cleland et al., 2012) explain observed vegetation change within communities. Finally, differences in trait plasticity among species may determine ability to respond to environmental change, and thus fitness in a warmer tundra (Berg and Ellers, 2010; Liancourt et al., 2015).

### 7.2.3 Predicting ecosystem function

Strong links between plant traits and ecosystem process provide a mechanism to incorporate vegetation change feedbacks into Earth system models (Verheijen et al., 2013). Generalizable relationships among plant traits (Chapter 3) offer opportunities to estimate unmeasured traits based on known trait relationships (Schrodt et al., 2015), including from remotely sensed data (Jetz et al., 2016). Biogeographic relationships in plant trait expression, both for individual traits (Bjorkman et al., in revision) and along key trait axes (Chapter 3, Chapter 6), constrain predictions of trait change in a warming tundra, and indicate which ecosystem functions are most likely to be affected by warming-induced vegetation change. For example, functions relating to plant height, such as albedo (Sturm, 2005; Loranty et al., 2014; Ménard et al., 2014) or snow dynamics (Sturm et al., 2001; Essery and Pomeroy, 2004; Myers-Smith and Hik, 2013) are likely to change more rapidly than functions relating to resource economics (Chapter 6, section 7.2.3). Finally, quantifiable relationships between plant traits and climatic variables (Bjorkman et al., in revision; Choler, 2005; Kichenin et al., 2013), and between plant traits and ecosystem functions (Chapter 6), can greatly enhance prediction of ecosystem function change over the coming century, particularly where future conditions or communities may have no current analogues (Edwards et al., 2005; Van Bodegom et al., 2012).
7.3 Mechanisms, rates, and relative importance of trait change

This thesis demonstrates that plant traits exert strong controls over ecosystem function from the site to biome scale. Differences in litter quality have a seven times greater effect on summer litter mass loss than differences in soil temperature alone across the circum-Arctic and alpine tundra biome (Chapter 5). Trait differences among species have also been demonstrated to alter albedo by 30-40% (Sturm, 2005; Williamson et al., 2016), increase snow depths by 10-25% (Sturm et al., 2001; Essery and Pomeroy, 2004), increase soil temperatures by 2-10 °C (Chapin et al., 2005; Paradis et al., 2016), decrease active layer depths by 9% (Blok et al., 2010), alter rates of nutrient cycling by up to 300% (Buckeridge et al., 2009 but see Myers-Smith and Hik, 2013) and alter soil carbon storage by over 200% (Parker et al., 2015; Christiansen et al., 2018; Lafleur and Humphreys, 2018). A critical question is thus not the extent to which plant traits determine ecosystem function, but the extent to which plant trait change determines ecosystem function change, particularly when compared with wider climatic change.

Community-level trait change can occur through four principal mechanisms: changing species abundance, species turnover, plasticity and evolution (Figure 7.3). The relative importance of these mechanisms, and the rate at which they occur, will thus be a key determinant of trait change in the tundra. Furthermore, the direction of trait change may differ between mechanisms (Chapter 6; Kichenin et al., 2013), making it difficult to predict overall direction of trait change at the community level (Suding et al., 2008).

7.3.1 Community-level processes: abundance and turnover

Differentiating the relative contributions of changing abundance versus species turnover to vegetation change is highly challenging, since most tundra synthesis studies have examined change at the functional group level (Walker et al., 2006; Elmendorf et al., 2012b, 2012a). Nevertheless, diversity measures across tundra sites remain largely unchanged despite warming (Myers-Smith et al., in revision; Hudson and Henry, 2009; Vellend et al., 2013). Where species-specific changes are recorded, warming has tended to change species abundance without altering community composition (Klanderud, 2008; Wilson and Nilsson, 2009). Widespread shrub expansion across the tundra is commonly driven by infilling from existing individuals, rather than by migration (Tape et al., 2006, 2012, Myers-Smith et al., 2011b, 2011a).
It is therefore likely that changes in species abundance comprise the majority of observed vegetation change in the tundra to date.

**Figure 7.3:** Mechanisms of trait change. Changes in community-level traits can occur through four mechanisms: changing species abundance (e.g. higher proportion of taller species), species turnover (e.g. new tall species), phenotypic plasticity (e.g. individuals of a species grow taller) and genetic evolution (e.g. taller species have greater fitness).

In contrast, species turnover requires the migration of new species and is dependent on reproduction, dispersal, recruitment and survival of new individuals (Engler et al., 2009; Elmendorf et al., 2015). Sexual reproduction and recruitment in the tundra is assumed to be low (Billings, 1987; Gough, 2006), except on bare soils following disturbance (Lantz et al., 2010), though reproductive success could be enhanced by warming (Klady et al., 2011). Nevertheless, there is evidence for latitudinal and altitudinal shifts in treeline (Harsch et al., 2009), shrubline (Myers-Smith, 2007; Hallinger et al., 2010; Myers-Smith and Hik, 2018), and species identity (Chen et al., 2011; Steinbauer et al., 2018). Thus, although species turnover is likely to occur slowly compared to abundance change, it comprises an important component of
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community-level trait change and may accelerate as the climate warms (Steinbauer et al., 2018).

7.3.2 Species-level processes: plasticity and evolution

Trait plasticity enables species and individuals to respond rapidly to environmental change on hourly to decadal scales (Shipley, 2000; Nicotra et al., 2010), and is itself a determinant of fitness (Shipley et al., 2016). Despite some evidence for trait change within species (see 7.2.1), this thesis suggests that within-species variation, and thus the magnitude of potential plastic responses, is low compared to differences arising from species turnover for many key plant traits (see also Bjorkman et al., in revision; Soudzilovskaia et al., 2013). Nevertheless, the potential for plastic responses in some traits, notably plant height (Hudson et al., 2011; Figure 7.2), combined with differences in plasticity among species and populations (Cleland et al., 2012; Liancourt et al., 2015; Figure 7.4), may play a strong role in shaping community assembly, fitness, and ultimately trait distributions in a warmer tundra.

A key unknown is the extent to which trait expression can track environmental change, and how this varies among species. Climate-trait relationships within species (e.g. Kichenin et al., 2013) may not equate to change over time if local genetic adaptation constrains plant responses (De Frenne et al., 2013). For example, high Arctic plant communities have showed little response to experimental warming, despite containing many of the same species as responsive plots at warmer sites (Hudson and Henry, 2010; Elmendorf et al., 2012a). In a common garden experiment conducted alongside this thesis, individuals of two shrub species (Salix pulchra, Salix richardsonii) from two populations separated by a 1,000km gradient were transplanted to a common garden approximately 3-5°C warmer than source sites. After four years, initial findings indicate that plant height, leaf length, leaf area and annual stem elongation show strong plastic responses to warming. However, trait responses vary substantially between populations, with southern willows demonstrating much greater trait change than northern willows (Figure 7.4). These findings suggest that, although the potential for plastic responses to warming may be high in some regions, genetic differences among populations could constrain trait change. Our findings mirror evidence for genetic differentiation among widespread tundra species, particularly for phenological traits (Bjorkman et al., 2017; Parker et al., 2017, Figure 7.4). Together, this evidence suggests that local adaptation could constrain trait responses to
warming, particularly at colder sites, and may require gene flow from warmer populations for trait change to occur (Jump and Peñuelas, 2005; Alsos et al., 2007).

**Figure 7.4:** Growth and leaf trait responses to warming differ between southern and northern populations of two widespread tundra willow species. Individuals of two species (*Salix pulchra, Salix richardsonii*) from two locations separated by a 1,000km gradient (Kluane Lake - southern alpine, Qikiqtaruk-Herschel Island - northern Arctic; Figure 1.3) were transplanted to a common garden approximately 3-5°C warmer (summer temperatures) than source sites. Populations demonstrated significant differences in (a) canopy height, (b) leaf length and (c) stem elongation, with rapid growth among southern individuals but slow growth among northern individuals. Lines indicate log-linear mixed model fit and 95% confidence intervals with sampling year and individual as hierarchical random effects and mother individual height and stem size as non-hierarchical random effects. Colours indicate source population (green = Kluane Lake, blue = Qikiqtaruk-Herschel Island). Populations also demonstrated significant but inconsistent differences in leaf traits, including (d) leaf area, (e) leaf fresh mass and (f) specific leaf area that indicated plastic responses to warmer conditions and differed between plant size and leaf economic traits.

### 7.3.3 Importance of trait change for ecosystem function
Overall, trait change in the tundra will likely lag behind warming trends, at least for economic traits. Firstly, the majority of trait variation occurs among species, so trait change will be primarily driven by species abundance or turnover (Chapter 3). Secondly, the majority of trait variation over space is driven by species turnover (Bjorkman et al., in revision; Soudzilovskaia et al., 2013), and thus community-level trait change will require migration of new species. Thirdly, environmental constraints to tundra trait distributions primarily apply to plant size traits, and not economic traits (Chapter 3). It is highly likely that a slower rate of species turnover compared to abundance change underpins the disconnect between rates of trait change over spatial gradients and change over time, identified by this thesis and other studies (Bjorkman et al., in revision; Elmendorf et al., 2015). Moreover, the importance of species identity and turnover points to the role community composition and functional diversity as regulators of key ecosystem processes, both in the tundra biome and globally (Tilman et al., 1997; Symstad et al., 1998; Allan et al., 2011).

A slow rate of trait change in the tundra biome suggests that trait feedbacks are less important than the direct impacts of climate change for functions related to economic traits, at least in the short term (Figure 7.5). Quantifying the direct relationships between warming and key ecosystem functions, taking into account large variation in site conditions across the tundra (Hodkinson et al., 1999), is therefore critical. In contrast, trait-climate feedbacks may exceed direct climate impacts on key ecosystem functions relating to plant size. We do not yet fully understand the net impact of changes in canopy height or leaf properties on several key functions, including albedo (Sturm, 2005; Williamson et al., 2016) and soil temperatures (Blok et al., 2010; Paradis et al., 2016). Quantification of trait feedbacks relating to plant size should thus be a future research priority. Finally, shifts in species identity are highly likely to occur over longer time scales (Edwards et al., 2005). Spatial relationships indicate that trait distributions will eventually shift towards ‘faster’ traits associated with rapid biogeochemical cycling (Reich, 2014; Chapter 6). Such trait changes could have profound implications for nutrient availability and carbon storage in the tundra, outweighing the direct effects of climate warming over the long term.
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7.4 Beyond warming: additional drivers of ecological change in the tundra

Lastly, the findings of this thesis emphasise the importance of predicting and modelling environmental changes beyond the direct impacts of warming. Differences in plant trait expression and soil moisture can mediate or even counteract warming effects, while additional factors that may be independent to warming, such as soil type, herbivory or photoperiod, could greatly constrain environmental change.

7.4.1 Trait change

A key message of this thesis is that quantifying trait change within the tundra is critical to predicting large-scale feedbacks to climate change. Indeed, inclusion of trait data and relationships within Earth system models can greatly change predictions. For example, Verheijen et al. (2015) found that incorporation of trait-climate relationships into an Earth system model resulted in a 33% reduction of the global carbon sink.
Plant height and leaf traits also constrain productivity estimates by accounting for species competition and turnover (Madani et al., 2018). Finally, direct use of trait data allows models to move beyond plant functional group classifications (Wullschleger et al., 2014), and to predict new trait combinations and feedbacks (Van Bodegom et al., 2012). Trait feedbacks thus have the potential to fill gaps in ecological knowledge and Earth system modelling, improving climate predictions (Wullschleger et al., 2014; Fisher et al., 2018).

### 7.4.2 Soil moisture

Soil moisture emerges as a key change driver across multiple dimensions (Figure 7.6). Soil moisture strongly influences trait relationships over biogeographic gradients, with stronger relationships in wetter sites (Bjorkman et al., in revision). Wetter sites are also experiencing more rapid vegetation change (Elmendorf et al., 2012b; Ackerman et al., 2017), including a greater probability of shrub expansion (Tape et al., 2006) and greater sensitivity of shrub growth (Myers-Smith et al., 2015a). Finally, soil moisture mediates key ecosystem processes, including productivity (Huemmrich et al., 2010), nutrient cycling (Chapin et al., 1988), nitrogen fixation (Rousk et al., 2018), and decomposition (Hicks Pries et al., 2013; Natali et al., 2015; Walker et al., in revision, Chapter 4). Soil moisture therefore mediates both trait change across the tundra, and the impacts of trait change on ecosystem function. Given large uncertainty surrounding future precipitation and soil moisture regimes (Seneviratne et al., 2010; IPCC, 2014), incorporating soil moisture into Earth system models and large-scale prediction of change in the tundra remains a major priority.
Figure 7.6 Soil moisture is a key driver of vegetation and ecosystem function change in tundra ecosystems. (a) Wetter sites have a greater probability of shrub expansion with warming (Elmendorf et al., 2012b); (b) Climate sensitivity of shrub growth increases with soil moisture (Myers-Smith et al., 2015b); (c) Canopy height is greater in wetter sites across biogeographic gradients (Bjorkman et al., in revision); (d) Increases in community litter decomposability with temperature are greater in wetter sites (Chapter 6); (e) Decomposition is greater in wetter sites (Chapter 5); (f) Net carbon losses are higher in wet sites compared to dry sites (Euskirchen et al., 2017).

7.4.3 Environmental constraints to trait change

The impact of warming on trait variation in the tundra may be restricted by several additional factors. Firstly, tundra systems are typically nutrient limited (Baddeley et al., 1994; DeMarco et al., 2014b). Release of nutrients through increased decomposition and changing soil conditions due to warming and permafrost thaw (Schuur et al., 2007; Keuper et al., 2012) may thus be a key driver of tundra vegetation change (Zamin and Grogan, 2012). However, in the long term, nutrient availability may constrain vegetation responses to warming (Barrett and Hollister, 2016) if growth responses outpace decomposition (Weintraub and Schimel, 2005). Secondly, herbivory mediates both vegetation change (Post and Pedersen, 2008; Olofsson et
al., 2009) and community-level trait characteristics (Speed et al., 2010; Kaarlejärvi et al., 2017). Changes in herbivore density may thus constrain trait responses to warming (Valladares et al., 2007). Thirdly, local or regional soil properties will likely change on longer timescales to climate change (Pearson and Dawson, 2003), yet act as a strong control on community composition (Eskelinen et al., 2009) and could constrain migration of species from warmer regions (Lafleur et al., 2010). Finally, the impact of photoperiod on potential growing season length could decouple trait-climate relationships in the tundra through controls on plant phenology (Keller and Körner, 2003; Semenchuk et al., 2016; Parker et al., 2017) or restricting the success of migrant species from warmer environments (Aitken et al., 2008).

7.5 Future directions for research

7.5.1 Incorporating trait gaps

This thesis has contributed to the development of a new tundra trait database (TTT; Bjorkman et al., in revision; Chapter S1), addressing the paucity of trait data for tundra species, and enabling assumptions underpinning trait-based ecology to be tested at the cold extremes of the planet. However, crucial data gaps remain. The majority of plant trait records are collected at a few, well-monitored locations, yet there is substantial variation in vegetation change at landscape and regional scales (Elmendorf et al., 2012a, 2012b; Guay et al., 2014; Bjorkman et al., in revision). Trait data collection has also tended to focus on above ground leaf or canopy traits, rather than on chemical and physiological traits (Eckstein et al., 1999) and below ground characteristics (Iversen et al., 2015). In particular, root traits vary substantially between species (Deslippe and Simard, 2011; Oulehle et al., 2016; Wang et al., 2016), predict community response to environmental change (Cornelissen et al., 2001; Soudzilovskaia et al., 2013), and influence key ecosystem processes such as soil carbon sequestration (Clemmensen et al., 2013). Yet despite up to 90% of tundra biomass being located below ground (Iversen et al., 2015), root trait data are still lacking for many tundra species (Bardgett et al., 2014; Iversen et al., 2015, 2017). Relationships among key plant traits, including linkages between above- and below-ground characteristics (Wardle et al., 2004; Tjoelker et al., 2005), offer an opportunity to address these trait gaps (Street et al., 2007; Schrodт et al., 2015), and could facilitate collection of key plant traits using aerial imagery (Van Wijk and Williams,
2005; Fraser et al., 2016; Asner et al., 2017; Eetu et al., 2018) or satellite data (Jetz et al., 2016).

7.5.2 Trait-based prediction of vegetation change.
Trait-based approaches offer strong potential to predict vegetation change and community assembly in a warming tundra. Plant traits demonstrate strong temperature relationships over biogeographic gradients (Bjorkman et al., in revision), demonstrate predictable patterns of trait change along key axes (Chapter 3, Chapter 6, Bjorkman et al., in revision), and explain vegetation change within tundra communities (Elmendorf et al., 2012b). A key next step is to test whether plant traits can directly predict community assembly by identifying ‘winners’ and ‘losers’ in response to environmental change. For example, tall (Klanderud, 2008) or economically acquisitive (Bret-Harte et al., 2001) species often outperform smaller, slower growing species in warming experiments. Phenologically sensitive species also tend to have improved growth, productivity and reproductive success in response to climate change (Cleland et al., 2012). Trait-based prediction of vegetation change could thus quantify ‘thermophilisation’ within the tundra, and more broadly could provide insight into processes of community assembly (Ackerly and Cornwell, 2007; Kraft et al., 2008; Venn et al., 2011; Kichenin et al., 2013).

7.5.3 Testing trait-based prediction of ecological process
The relationships between plant traits and key ecosystem functions facilitate prediction of ecosystem function change at large spatial scales and under future warming scenarios (Van Bodegom et al., 2012). At present, trait-based predictions of ecological function are based on statistical modelling approaches that combine plot-level community composition with biome-scale trait databases. A remaining step is to validate such modelling approaches by 1) comparing modelled and field-measured trait distributions of tundra vegetation communities, and 2) testing how well modelled community-level trait characteristics predict ecosystem processes. Such tests are required to enable trait-based prediction of vegetation and ecosystem function change to be incorporated into Earth system modelling (Verheijen et al., 2015), and thus enable plant functional traits to fulfil their promise of predicting community responses and feedbacks to global change.


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Shaver, G.R., Syndonia Bret-Harte, M., Jones, M.H., Johnstone, J., Gough, L., Launde, J.,
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Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares,


S1. Supporting Manuscripts

Work undertaken as part of this PhD has contributed to two additional research papers and one data paper. These manuscripts are not included in the main body of the thesis, but are nonetheless integral to the results presented. This chapter outlines the abstracts of these three additional supporting manuscripts.
S1.1 Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change

The following manuscript, ‘Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change’ is in revision in *Ecological Monographs*.

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**Abstract**

The Arctic tundra is warming rapidly, yet the exact mechanisms linking warming and observed ecological changes are often unclear. Understanding mechanisms of change requires long-term monitoring of multiple ecological parameters. We present the findings of a collaboration between government scientists, local people, park rangers and academic researchers that provides insight into changes in plant composition, phenology and growth over 18 years on Qikiqtaruk–Herschel Island, Canada. Qikiqtaruk is an important focal research site located at the latitudinal tall shrub line in the western Arctic. This unique ecological monitoring program indicates the following findings: 1) a nine day per decade advance of spring phenology, 2) a doubling of average plant canopy height per decade, but no directional change in shrub radial growth and 3) a doubling of shrub and graminoid abundance and a decrease by half in bare ground cover per decade. Ecological changes are concurrent with satellite-observed greening and when integrated suggest that indirect warming from increased growing season length and active layer depths, rather than warming summer air temperatures alone, could be important drivers of the observed tundra vegetation change. Our results highlight the vital role that long-term and multi-parameter ecological monitoring plays in both the detection and attribution of global change.
S1.2 Changes in plant functional traits across a warming tundra biome

The following manuscript, ‘Changes in plant functional traits across a warming tundra biome’ is in revision in *Nature*.


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Abstract

Rapid climate warming in Arctic and alpine regions is driving changes in the structure and composition of tundra plant communities, with unknown consequences for ecosystem functioning. Because plant functional traits are directly related to vital ecosystem processes such as primary productivity and decomposition, understanding trait-environment relationships is critical to predicting high-latitude climate feedbacks, yet such relationships have never been quantified at the biome scale. Here, we explore the biome-wide relationships between temperature, soil moisture, and key plant functional traits (plant height, leaf area, leaf nitrogen content (leaf N), specific leaf area (SLA), and leaf dry matter content (LDMC), as well as community woodiness and evergreenness). We integrated more than 56,000 trait observations with nearly three decades of plant community vegetation surveys at 117 Arctic and alpine tundra sites spanning the Northern Hemisphere. We found strong spatial relationships between summer temperature and community height, SLA, and LDMC. Soil moisture had a marked influence on the strength (SLA and LDMC) and direction (leaf area and leaf N) of the temperature-trait relationship, highlighting the potentially important influence of changes in water availability on future plant trait change. Over the past three decades, community plant height increased with warming across all sites, but other traits lagged far behind the rates of change predicted from spatial temperature-trait relationships. Our findings highlight the challenge of using space-for-time substitution to predict the near-term consequences of future warming on functional composition and suggest that tundra ecosystem functions tied closely to plant height (e.g., carbon uptake) will show the most rapid changes with warming. Our results reveal the strength with which environmental factors shape biotic communities at the coldest extremes of the planet and will enable improved projections of tundra functional change with climate warming.
S1.3 Tundra Trait Team: A database of plant traits spanning the tundra biome

The following data paper, ‘Tundra Trait Team: A database of plant traits spanning the tundra biome’ is in revision in Global Ecology and Biogeography.


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59. Aarhus University, Denmark
60. Florida International University, USA
61. Lomonosov Moscow State University, Russia
62. Griffith University, Australia
63. Greifswald University, Germany
64. Leiden University, The Netherlands
65. University of California Riverside, USA
66. Norwegian University of Science and Technology, Norway
67. University of Colorado, Boulder, USA
68. University of Alaska Fairbanks, USA
69. University of Waterloo, Canada
70. Université Laval, Canada
71. Deakin University, Australia
72. University of Bonn, Germany
Abstract

Motivation: The Tundra Trait Team (TTT) database includes field-based measurements of key traits related to plant form and function at multiple sites across the tundra biome. This dataset can be used to address theoretical questions about plant strategy and trade-offs, trait-environment relationships and environmental filtering, and trait variation across spatial scales, to validate satellite data, and to inform earth system model parameters.

Main types of variable contained: The database contains 81,537 measurements of 18 plant traits. The most frequently measured traits (>1,000 observations each) include plant height, leaf area, specific leaf area, leaf fresh and dry mass, leaf dry matter content, leaf nitrogen content, leaf carbon content, leaf phosphorus content, seed mass, and stem specific density.

Spatial location and grain: Measurements were collected in tundra habitats in both the northern and southern hemispheres, including Arctic sites in Alaska, Canada, Greenland, Fennoscandia, and Siberia and alpine sites in the European Alps, Colorado Rockies, Caucasus, Ural Mountains, Pyrenees, Australian Alps, and Central Otago Mountains (New Zealand). More than 99% of observations are georeferenced.

Time period and grain: All data were collected between 1964 and 2016. A small number of sites have repeated trait measurements at two or more time periods.

Major taxa and level of measurement: Trait measurements were made on 858 terrestrial vascular plant species growing in tundra habitats. Most observations are on individuals (87%), while a small number represent plot or site means or maximums per species.

Software format: csv file and GitHub repository with data cleaning scripts in R; contribution to TRY plant trait database (www.try-db.org) to be included in the next version release.
Chapter S1. Supporting manuscripts
S2. Supporting information for Chapter 3: ‘Global plant trait relationships extend to the climatic extremes of the tundra biome’

Below are all supplementary methods, tables and figures supporting the analyses set out in ‘Global plant trait relationships extend to the climatic extremes of the tundra biome’.

S2.1 Extended Methods

S2.1.1 Tundra biome definition
In line with previous biome-scale assessments of tundra vegetation community change (Bliss et al., 1981; Elmendorf et al., 2012; Myers-Smith et al., 2015), we defined the tundra biome as the vegetated regions above treeline at high latitude and high altitude. Tundra species were identified as those present in sampling plots from two biome-scale experiments, the International Tundra Experiment (ITEX) (Henry and Molau, 1997) and associated sites (Elmendorf et al., 2012), and the sUMMITDiv network (Steinbauer et al., 2018), or those present at trait collection sites with a mean annual temperature below 0°C. Tundra plant communities include many widely-distributed and locally common species that are found across large geographical gradients and a variety of environments (Henry and Molau, 1997). We included trait records of tundra species collected outside of tundra environments in this study because i) we were specifically interested in the maximum potential within-species variation among tundra species, ii) defining tundra environments on a purely climatic basis (excluding biotic community in the definition) is very difficult and would require arbitrary decisions regarding biome boundaries, and iii) many trait records in the TRY database do not contain georeferenced collection coordinates and thus would be impossible to classify based on environment.

S2.1.2 Trait selection
We selected six plant traits: plant height (PH, maximum measured height), seed mass (SM, dry mass), leaf area per leaf (LA, fresh leaf area), leaf mass per area (LMA, ratio of leaf dry mass to fresh leaf area), leaf dry matter content (LDMC, ratio
of leaf dry mass to fresh leaf mass), and leaf nitrogen (LN, nitrogen per unit leaf dry mass). These six traits are considered to represent fundamental dimensions of ecological strategy (Weiher et al., 1999; Díaz et al., 2016) and are commonly measured in the tundra, thus maximizing trait coverage.

S2.1.3 Trait data

Trait data collection

We extracted trait data from the TRY 3.0 database (Kattge et al., 2011, available at www.try-db.org; Chapter S3) for tundra species. We extracted traits of all tundra species from the TRY database regardless of location to maximize the capture of trait variation per species. We supplemented TRY data with additional trait data from the “Tundra Trait Team” (TTT) database (Bjorkman et al., GEB in revision). All species names from ITEX, TRY and TTT were matched to accepted names in The Plant List using the R package Taxonstand (v. 1.8) before merging the datasets (Cayuela et al., 2012). We assigned species to four traditional functional groups - evergreen shrubs, deciduous shrubs, graminoids, and forbs - based on previous classification of ITEX species (Elmendorf et al., 2012). We excluded SSD from all analyses, except for comparisons with (Díaz et al., 2016; Fig. S2.8), since SSD had low collection coverage in the tundra and was available for too few species (n=52). We also extracted trait data and collection site coordinates from TRY 3.0 for all global species to provide global context in geographical-, climate- and trait-space analyses following previously published approaches in Kattge et al. (2011) and Díaz et al. (2016).

Data cleaning - TRY

TRY trait data were subjected to a multi-step cleaning process. Firstly, all values that did not represent individual measurements or species means were excluded. Secondly, we identified overlapping datasets within TRY and removed duplicate observations whenever possible. The following datasets were identified as having partially overlapping observations: GLOPNET – Global Plant Trait Network Database, The LEDA Traitbase, Abisko & Sheffield Database, Tundra Plant Traits Database, and KEW Seed Information Database (SID).

Thirdly, we removed duplicates within each TRY dataset (e.g., if a value is listed once as “mean” and once as “best estimate”) by first calculating the ratio of
duplicated values within each dataset, and then removing duplicates from datasets with more than 30% duplicated values. This cut-off was determined by manual evaluation of datasets at a range of thresholds. Datasets with fewer than 30% duplicated values were not cleaned in this way as any internally duplicate values were assumed to be true duplicates (i.e. two different individuals were measured and happened to have the same measurement value).

Finally, we removed all species mean observations from the “Niwot Alpine Plant Traits” database and replaced them with the original individual observations as provided by the trait collector (Marko J. Spasojevic) in order to ensure all trait measurements were for individuals.

Data cleaning – TRY & TTT combined
Both datasets were checked for improbable values, with the goal of excluding likely errors or measurements with incorrect units but without excluding true extreme values. It was particularly important to avoid artificial reduction in the range of trait values in this study since we were explicitly interested in trait variation. We followed a series of data-cleaning steps, in each case estimating an error risk for a given observation (x) by calculating the difference between x and the mean (excluding x) of the group in question and then dividing by the standard deviation of the group.

We employed a hierarchical data cleaning method, because the standard deviation of a trait value is related to the mean and sample size. First, we checked individual records against the entire distribution of observations of that trait and removed any records with an error risk greater than eight (i.e., a value more than eight standard deviations away from the trait mean). For species that occurred in four or more unique datasets within TRY or TTT (i.e., different data contributors), we estimated a species mean per dataset and removed observations for which the species mean error risk was greater than three (i.e., the species mean of that dataset was more than three SD’s away from the species mean across all datasets). For species that occurred in fewer than four unique datasets, we estimated a genus mean per dataset and removed observations in datasets for which the error risk based on the genus mean was greater than 3.5. Finally, we compared individual records directly to the distribution of values for that species. For species with fewer than four records we did not remove any values. For species with more than four records, we excluded values...
above an error risk $Y$, where $Y$ was dependent on the number of records of that species and ranged from an error risk of 2.25 for species with fewer than 10 records to an error risk of four for species with more than 30 records. This procedure was performed on the complete tundra trait database – including species and traits not presented here. In total, 3,515 observations (2.8%) were removed. In all cases, we visually checked the excluded values against the distribution of all observations for each species to ensure that our trait cleaning protocol was reasonable.

All trait observations with latitude/longitude information were mapped and checked for illogical values (e.g., falling in the ocean). These values were corrected from the original publications or by contacting the data contributor whenever possible. Where locations could not be verified, geo-referenced coordinates were removed and the trait data not included in scale-related analyses.

**Final trait database**

After cleaning out duplicates and suspected mistakes, we retained 51,657 unique trait observations (of which 20,991 were already in TRY and 30,616 were newly contributed by the Tundra Trait Team) across the six traits of interest. Of the 447 identified species in the ITEX dataset, 397 (89%) had trait data available from TRY or TTT for at least one trait (range 60-100% per site). Those species without trait data generally represent rare or uncommon species unique to each site. On average, trait data were available for 97% of total plant cover across all sites (range 39-100% per site; Table S1).

Data compiled through the Tundra Trait Team are available in Bjorkman et al., (GEB in revision), will be submitted to the TRY trait database, and made publicly available using the Polar Data Catalogue (https://www.polardata.ca/). The total TTT database submitted to TRY will include traits not considered in this study as well as tundra species that do not occur in our vegetation survey plots, for a total of 54,210 trait observations on 530 species. For more information on trait data and trait cleaning methods see Bjorkman et al. Nature in revision and Bjorkman et al. GEB in revision.
S2.1.4 Climate data

Calculation of climate space
To plot the distribution of tundra trait data within climate space, we used the coordinates of all unique collection sites for both tundra (TRY and TTT) and global (TRY) datasets.

We extracted CHELSA climate variables (mean annual temperature – BIO10_1 and mean annual precipitation – BIO10_12; Karger et al., 2017, http://chelsa-climate.org/) for all trait observations with latitude/longitude values recorded (39,573 records in total, 12,434 of which were from TRY and 27,139 from TTT). Because most observations did not include information about elevation, temperature estimates for individual trait observations were not corrected for elevation.

Temperature class of tundra species
We calculated the ‘temperature class’ of tundra species based on the mean summer temperature of the coldest International Tundra Experiment (ITEX) site at which each species was observed, assumed to represent the cold limit of each species’ range. Mean summer temperature was considered to be the most ecologically meaningful climatic variable since it captures conditions during the growing season for each plant species. We extracted summer temperatures for ITEX sites from the CHELSA dataset based on BioClim variable BIO10_10. We assigned species to three temperature classes: Group 1 (Cold tundra) = summer temperature of coldest site less than 5°C, Group 2 (Mid tundra) = summer temperature of coldest site greater than 5°C but less than 10°C, Group 3 (Warm tundra) = summer temperature of coldest site greater than 10°C.

S2.1.5 Analysis
All analyses were conducted in R (v. 3.3.3). Code is available at github.com/hjdtomath/Tundra_trait_variation.

Analysis of trait relationships
We performed principal component analysis (PCA) on plant traits for all global species, and for tundra species only using the R package ‘prcomp’. As far as possible, we replicated the methods outlined in Díaz et al. (2016), though this was
not always possible due to the use of gap-filled traits and additional data not included in TRY in Díaz et al. (2016). We log transformed trait values to account for log-normal distributions, which is considered appropriate for data with different measurement scales Díaz et al. (2016). To test whether the inclusion of SSD altered results, and for comparison with Díaz et al. (2016), we performed supplementary analysis using a conversion from SSD to LDMC based on the correlation between these two traits (Büntgen et al., 2014; Díaz et al., 2016), since LDMC and SSD individually have fewer trait observations than other traits at the global scale. Although only an approximate conversion, this greatly increases the number of species available for the analyses and does not affect the distribution of trait-space or direction of trait loadings (Fig S2.8). We did not use converted values in the main analysis to avoid introducing additional sources of variation.

To visualize trait-space, we plotted the first two PCA axes and direction and weighting of trait loadings (Figure 3.2). We performed PCA on the full global dataset (including tundra data) and highlighted tundra species within the overall distribution to identify the location of tundra species within global trait-space. We repeated PCA using tundra species only to compare global trait relationships with tundra trait relationships. We compared all pairwise trait correlations for both global and tundra species (Fig S2.2) to investigate consistency in trait-trait relationships, and investigated the strength and direction of trait loadings for global and tundra analyses to compare the location and relative importance of PCA axes (Fig S2.3).

To investigate whether the location of species within tundra trait-space or along the two major axes of variation was influenced by climate, we categorised species according to temperature class (see above). We subsampled 14 species from each temperature class (the minimum number of species per temperature class) and plotted the distribution over 1,000 sampling runs (Fig S2.1) to account for the different number of species in each temperature class. We plotted the distribution of species along PCA axes for each temperature class to test whether trait variation within multivariate trait-space was influenced by the species’ thermal range (Figure 2.1).
**Variance partitioning**

To investigate the sources of trait variation in the tundra, we conducted variance partitioning by fitting a generalised linear mixed-effects model to the variance across nested classification hierarchy (functional group/species) using the R package `nlme`. We then conducted a variance component analysis on this model using the `varcomp` function in the R package `ape`. Partitioning was performed on a trait-by-trait basis, so does not account for co-variation between traits. We used unexplained variance to represent the within-species variation (including within-individual variation), though some unexplained variation could also represent measurement error. To complement variance partitioning, we also calculated the coefficient of variation (CV; the ratio of the standard deviation to the mean) to compare variation among traits. CV was calculated for each trait for all species.

**Variance partitioning across spatial scale**

To assess how variance explained by differences within- and between-species varied with spatial scale, we iteratively grouped sites based on geographic proximity. We calculated the geographic distance between all trait sampling sites using the R package `geosphere`. We excluded sampling sites with fewer than three species per site, or fewer than two trait observations per species. For a given trait sampling site, we conducted variance partitioning analysis at the site scale (scale = 0). We then added data from the nearest site (shortest geographical distance) and conducted variance partitioning analysis on this expanded dataset (spatial scale = distance from starting site to most distant site). We added sites iteratively until all sites were included i.e. the biome-scale was reached. We repeated this analysis across all trait sampling sites. To examine whether sources of trait variance were affected by differences in species richness at different geographical scales, we also calculated the species richness (number of unique species for which we have trait measurements, i.e. size of the measured species pool) of the dataset at each sampling step.

To summarise the relationship between variance explained, spatial scale and species richness, we performed a breakpoint analysis with one break point using the R package `segmented`. To calculate errors, we grouped trait observation sites into 5km or 1 species bins and calculated the 95% intervals of the spread of values. These were plotted as error bounds using a second-order polynomial smooth. We
visualised all analyses with spatial scale and species richness presented on a \( \log_{10} \) scale to highlight change at small scales. For non-logged figures see Figs S2.6-7. To investigate if differences in the contribution if within-species and among-species variation to total trait variation were significant, we additionally grouped data into 10 equal bins, and tested the significance of source of variance using linear models, with a significance threshold of 0.05. We highlighted insignificant bins on figures as grey shaded areas, which indicate scales at which the amount of within-species variation is not significantly different from among-species variation. Finally, we examined 1) the mean contribution of within- and among-species variation to overall trait variation, and 2) proportion of sampling combinations for which within-species variation accounted for at least one third and one half of overall trait variation above and below each break point (Fig S2.4).

All analyses and results not presented in the main text are presented in the following figures and tables.
S2.3 Supplementary Tables

**Table S2.1.** Number of overall observations per trait, and those with latitude/longitude information for tundra species. The minimum and mean percent of species per site with at least one trait observation, and the minimum and mean percent cover (abundance) of species per site with at least one trait observation. The maximum % species and % cover is 100 for all traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Num. of observations</th>
<th>Num. obs. w/ coordinates</th>
<th>% species (min)</th>
<th>% species (mean)</th>
<th>% cover (min)</th>
<th>% cover (mean)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Dry Matter Content</td>
<td>6,552</td>
<td>6,242</td>
<td>19</td>
<td>67.5</td>
<td>5</td>
<td>80.5</td>
</tr>
<tr>
<td>Leaf Area</td>
<td>9,067</td>
<td>8,820</td>
<td>20</td>
<td>82.1</td>
<td>10</td>
<td>90.0</td>
</tr>
<tr>
<td>Leaf N</td>
<td>4,420</td>
<td>3,860</td>
<td>29</td>
<td>72.1</td>
<td>30</td>
<td>86.8</td>
</tr>
<tr>
<td>Height</td>
<td>19,396</td>
<td>18,176</td>
<td>48</td>
<td>94.0</td>
<td>38</td>
<td>96.1</td>
</tr>
<tr>
<td>Seed Mass</td>
<td>2,410</td>
<td>915</td>
<td>20</td>
<td>71.6</td>
<td>4</td>
<td>80.4</td>
</tr>
<tr>
<td>Specific Leaf Area</td>
<td>9,817</td>
<td>8,793</td>
<td>20</td>
<td>78.0</td>
<td>10</td>
<td>87.3</td>
</tr>
</tbody>
</table>
**S2.3 Supplementary Figures**

**Fig. S2.1:** Distribution of tundra species along the two dimensions of trait variation, grouped by ‘temperature class’ of species. Curves indicate the density distribution of species along PCA axes. Colours indicate temperature category, corresponding to the summer temperature of the coldest ITEX plot for each species (Cold < 5°C, Mid < 10 °C, Warm > 10 °C).
Fig. S2.2: Comparison of trait distributions and trait correlations among tundra (blue) and global vascular plant species (grey). Lower left panels: pairwise trait correlations among the six plant traits tested in this study (leaf area, seed mass, plant height, LMA – leaf mass per area, leaf nitrogen, LDMC – leaf dry matter content). Points represent the mean value for each species. Solid lines indicate fit for tundra species, dashed lines indicate fit for global species. Diagonal panels: smoothed distribution of log transformed trait values for tundra and global plant species.
Fig. S2.3: Comparison of trait loadings for the first two PCA axes for tundra and global vascular plant species. Colours indicate traits (blue = plant height, red = leaf area, grey = seed mass, green = leaf nitrogen, yellow = leaf mass per area (LMA), brown = leaf dry matter content (LDMC)). Solid, darker bars indicate loadings for global species; dashed and lighter coloured bars indicate loadings for tundra species. The relative importance of PCA axes is reversed for tundra species, such that PCA 1 for global species corresponds with PCA 2 for tundra species.
Fig. S2.4: The proportion of sites for which within-species variation accounts for at least half of trait variation (a-f) or at least one third of trait variation (g-l) among tundra species. Bars indicate the proportion of sites above and below the break point of change in source of variation over geographical scale (Figure 4, Figure S5).
Fig. S2.5: Sources of trait variation across geographical scale (a-b) and species richness (c-d) for leaf dry matter content and seed mass (plant height, leaf area, leaf mass per area and leaf nitrogen shown in Fig. 3.4). Variance partitioning occurs over incrementally increasing sampling steps, beginning at a given trait collection site and iteratively adding sites based on geographical proximity until the whole biome is represented. The process is repeated for every trait-sampling site. Points indicate contribution to total trait variation from between-species variation (red) and within-species variation (blue) at every sampling step. Coloured lines indicate linear break point model fit with one break point and black dashed line indicates break point location. Error bounds indicate 95% of variation across sampling sites. Grey box indicates where the difference between among- and within-species richness is not significant ($P > 0.05$). The x-axis in (a-b) represents trait variation over geographical scale, where scale represents the maximum distance from the initial sampling site, presented on a log$_{10}$ scale. The x-axis in (c-d) represents trait variation with species richness, presented on a log$_{10}$ scale.
**Fig. S2.6:** Sources of trait variation across non-log\(_{10}\) transformed geographical scale for leaf area, plant height, leaf mass per area, leaf nitrogen, leaf dry matter content and seed mass (as opposed to log\(_{10}\) transformed geographical scale in Fig. 3.4). Variance partitioning occurs over incrementally increasing sampling steps, beginning at a given trait collection site (first step) and iteratively adding sites based on geographical proximity until the whole biome is represented (final step). The process is repeated for every trait-sampling site. Points indicate contribution to total trait variation from between-species variation (red) and within-species variation (blue) at every sampling step. Coloured lines indicate linear break point model fits with one break point. Dashed line indicates break point location. Error bounds indicate 95% of variation across sampling sites.
Fig. S2.7: Sources of trait variation with non-log$_{10}$ transformed species richness for leaf area, plant height, leaf mass per area, leaf nitrogen, leaf dry matter content and seed mass (as opposed to log$_{10}$ transformed species richness in Fig. 3.4). Variance partitioning occurs over incrementally increasing sampling steps, beginning at a given trait collection site (first step) and iteratively adding sites based on geographical proximity until the whole biome is represented (final step). The process is repeated for every trait-sampling site. Points indicate contribution to total trait variation from between-species variation (red) and within-species variation (blue) at every sampling step. Coloured lines indicate linear break point model fits with one break point. Dashed line indicates break point location. Error bounds indicate 95% of variation across sampling sites.
**Fig. S2.8:** Distribution of trait-space as defined by six plant traits as in Fig. 3.2, but with the inclusion of trait values converted from specific stem density to leaf dry matter content based on trait co-variation. Height = adult plant height, LMA = leaf mass per area, Leaf N = leaf nitrogen, LDMC = leaf dry matter content. (a) Location of tundra species within global trait-space, following Díaz et al. (2016). Points represent mean trait values for each of global plant species defined by two component axes. Grey points represent 1,744 plant species in the global TRY dataset; blue points represent 220 tundra species. Arrows indicate the direction and weighting of trait vectors for all observations. (b) Distribution of trait space for tundra species only. Points represent mean trait values for tundra species, coloured by ‘temperature class’. Temperature class corresponds to the mean summer temperature of the coldest International Tundra Experiment (ITEX) site where the species is found (Group 1 – cold tundra: < 5°C, Group 2 – mid tundra: < 10°C, Group 3 – warm tundra: > 10 °C). Arrows represent direction and magnitude of trait loadings.
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S3. Contributing references to published studies from the TRY database used in analyses.

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Bares, J., Chapin, T., Cornellissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom,
P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J.,
Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L.,
Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R.
S4. Supporting information for Chapter 4: ‘Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome’

Below are all supplementary tables and figures supporting the analyses set out in ‘Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome’.

S4.1 Supplementary Tables

Table S4.1 Studies employing an ‘evergreen shrub - deciduous shrub - graminoid - forb’ functional group classification (or close variant) to examine the response of tundra communities to environmental change over the past two decades. Studies were identified based on a literature search on Web of Science using the search terms ‘tundra’ and ‘plant functional group’ or ‘plant functional type’. Studies are grouped by whether they found clear differences in functional group response (Yes: clear differences were found between some (but not necessarily all) functional groups; Not clear: differences between groups were inconsistent among sites or over time; No: No significant differences in functional group response). Studies vary in duration from 2-30 years and incorporate a range of bioclimatic contexts and experimental types. For full meta-analyses of functional group response see Dormann & Woodin (2002) and Dorrepaal (2007).
### Differences in response among plant functional groups

<table>
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<th>Environmental variable</th>
<th>Yes</th>
<th>Not clear</th>
<th>No</th>
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<td>Warming (experimental)</td>
<td>Arft et al., 1999; Klanderud &amp; Totland, 2005; Wahren et al., 2005; Jägerbrand et al., 2009; Klady et al., 2011; Smith et al., 2012; Wang et al., 2012; Elmendorf et al., 2012a; Post, 2013; Zamin et al., 2014; DeMarco et al., 2014; Mclaughlin et al., 2014; Kremers et al., 2015; Alatalo et al., 2016; Livensperger et al., 2016</td>
<td>Van Wijk et al., 2003; Dorrepaal, 2007; Kudo et al., 2010; Alatalo et al., 2014</td>
<td>Jonasson et al., 1999; Hollister et al., 2005; Klanderud, 2008; Zhao et al., 2013; Little et al., 2015</td>
</tr>
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<td>Warming (ambient)</td>
<td>Epstein et al., 2004; Molau et al., 2005; Elmendorf et al., 2012b; Kaaerlejärvi et al., 2012; Fraser et al., 2014; Van Der Wal &amp; Stien, 2014; Venn et al., 2014</td>
<td>-</td>
<td>Hill &amp; Henry, 2011; Villarreal et al., 2012; Pattison et al., 2015; Damgaard et al., 2016</td>
</tr>
<tr>
<td>Warming (gradient)</td>
<td>-</td>
<td>Epstein et al., 2008</td>
<td>Klanderud, 2008</td>
</tr>
<tr>
<td>Fertilization</td>
<td>Graglia et al., 2001; Dormann &amp; Woodin, 2002; Gough et al., 2002; Klanderud &amp; Totland, 2005; Jägerbrand et al., 2009; Laiho et al., 2012; Smith et al., 2012; Yano et al., 2013; Zamin et al., 2014; Oulehle et al., 2016; Wang et al., 2016a</td>
<td>Grellmann, 2002; Gough &amp; Hobbie, 2003; Van Wijk et al., 2003; Dorrepaal, 2007; Onipchenko et al., 2012; Manninen &amp; Tolvanen, 2013; Alatalo et al., 2014; Sundqvist et al., 2014</td>
<td>Jonasson et al., 1999; Shaver et al., 2001; Bret-Harte et al., 2004, 2008; Madan et al., 2007; Sundqvist et al., 2014; Little et al., 2015</td>
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<td>Herbivory</td>
<td>González et al., 2010; Yu et al., 2011; Wang et al., 2012; Post, 2013; Vowles et al., 2017</td>
<td>Grellmann, 2002; Speed et al., 2010; Johnson et al., 2011; Saccone et al., 2014</td>
<td>Austrheim et al., 2008; Damgaard et al., 2016</td>
</tr>
<tr>
<td>Soil Moisture</td>
<td>Bubier &amp; Crill, 2003; Hu et al., 2013; Winkler et al., 2016</td>
<td>Saccone et al., 2014; Saccone &amp; Virtanen, 2016</td>
<td>Dormann &amp; Woodin, 2002</td>
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<td>Snow depth</td>
<td>Molau et al., 2005; Wahren et al., 2005; Wipf &amp; Rixen, 2010; Smith et al., 2012</td>
<td>Saccone et al., 2017</td>
<td>Rumpf et al., 2014; Gaasch &amp; Seastedt, 2015; Saccone et al., 2017</td>
</tr>
<tr>
<td>Permafrost thaw</td>
<td>Schuur et al., 2007</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Light manipulation</td>
<td>Gough et al., 2002</td>
<td>Dormann &amp; Woodin, 2002; Van Wijk et al., 2003</td>
<td>-</td>
</tr>
<tr>
<td>CO₂ fertilization</td>
<td>-</td>
<td>-</td>
<td>Dormann &amp; Woodin, 2002</td>
</tr>
</tbody>
</table>
Table S4.2 Number of trait observations and species with available trait data for the six main traits (plant height, specific leaf area, leaf dry matter content, leaf nitrogen, seed mass) and two supplementary traits (stem specific density, leaf lifespan) used in analysis.

<table>
<thead>
<tr>
<th>Trait name</th>
<th>All trait observations</th>
<th>Only species with trait data for all traits</th>
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<td></td>
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</tr>
<tr>
<td>Plant height</td>
<td>26,448</td>
<td>742</td>
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<tr>
<td>Specific leaf area</td>
<td>15,406</td>
<td>562</td>
</tr>
<tr>
<td>Leaf dry matter content</td>
<td>11,691</td>
<td>473</td>
</tr>
<tr>
<td>Leaf nitrogen</td>
<td>6,352</td>
<td>471</td>
</tr>
<tr>
<td>Seed mass</td>
<td>4,230</td>
<td>637</td>
</tr>
<tr>
<td>Stem specific density</td>
<td>1,214</td>
<td>66</td>
</tr>
<tr>
<td>Leaf lifespan</td>
<td>237</td>
<td>129</td>
</tr>
</tbody>
</table>
Table S4.3 Similarity in species composition between traditional functional groups and trait-based classifications ($k$-means = k-means clustering; HCA = hierarchical agglomerative clustering), calculated as the proportion of consistently classified species out of all species. Post-hoc groups were matched to functional groups based on the maximum correspondence of each individual functional group, rather than based on overall correspondence across all functional groups as in the main analysis. Any changes to similarity using these grouping are indicated in bold, with similarities for groupings used in main analysis indicated in brackets. Only deciduous shrub and graminoids species changed between grouping approaches. Maximising the deciduous shrub grouping using this alternative approach resulted in an increase in correspondence for deciduous shrubs but an overall decrease across all groups.

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Functional groups vs. K-means</th>
<th>Functional groups vs. HCA</th>
<th>K-means vs. HCA</th>
<th>All Methods</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Similarity between group species composition – Deciduous shrubs maximised</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All groups</td>
<td>33% (42%)</td>
<td>33% (43%)</td>
<td>74% (74%)</td>
<td>28% (35%)</td>
</tr>
<tr>
<td>Evergreen shrubs</td>
<td>89% (89%)</td>
<td>94% (94%)</td>
<td>94% (94%)</td>
<td>89% (89%)</td>
</tr>
<tr>
<td>Deciduous shrubs</td>
<td>33% (0%)</td>
<td>33% (13%)</td>
<td>87% (87%)</td>
<td>33% (0%)</td>
</tr>
<tr>
<td>Graminoids</td>
<td>9% (52%)</td>
<td>9% (51%)</td>
<td>78% (78%)</td>
<td>6% (42%)</td>
</tr>
<tr>
<td>Forbs</td>
<td>37% (37%)</td>
<td>37% (37%)</td>
<td>69% (69%)</td>
<td>30% (30%)</td>
</tr>
</tbody>
</table>
Table S4.4 List of species that are consistently categorized to corresponding groups (104 out of 295) among traditional plant functional groups, k-means clustering, and hierarchical agglomerative clustering.

<table>
<thead>
<tr>
<th>Species</th>
<th>Functional Group</th>
<th>Species</th>
<th>Functional Group</th>
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</thead>
<tbody>
<tr>
<td><em>Andromeda polifolia</em></td>
<td>Ever. Shrub</td>
<td><em>Anemone narcissiflora</em></td>
<td>Forb</td>
</tr>
<tr>
<td><em>Calluna vulgaris</em></td>
<td>Ever. Shrub</td>
<td><em>Anemone nemorosa</em></td>
<td>Forb</td>
</tr>
<tr>
<td><em>Cassiope tetragona</em></td>
<td>Ever. Shrub</td>
<td><em>Angelica archangelica</em></td>
<td>Forb</td>
</tr>
<tr>
<td><em>Diapensia lapponica</em></td>
<td>Ever. Shrub</td>
<td><em>Anthriscus sylvestris</em></td>
<td>Forb</td>
</tr>
<tr>
<td><em>Dryas integrifolia</em></td>
<td>Ever. Shrub</td>
<td><em>Anthyllis vulneraria</em></td>
<td>Forb</td>
</tr>
<tr>
<td><em>Dryas octopetala</em></td>
<td>Ever. Shrub</td>
<td><em>Arnica montana</em></td>
<td>Forb</td>
</tr>
<tr>
<td><em>Empetrum nigrum</em></td>
<td>Ever. Shrub</td>
<td><em>Astragalus frigidus</em></td>
<td>Forb</td>
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<tr>
<td><em>Harrimanella hypnoides</em></td>
<td>Ever. Shrub</td>
<td><em>Athyrium filix-femina</em></td>
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<tr>
<td><em>Ledum palustre</em></td>
<td>Ever. Shrub</td>
<td><em>Biscutella laevigata</em></td>
<td>Forb</td>
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<tr>
<td><em>Linnaea borealis</em></td>
<td>Ever. Shrub</td>
<td><em>Caltha palustris</em></td>
<td>Forb</td>
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<tr>
<td><em>Loiseleuria procumbens</em></td>
<td>Ever. Shrub</td>
<td><em>Carlina acaulis</em></td>
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<tr>
<td><em>Phylloco caerulea</em></td>
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<td><em>Carum carvi</em></td>
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<td><em>Rhododendron lapponicum</em></td>
<td>Ever. Shrub</td>
<td><em>Crepis paludosa</em></td>
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<td><em>Thymus praecox</em></td>
<td>Ever. Shrub</td>
<td><em>Filipendula ulmaria</em></td>
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<td><em>Vaccinium oxyccocus</em></td>
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<td><em>Gentiana purpurea</em></td>
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<td><em>Anthoxanthum odoratum</em></td>
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<tr>
<td><em>Arctagrostis latifolia</em></td>
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<td><em>Geum rivale</em></td>
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<td><em>Briza media</em></td>
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<td><em>Hieracium laevigatum</em></td>
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<tr>
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<td><em>Hieracium prenanthoides</em></td>
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<tr>
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<td><em>Hieracium umbellatum</em></td>
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<tr>
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<td><em>Lomelosia caucasic</em></td>
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<tr>
<td><em>Carex canescens</em></td>
<td>Graminoid</td>
<td><em>Lupinus arcticus</em></td>
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<tr>
<td><em>Carex caryophyllela</em></td>
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<tr>
<td>------------------------------</td>
<td>------------</td>
<td>---------------------------------</td>
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<td>Carex flacca</td>
<td>Graminoid</td>
<td>Melampyrum sylvaticum</td>
<td>Forb</td>
</tr>
<tr>
<td>Carex flava</td>
<td>Graminoid</td>
<td>Menyanthes trifoliata</td>
<td>Forb</td>
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<tr>
<td>Carex montana</td>
<td>Graminoid</td>
<td>Persicaria bistorta</td>
<td>Forb</td>
</tr>
<tr>
<td>Carex nigra</td>
<td>Graminoid</td>
<td>Petasites frigidus</td>
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<tr>
<td>Carex pilulifera</td>
<td>Graminoid</td>
<td>Peucedanum ostruthium</td>
<td>Forb</td>
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<td>Carex saxatilis</td>
<td>Graminoid</td>
<td>Pimpinella major</td>
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<td>Carex sempervirens</td>
<td>Graminoid</td>
<td>Plantago atrata</td>
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<td>Carex umbrosa</td>
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<td>Potentilla anserina</td>
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<td>Deschampsia cespitosa</td>
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<td>Ranunculus montanus</td>
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<td>Ranunculus trichophyllus</td>
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<td>Rhinanthus minor</td>
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<td>Rubus chamaemorus</td>
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<td>Hierochloe alpina</td>
<td>Graminoid</td>
<td>Rumex acetosa</td>
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<td>Forb</td>
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<tr>
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<td>Forb</td>
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<tr>
<td>Anemone alpina</td>
<td>Forb</td>
<td>Vicia cracca</td>
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</tbody>
</table>
S4.2 Supplementary Figures

**Figure S4.1** Distribution of tundra plant traits represented by four traditional tundra plant functional groups. Distributions in panels (a-f) are based on species-level means for the 295 tundra species for which data are available, as presented in Fig 4.2. Distributions in panels (g-l) are based on all available trait data for the 295 tundra species for which data are available for all six plant traits of interest. The use of all trait data accounts for within-species trait variation within functional groups, but is biased by species with greater availability of trait data for some species. Trait values are presented on the x axis in untransformed units on a log scale.
Figure S4.2 Abundance, but not number of observations increases likelihood that species will be consistently classified across the three sampling methods (functional groups, k-means clustering, hierarchical agglomerative clustering). Plant traits represented are plant height (PH), leaf area (LA), seed mass (SM), specific leaf area (SLA), leaf dry matter content (LDMC) and lean nitrogen per unit mass (LN). a) Number of trait observations for species that were consistently and inconsistently classified across clustering methods. Differences are not statistically significant (Wilcoxon test, $P = 0.11$). b) Relative abundance of species that were consistently and inconsistently classified across clustering methods. Differences are statistically significant (Wilcoxon test, $P = 0.02$). c) Relationship between number of trait observations and relative abundance of species. Point colours indicate if species were consistently classified. Line indicates linear model fit (LM, stats), and shaded area the 95% confidence intervals. d) Multivariate distribution of six plant traits for tundra species, indicating species that were consistently classified across grouping methods. Species that were consistently classified (red points, 104 out of 295 species) occupied a significantly different region of trait-space (PERMANOVA, $P < 0.001$) and tended to have larger growth forms and more extreme economic traits (highly conservative or highly acquisitive). Inconsistently classified species (grey points) tended to be located closer towards the centre of the overall tundra trait distribution.
Figure S4.3 Alternative classification schemes increase the trait variation explained by traditional functional groups, but in line with expectations resulting from an increased number of groups. a-c) Clustering of species in multivariate trait-space according to a) the four-group classification in the main analysis, b) four-group k-means clustering, and c) four-group hierarchical-agglomerative sampling. d-f) variance explained by four-group clusters for all traits (white), only size-related traits (red) and only economic traits (blue). g-i) Clustering of species in multivariate trait-space according to g) a six-group functional group classification (evergreen shrubs (blue), deciduous shrubs (green), grasses (orange), sedges (red), rushes (brown), forbs (purple)), h) six-group k-means clustering, and i) six-group hierarchical-agglomerative sampling. j-l) variance explained by six-group clusters for all traits, only size-related traits, and only economic traits. m-o) Clustering of species in multivariate trait-space according to m) a seven-group functional group classification (dwarf evergreen shrubs (blue), dwarf deciduous shrubs (light green), tall deciduous shrubs (dark green), grasses (orange), sedges (red), rushes (brown), forbs (purple)). We classified shrubs with a mean height greater than 30cm as tall shrubs; there were no tall evergreen shrubs with available trait data for all six traits according to this classification. n) seven-group k-means clustering, and o) seven-group hierarchical-agglomerative sampling. p-r) variance explained by seven-group clusters for all traits, only size-related traits, and only economic traits. Functional space was defined based on plant height (PH), seed mass (SM), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen content (LN). Ellipses represent 95% confidence interval of functional group distributions. Arrows indicate direction and weighting of each trait.
**Figure S4.4** Variation in multivariate trait expression explained by traditional functional groups for all possible trait combinations, including a) stem density and b) leaf lifespan. Previous analyses (Díaz et al., 2016) have used stem density rather than leaf dry matter content, but this trait was unavailable for the majority of tundra species and is highly correlated with LDMC (Büntgen et al., 2014). Inclusion of stem density increases explanatory power of functional groups to 55%, but stem density data are available for only 53 species and so may not represent biome-scale patterns. Inclusion of leaf lifespan increased explanatory power of functional groups to 41%, but leaf lifespan data have only 146 available observations across 102 species, and so also may not represent biome-scale patterns. Distribution of tundra plant traits represented by the four traditional tundra plant functional groups for c) stem specific density and d) leaf lifespan reveal that differences among groups are driven by shrub vs non-shrub species (stem specific density), and evergreen shrubs (leaf lifespan). Trait values are presented on the x axis in untransformed units on a log scale.
Figure S4.5 Variance explained by traditional functional groups is consistent across a) the species-level mean of trait distributions (main analysis), b) the 25th percentile of species-level trait distributions, and c) the 75th percentile of species-level trait distributions. Functional space was defined based on plant height (PH), seed mass (SM), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen content (LN). Individual species are represented by points and functional groups by point colour (blue = evergreen shrub, green = deciduous shrub, yellow = graminoid, purple = forb). Ellipses represent 95% confidence interval of functional group distributions. Arrows indicate direction and weighting of each trait.
Figure S4.6 – Distribution of species-level traits represented by the four traditional tundra plant functional groups. Distributions are based on species-level mean traits using only georeferenced trait data from locations north of 60°N. Note that only 57 tundra species have available trait data from these locations (compared to 295 species using the full dataset). Trait values are presented on the x axis in untransformed units on a log scale. Significance of distributions is indicated by symbols (pairwise wilcoxon test; * = $P < 0.05$; ** = $P < 0.01$, *** = $P < 0.001$).
Figure S4.7 Distribution of tundra species in functional trait space using only georeferenced trait data from locations north of 60°N. Note that only 57 tundra species have available trait data from these locations compared to 295 species using the full dataset. Inset plots indicate PCA multivariate distribution of six plant traits for two tundra sites (a) Qikiqtaruk, (b) Abisko, and for c) the Arctic tundra. Georeferenced trait collection locations are indicated by grey circles and modelled site locations by red circles.

Functional space was defined based on plant height (PH), seed mass (SM), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen content (LN). Individual species are represented by points and functional groups by point colour (blue = evergreen shrub, green = deciduous shrub, yellow = graminoid, purple = forb). Ellipses represent 95% confidence interval of functional group distributions. Arrows indicate direction and weighting of each trait.
Figure S4.8 Trait variation explained by traditional functional groups for all possible trait combinations using only georeferenced trait data from locations north of 60°N. Functional groups best explain combinations of only economic traits (a) or those containing leaf dry matter content (LDMC) (b), and worst explain combinations of only morphological traits (a) or those containing plant height or seed mass (c). Note that only 57 tundra species have available trait data from these locations (compared to 295 species using the full dataset). Points indicate the mean variance explained (PERMANOVA $R^2$) by functional groups and coloured to visualise the importance of different trait combinations.
Figure S4.9 Comparison of group structure, trait variation explained, and group composition between traditional functional groups and post-hoc classifications using only georeferenced trait data from locations north of 60°N. Note that only 57 tundra species have available trait data from these locations (compared to 295 species using the full dataset). (a-c): PCA visualization of species clusters as defined by (a) traditional functional groups, (b) k-means clustering, and (c) hierarchical-agglomerative clustering (HCA). Species are indicated by points and group distribution by ellipses. Colours indicate groups (dark blue = evergreen shrub, green = deciduous shrub, yellow = graminoid, purple = forb). Post-hoc classifications are matched with functional groups based on maximum species correspondence between grouping methods, such that each post-hoc classification corresponds with a traditional functional group. (d-f): Trait variation explained by (d) traditional functional groups, (e) k-means, and (f) HCA for multivariate combinations of all six plant traits (white), structural traits only (red), and economic traits only (light blue). (g): Comparison of group composition across clustering methods. The stacked bars represent individual species and are ordered by traditional functional group (species order remains consistent across columns). The colour of each stacked bar represents the group to which species were assigned by each classification method (classification can change across columns). For example, a species categorised as a graminoid by traditional functional groups can be categorised in the group most corresponding to forbs by post-hoc classifications.


Klanderud, K., Totland, Ø., 2005. Simulated Climate Change Altered Dominance Hierarchies


S5. Supporting information for Chapter 5: ‘Litter quality outweighs environmental drivers of litter decomposition across the tundra biome’

Below are all supplementary methods, tables and figures supporting the analyses set out in ‘Litter quality outweighs environmental drivers of litter decomposition across the tundra biome’.

S5.1 Extended Methods

S5.1.1 Site Descriptions

We established 248 decomposition sites across 25 geographic regions across the circum-Arctic and alpine tundra (Table S5.1). Mean annual temperatures ranged from 12.7°C at the warmest site to -10.2°C at the coldest site. Sites were largely above treeline though some subarctic and alpine sites extended below treeline.

S5.1.2 Decomposition experiment

We measured decomposition using two types of tea – a labile green tea and a recalcitrant rooibos tea – following the Tea Bag Index methodology (Keuskamp et al., 2013). The two tea types represent dried leaves of two shrubs species (*Camellia sinensis* – green tea) and (*Aspalathus linearis* – rooibos tea), that vary in their leaf traits and chemistry (Graham, 1992; Krafczyk and Glomb, 2008; Keuskamp et al., 2013). Although not native to the tundra, decomposition of these two tea types are comparable with a range of tundra species (Fig S5.1), and allow comparison across global sites (Keuskamp et al., 2013; Djukic et al., 2018). Mass loss via leaching of these tea bags is also comparable with previous findings for litter bags (24 hour mass loss: 14% (rooibos tea) - 37% (green tea); 8 - 32% in litter leaching studies, Bokhorst et al., 2010).

We buried tea bags at 5 cm depth for three time periods – three months (summer), nine months (winter) and twelve months (year). Due to the logistical constraints of accessing some sites, not all incubations were carried out at all sites. We buried a minimum of four tea bag replicates at each site for each time period. Tea bags were buried, rather than placed on the surface, to increase likelihood of recovery across the time periods covered in this experiment, and for consistency with the global
standardised Tea Bag Index protocol (Keuskamp et al., 2013). Surface litter likely experiences greater fluctuations in temperature and moisture that may reduce decomposition (Bokhorst et al., 2010), and we found that annual mass loss of surface litter was reduced compared to buried litter in green tea, but not rooibos tea, within a common site (Fig S5.9). However, litter is commonly mixed into tundra soils through cryoturbation processes (Sistla et al., 2013), while using a buried litter substrate also serves as a proxy for soil organic matter decomposition (Eskelinen et al., 2009).

We weighed tea bags prior to burial, including both the bag and tag. Upon recovery, we dried bags at 70°C for at least 48 hours, removed any attached soil or roots, and reweighed tea bags. We subtracted the mass of the bag and label to determine the mass of the tea only, and the initial weights were corrected to account for loss of material in transit to field sites.

**S5.2.3 Decomposition variables**

We calculated three indices of decomposition: (1) overall mass loss (final mass divided by initial mass) for each tea type. (2) The stabilisation factor (S), which describes the proportion of potentially decomposable compounds (the hydrolysable fraction, \(H_g\)) remaining upon stabilisation of decomposition. S is calculated using only green tea, for which decomposition assumed to stabilise within three months of burial (Keuskamp et al., 2013, Fig S5.8), whereby:

**Equation 1:**

\[ S = 1 - \left( \frac{a_g}{H_g} \right) \]

where \(a_g\) is the decomposable fraction (mass loss) of green tea and \(H_g\) is the hydrolysable fraction of green tea. (3) The decomposition rate (k), which represents the rate at which decomposable compounds are lost during decomposition. This two pool decomposition constant was calculated based on the methodology outlined in Keuskamp et al. (2013), and is calculated using only rooibos tea, for which decomposition is assumed not to have stabilised during the incubation periods covered by this analysis (Keuskamp et al., 2013, Fig S5.8).

**Equation 2:**

\[ k = \ln \left( \frac{a_r}{M_{t(r)} - a_r} \right) x \frac{1}{t} \]
where M is equal to the mass of rooibos tea at time point t (days) and $a_r$ is the decomposable fraction of rooibos tea. $a_r$ is calculated from the hydrolysable fraction of rooibos tea ($H_r$) and stabilisation factor ($S$), whereby $a_r = H_r (1 - S)$.

**S5.1.4 Environmental variables**

Where possible, we measured local environmental variables at decomposition sites for the duration of the incubation period. Soil temperatures were measured using digital ibuttons (DS1921G Thermochron iButtons, Maxim, San Jose, CA, US) or HOBO data loggers (HOBO RX3000 Remote Monitoring Station Data Logger, Onset Computer Corporation, Pocasset, MA). Soil moisture (percent volumetric water content) was measured using hand-held moisture probes or permanently installed HOBO data loggers at 5 cm depth. Where site-measured data were not available, notably for air temperature, we used local weather station data, provided either by local research stations or from publicly available sources. All environmental data were trimmed to the corresponding incubation period for analyses. Sites that did not have available environmental data were excluded from relevant analyses.

**S5.1.5 Gridded climate variables**

We used ‘Climatologies at high resolution for the earth’s land surface areas’ data (CHELSA, 0.0083 x 0.0083 degree resolution, Karger et al., 2017) to provide gridded temperature and precipitation data for all sites, and to extrapolate decomposition across the tundra biome. We extracted climatologies (covering the time period 1979 to 2013) for summer, winter and annual temperature and precipitation. We used European Space Agency (ESA) Climate Change Initiative combined soil moisture data product (0.25 x 0.25-degree resolution, Dorigo et al., 2017) to provide modelled soil moisture for all sites and to extrapolate decomposition across the tundra. We used daily data for the period 1979 to 2013 to build climatologies (summer, winter, year) to align with CHELSA data.

We compared site measured environmental data to gridded climate data using Bayesian hierarchical models with grid cell and site as nested random effects using the R package MCMCglmm (Hadfield, 2010). Site measured temperature variables correlated closely with gridded temperature data, exhibiting a close to 1:1 relationship (Fig S5.10). Site measured moisture weakly correlated with average ESA soil moisture data, and showed no relationship with long-term CHELSA precipitation data. This discrepancy may result from greater inter-annual variability in moisture or
precipitation compared to temperature (Seneviratne et al., 2010), or high within-site variation in soil moisture that is not captured at the grid cell scale.

S5.1.6 Environmental Relationships – individual variables

Analyses of environmental relationships were conducted in the statistical programming language Stan run through R (v. 3.3.3.) using packages rjags (v.4.6; Plummer, 2016) and rstan (v. 2.17.3; Stan Development Team, 2018). Code is available at github.com/hjdthomas/Tundra_teabag_experiment.

The relationship between each decomposition metric and environmental variables (EV) was estimated from a Bayesian hierarchical model, with climatic variables as the predictor variable and decomposition as the predictor variable, with grid cell (g), site (s) and plot (p) as random effects, varying by tea type (t):

**Equation 3:**

\[\text{decomp}_{p,t} \sim \text{Normal}(\alpha_{p,t} + \alpha_{s,t} + \alpha_{g,t}, \sigma)\]

We estimated relationships over space at the level at which environmental variables were measured, including incubation length (days) as a fixed effect. For example, relationships for gridded climate data were estimated at the level of the grid cell (g), with site (s) and plot (p) and as nested hierarchical random effects. Relationships for site-measured variables were estimated at the site level, with plot (p) as a random effect. If environmental variables were measured at the plot level, we summarised variables to the site level carried forward the standard deviation among plots into models. If there was only one teabag per plot, one plot per site or one site per grid cell, there was only one tea bag in a plot, or there was only one site in a grid cell, \(a_{p,t}\) or \(a_{s,t}\) was set to zero. Note that data availability differs for each environmental variable.

**Equation 4:**

\[\alpha_{g,t} \sim \text{Normal}(\gamma_0 + \gamma_1 \ast \text{EV}_{g,t} + \gamma_2 \ast \text{days}_{g,t}, \theta)\]
\[\alpha_{p,t} \sim \text{Normal}(0, \sigma_1)\]
\[\alpha_{s,t} \sim \text{Normal}(0, \sigma_2)\]
We modelled all incubation periods separately due large differences in the availability of environmental data and qualitative differences between seasons such as frozen ground during the winter.

**S5.1.7 Environmental Relationships – temperature and moisture interactions**

We modelled the relationships over space accounting for temperature and moisture within the same model (for site-measure temperature and moisture, for gridded temperature – CHELSA and gridded moisture – ESA) using the same model structure but including an interaction term between these two environmental variables.

*Equation 5:*

\[
\alpha_{g,t} \sim \text{Normal}(\gamma_0 + \gamma_1 \cdot \text{temp}_{g,t} + \gamma_2 \cdot \text{moisture}_{g,t} + \gamma_3 \cdot \text{temp}_{g,t} \cdot \text{moisture}_{g,t} + \gamma_4 \cdot \text{days}_{g,t}, \theta)
\]

We ran models using data in original units, and also using standardised environmental variables and incubation length using mean zero, unit variance scaling to allow comparison across variables.

**S5.1.8 Environmental Relationships – within grid cells**

We modelled the relationship between decomposition metrics and environmental variables (single variables only) within grid cells using the same model structure, but standardising all environmental variables within a grid cell using mean zero, unit variance scaling. Grid cells with only one site or plot per grid cell were removed from this analysis.

**S5.1.9 Mapping decomposition**

We used model estimates from the gridded climate variable model (Equation 5) to map decomposition over space based on summer temperature and moisture for tundra and subarctic climate regions. We used gridded temperature of the warmest quarter (CHELSA bio10) and gridded summer moisture (ESA, June-July-August) as environmental variables. We used the coefficients for green tea and assumed the mean incubation length across summer treatments (81 days). We masked estimates to tundra and subarctic climate regions based on the Köppen-Geiger climate classification (Kottek et al., 2006, regions ET, Dsc, Dsc, Dwc, Dwd, Dfc, Dfd).
### S5.2 Supplementary Tables

**Table S5.1:** Summary of geographic locations used in main study, indicating number of sites and plots, number of tea bag replicates, and mean temperatures.

<table>
<thead>
<tr>
<th>Geographic Region</th>
<th>Number of sites</th>
<th>Number of plots</th>
<th>Number of tea bags</th>
<th>Mean temperature (°C) (year / summer / winter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine Japan</td>
<td>45</td>
<td>46</td>
<td>776</td>
<td>6.7 / 18.7 / -4.5</td>
</tr>
<tr>
<td>Auðukúluheiði, Iceland</td>
<td>3</td>
<td>3</td>
<td>110</td>
<td>0.9 / 8.6 / -5.0</td>
</tr>
<tr>
<td>Australian Alps</td>
<td>1</td>
<td>18</td>
<td>191</td>
<td>4.7 / 11.4 / -1.5</td>
</tr>
<tr>
<td>Disko Island, Greenland</td>
<td>7</td>
<td>7</td>
<td>112</td>
<td>-4.0 / 7.1 / -15.4</td>
</tr>
<tr>
<td>Fairbanks, Alaska</td>
<td>7</td>
<td>14</td>
<td>56</td>
<td>-4.8 / 14.3 / -22.0</td>
</tr>
<tr>
<td>Gothic Mountain, Colorado, USA</td>
<td>5</td>
<td>5</td>
<td>95</td>
<td>2.2 / 13.4 / -8.1</td>
</tr>
<tr>
<td>Italian Alps</td>
<td>2</td>
<td>14</td>
<td>116</td>
<td>-1.6 / 7.5 / -10.1</td>
</tr>
<tr>
<td>Kangerlussuaq, Greenland</td>
<td>2</td>
<td>2</td>
<td>36</td>
<td>-5.6 / 7.5 / -16.6</td>
</tr>
<tr>
<td>Khanyymey, western Siberia</td>
<td>2</td>
<td>2</td>
<td>15</td>
<td>-3.6 / 15.4 / -21.1</td>
</tr>
<tr>
<td>Kluane, Yukon, Canada</td>
<td>15</td>
<td>72</td>
<td>757</td>
<td>-3.1 / 8.8 / -14.1</td>
</tr>
<tr>
<td>Lofoten Islands, Norways</td>
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<td>16</td>
<td>55</td>
<td>5.8 / 12.6 / 0.8</td>
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<tr>
<td>Narsarsuaq, Greenland</td>
<td>10</td>
<td>49</td>
<td>450</td>
<td>-3.3 / 6.6 / -12.0</td>
</tr>
<tr>
<td>Northern Norway</td>
<td>35</td>
<td>62</td>
<td>119</td>
<td>0.5 / 11.9 / -9.7</td>
</tr>
<tr>
<td>Northern Sweden</td>
<td>56</td>
<td>122</td>
<td>467</td>
<td>-2.1 / 9.9 / -12.8</td>
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<tr>
<td>Qikiqtaruk-Herschel Island, Yukon, Canada</td>
<td>9</td>
<td>14</td>
<td>224</td>
<td>-9.4 / 7.6 / -24.3</td>
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<td>1</td>
<td>5</td>
<td>-9.4 / 6.4 / -26.6</td>
</tr>
<tr>
<td>Svalbard</td>
<td>25</td>
<td>109</td>
<td>468</td>
<td>-6.3 / 4.2 / -14.7</td>
</tr>
<tr>
<td>Swiss Alps</td>
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<td>61</td>
<td>256</td>
<td>-1.00 / 8.0 / -9.4</td>
</tr>
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<td>Peistareykir, Iceland</td>
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<td>2</td>
<td>72</td>
<td>1.7 / 8.9 / -3.5</td>
</tr>
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<td>Pingvellir, Iceland</td>
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<td>1</td>
<td>40</td>
<td>4.0 / 10.7 / -1.1</td>
</tr>
<tr>
<td>Tazovsky, western Siberia</td>
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<td>1</td>
<td>8</td>
<td>-7.4 / 12.5 / -25.1</td>
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<td>Toolik Lake, Alaska, USA</td>
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<td>7</td>
<td>140</td>
<td>-10.2 / 10.4 / -26.6</td>
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<td>Trail Valley, NWT, Canada</td>
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<td>30</td>
<td>180</td>
<td>-9.1 / 12.0 / -27.2</td>
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<tr>
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<td>2</td>
<td>40</td>
<td>-3.9 / 9.9 / -20.8</td>
</tr>
<tr>
<td>Urengoy, western Siberia</td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>-6.3 / 13.7 / -24.0</td>
</tr>
</tbody>
</table>
Table S5.2 Model outputs for individual environmental variable – decomposition relationships. Bold rows designate relationships (slope parameter) for which the credible interval does not cross zero (i.e., the relationship is “significant”). Sample size indicates number of tea samples available to test relationships. Effective sample size indicates number of convergent model runs.

<table>
<thead>
<tr>
<th>Environ. Variable</th>
<th>Decomp. variable</th>
<th>Time period</th>
<th>Type</th>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>97.5%</th>
<th>Sample size</th>
<th>Effective sample size</th>
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</thead>
<tbody>
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<td>Air temp. (measured)</td>
<td>Mass loss</td>
<td>Summer</td>
<td>G</td>
<td>Intercept</td>
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<td>0.006</td>
<td>0.522</td>
<td>0.538</td>
<td>1,913</td>
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<td>Mass loss</td>
<td>Summer</td>
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<td>Intercept</td>
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<td>0.159</td>
<td>0.182</td>
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<td>Air temp. (measured)</td>
<td>Mass loss</td>
<td>Summer</td>
<td>G</td>
<td>Slope</td>
<td>0.003</td>
<td>0.002</td>
<td>-0.002</td>
<td>0.000</td>
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<td>Summer</td>
<td>R</td>
<td>Slope</td>
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<td>0.002</td>
<td>-3.99e-04</td>
<td>0.000</td>
<td>1,913</td>
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<td>G</td>
<td>Intercept</td>
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<td>Summer</td>
<td>R</td>
<td>Intercept</td>
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<td>Summer</td>
<td>G</td>
<td>Intercept</td>
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<td>0.013</td>
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<td>Air temp. (CHELSA)</td>
<td>Mass loss</td>
<td>Summer</td>
<td>R</td>
<td>Slope</td>
<td>0.012</td>
<td>0.002</td>
<td>0.008</td>
<td>0.016</td>
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<td>Air temp. (CHELSA)</td>
<td>Mass loss</td>
<td>Summer</td>
<td>G</td>
<td>Intercept</td>
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<tr>
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<td>G</td>
<td>Slope</td>
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<td>0.001</td>
<td>0.003</td>
<td>0.005</td>
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<tr>
<td>Precip. (CHELSA)</td>
<td>Mass loss</td>
<td>Summer</td>
<td>R</td>
<td>Slope</td>
<td>0.003</td>
<td>0.001</td>
<td>0.002</td>
<td>0.004</td>
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<td>15,000</td>
</tr>
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<td>Moisture (ESA)</td>
<td>Mass loss</td>
<td>Summer</td>
<td>G</td>
<td>Intercept</td>
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<td>Intercept</td>
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<tr>
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<td>Mass loss</td>
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<td>G</td>
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<td>15,000</td>
</tr>
<tr>
<td>Air temp. (CHELSA)</td>
<td>k</td>
<td>Summer</td>
<td>R</td>
<td>Slope</td>
<td>1.84e-04</td>
<td>1.22e-04</td>
<td>-5.34e-05</td>
<td>4.25e-04</td>
<td>1,403</td>
<td>15,000</td>
</tr>
<tr>
<td>Precip. (CHELSA)</td>
<td>k</td>
<td>Summer</td>
<td>R</td>
<td>Intercept</td>
<td>0.011</td>
<td>0.001</td>
<td>0.010</td>
<td>0.012</td>
<td>1,403</td>
<td>15,000</td>
</tr>
<tr>
<td>Precip. (CHELSA)</td>
<td>k</td>
<td>Summer</td>
<td>R</td>
<td>Slope</td>
<td>1.10e-05</td>
<td>3.24e-05</td>
<td>-5.34e-05</td>
<td>7.46e-05</td>
<td>1,403</td>
<td>15,000</td>
</tr>
<tr>
<td>Moisture (ESA)</td>
<td>k</td>
<td>Summer</td>
<td>R</td>
<td>Intercept</td>
<td>0.011</td>
<td>0.001</td>
<td>0.010</td>
<td>0.012</td>
<td>1,108</td>
<td>15,000</td>
</tr>
<tr>
<td>Moisture (ESA)</td>
<td>k</td>
<td>Summer</td>
<td>R</td>
<td>Slope</td>
<td>1.24e-05</td>
<td>1.61e-04</td>
<td>-2.99e-04</td>
<td>3.30e-04</td>
<td>1,108</td>
<td>15,000</td>
</tr>
</tbody>
</table>
**Table S5.3** Model outputs for environmental variable – decomposition relationships within grid cells. Bold rows designate relationships (slope parameter) for which the credible interval does not cross zero (i.e., the relationship is “significant”). Sample size indicates number of tea samples available to test relationships. Effective sample size indicates number of convergent model runs. Variables are standardized within grid cells using mean zero, unit variance scaling. All models are for summer incubations only.

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>Decomp variable</th>
<th>Tea Type</th>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>97.5%</th>
<th>Sample size</th>
<th>Effective sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temp.</td>
<td>Mass loss</td>
<td>G</td>
<td>Intercept</td>
<td>0.844</td>
<td>0.108</td>
<td>0.636</td>
<td>1.060</td>
<td>1,504</td>
<td>5,206</td>
</tr>
<tr>
<td>Air temp.</td>
<td>Mass loss</td>
<td>R</td>
<td>Intercept</td>
<td>-1.042</td>
<td>0.103</td>
<td>-1.245</td>
<td>-0.840</td>
<td>1,504</td>
<td>6,363</td>
</tr>
<tr>
<td>Air temp.</td>
<td>Mass loss</td>
<td>G</td>
<td>Slope</td>
<td>-0.047</td>
<td>0.043</td>
<td>-0.130</td>
<td>0.039</td>
<td>1,504</td>
<td>1,345</td>
</tr>
<tr>
<td>Air temp.</td>
<td>Mass loss</td>
<td>R</td>
<td>Slope</td>
<td>0.011</td>
<td>0.021</td>
<td>-0.030</td>
<td>0.054</td>
<td>1,504</td>
<td>6,516</td>
</tr>
<tr>
<td>Soil temp.</td>
<td>Mass loss</td>
<td>G</td>
<td>Intercept</td>
<td>0.799</td>
<td>0.105</td>
<td>0.593</td>
<td>1.001</td>
<td>1,446</td>
<td>444</td>
</tr>
<tr>
<td>Soil temp.</td>
<td>Mass loss</td>
<td>R</td>
<td>Intercept</td>
<td>-0.845</td>
<td>0.104</td>
<td>-1.043</td>
<td>-0.641</td>
<td>1,446</td>
<td>243</td>
</tr>
<tr>
<td>Soil temp.</td>
<td>Mass loss</td>
<td>G</td>
<td>Slope</td>
<td>0.146</td>
<td>0.026</td>
<td>0.093</td>
<td>0.197</td>
<td>1,446</td>
<td>489</td>
</tr>
<tr>
<td>Soil temp.</td>
<td>Mass loss</td>
<td>R</td>
<td>Slope</td>
<td>0.075</td>
<td>0.024</td>
<td>0.028</td>
<td>0.122</td>
<td>1,446</td>
<td>540</td>
</tr>
<tr>
<td>Moisture</td>
<td>Mass loss</td>
<td>G</td>
<td>Intercept</td>
<td>6.84e-01</td>
<td>1.35e-01</td>
<td>4.23e-01</td>
<td>9.49e-01</td>
<td>917</td>
<td>1,075</td>
</tr>
<tr>
<td>Moisture</td>
<td>Mass loss</td>
<td>R</td>
<td>Intercept</td>
<td>-0.928</td>
<td>0.139</td>
<td>-1.206</td>
<td>-0.660</td>
<td>917</td>
<td>1,083</td>
</tr>
<tr>
<td>Moisture</td>
<td>Mass loss</td>
<td>G</td>
<td>Slope</td>
<td>0.081</td>
<td>0.052</td>
<td>-0.018</td>
<td>0.184</td>
<td>917</td>
<td>390</td>
</tr>
<tr>
<td>Moisture</td>
<td>Mass loss</td>
<td>R</td>
<td>Slope</td>
<td>0.057</td>
<td>0.043</td>
<td>-0.027</td>
<td>0.141</td>
<td>917</td>
<td>553</td>
</tr>
</tbody>
</table>
Table S5.4 Model outputs for temperature – decomposition relationships, including an interaction with soil moisture. Bold rows designate relationships (slope parameter) for which the credible interval does not cross zero (i.e., the relationship is “significant”). Sample size indicates number of tea samples available to test relationships. Effective sample size indicates number of convergent model runs. Environmental variables are unscaled and in original units. All models are for summer incubations only.

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>Decompos variable</th>
<th>Tea Type</th>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>97.5%</th>
<th>Sample size</th>
<th>Effective sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss G</td>
<td>Intercept</td>
<td>0.513</td>
<td>0.014</td>
<td>0.487</td>
<td>0.540</td>
<td>624</td>
<td>5,842</td>
<td></td>
</tr>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss G</td>
<td>Temp. slope</td>
<td>0.028</td>
<td>0.005</td>
<td>0.018</td>
<td>0.036</td>
<td>624</td>
<td>5,700</td>
<td></td>
</tr>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss G</td>
<td>Moisture slope</td>
<td>0.002</td>
<td>0.001</td>
<td>0.001</td>
<td>0.003</td>
<td>624</td>
<td>5,299</td>
<td></td>
</tr>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss G</td>
<td>Interaction</td>
<td>-7.34e-05</td>
<td>2.55e-04</td>
<td>-5.86e-04</td>
<td>4.22e-04</td>
<td>624</td>
<td>5,206</td>
<td></td>
</tr>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss R</td>
<td>Intercept</td>
<td>0.169</td>
<td>0.011</td>
<td>0.148</td>
<td>0.190</td>
<td>624</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss R</td>
<td>Temp. slope</td>
<td>0.006</td>
<td>0.004</td>
<td>-0.001</td>
<td>0.014</td>
<td>624</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Measured soil temp. x moisture</td>
<td>Mass loss R</td>
<td>Moisture slope</td>
<td>4.84e-04</td>
<td>0.001</td>
<td>-0.001</td>
<td>0.001</td>
<td>624</td>
<td>11,411</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss G</td>
<td>Intercept</td>
<td>0.580</td>
<td>0.009</td>
<td>0.561</td>
<td>0.598</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss G</td>
<td>Temp. slope</td>
<td>0.019</td>
<td>0.002</td>
<td>0.015</td>
<td>0.023</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss G</td>
<td>Moisture slope</td>
<td>0.009</td>
<td>0.003</td>
<td>0.004</td>
<td>0.014</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss G</td>
<td>Interaction</td>
<td>0.001</td>
<td>0.001</td>
<td>-6.46e-04</td>
<td>0.002</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss R</td>
<td>Intercept</td>
<td>0.216</td>
<td>0.009</td>
<td>0.198</td>
<td>0.233</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss R</td>
<td>Temp. slope</td>
<td>0.012</td>
<td>0.002</td>
<td>0.008</td>
<td>0.016</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss R</td>
<td>Moisture slope</td>
<td>0.004</td>
<td>0.003</td>
<td>-0.001</td>
<td>0.009</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
<tr>
<td>Gridded temp. x moisture</td>
<td>Mass loss R</td>
<td>Interaction</td>
<td>0.001</td>
<td>0.001</td>
<td>3.77e-05</td>
<td>0.003</td>
<td>2,234</td>
<td>15,000</td>
<td></td>
</tr>
</tbody>
</table>
**Table S5.5** Model outputs for relationships between measured environmental variables and gridded environmental variables. Bold rows designate relationships (slope parameter) for which the credible interval does not cross zero (i.e., the relationship is “significant”). Sample size indicates number of sites available to test relationships. Effective sample size indicates number of convergent model runs.

<table>
<thead>
<tr>
<th>Measured variable</th>
<th>Gridded variable</th>
<th>Parameter</th>
<th>Mean</th>
<th>2.5%</th>
<th>97.5%</th>
<th>Sample size</th>
<th>Effective sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature</td>
<td>CHELSA air temperature</td>
<td>Intercept</td>
<td>-0.225</td>
<td>-1.596</td>
<td>1.194</td>
<td>151</td>
<td>15,000</td>
</tr>
<tr>
<td>Air temperature</td>
<td>CHELSA air temperature</td>
<td>Slope</td>
<td>0.877</td>
<td>0.474</td>
<td>1.013</td>
<td>151</td>
<td>15,000</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>CHELSA air temperature</td>
<td>Intercept</td>
<td>-2.259</td>
<td>-3.507</td>
<td>-1.013</td>
<td>134</td>
<td>15,000</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>CHELSA air temperature</td>
<td>Slope</td>
<td>1.24</td>
<td>1.130</td>
<td>1.352</td>
<td>134</td>
<td>15,000</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>CHELSA precipitation</td>
<td>Intercept</td>
<td>16.876</td>
<td>14.625</td>
<td>19.197</td>
<td>79</td>
<td>15,000</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>CHELSA precipitation</td>
<td>Slope</td>
<td>-0.120</td>
<td>-0.170</td>
<td>-0.074</td>
<td>79</td>
<td>11,445</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>ESA soil moisture</td>
<td>Intercept</td>
<td>24.405</td>
<td>22.237</td>
<td>26.612</td>
<td>39</td>
<td>15,000</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>ESA soil moisture</td>
<td>Slope</td>
<td>0.061</td>
<td>-0.004</td>
<td>0.128</td>
<td>39</td>
<td>15,000</td>
</tr>
</tbody>
</table>
Supplementary Figures

Figure S1: Tea types are representative of the decomposition of a range of tundra plant species. Annual mass loss of green and rooibos tea compared to mass loss of a range of representative tundra species. Tea types are indicated by red (rooibos tea) and green (green tea) bars. Tundra species were collected from two sites: the Kluane Range Mountains, Yukon, Canada (62°N) and Qikiqtaruk-Herschel Island, Yukon, Canada (70°N). All litter and tea were decomposed for one year in a common litter bed at Kluane Lake following methods outlined in Cornelissen et al (2007).
Figure S5.2: Relationships between decomposition (mass loss), measured environmental variables (a-c), and gridded climate data (d-f) for year-long tea incubations, as opposed to summer incubations in main text (Fig 5.3) or winter incubations (Fig S5.3). Points indicate individual tea bag replicates across all sites. Lines indicate hierarchical Bayesian model fit with 95% credible intervals. Colours indicate tea type (red = rooibos tea, green = green tea). See also Table S5.2.
Figure S5.3: Relationships between decomposition (mass loss), measured environmental variables (a-c), and gridded climate data (d-f) for winter tea incubations, as opposed to summer incubations in main text (Fig 5.3) or year-long incubations (Figure S5.2). Points indicate individual tea bag replicates across all sites. Lines indicate hierarchical Bayesian model fit with 95% credible intervals. Colours indicate tea type (red = rooibos tea, green = green tea). See also Table S5.2.
Figure S5.4: Relationships between stabilisation factor (S), measured environmental variables (a-c), and gridded climate data (d-f) for summer tea incubations, as opposed to summer mass loss in main text (Fig 5.3). S represents the proportion of labile material remaining once decomposition has stabilised, and thus long-term carbon storage. Points indicate individual tea bag replicates across all sites. Lines indicate hierarchical Bayesian model fit with 95% credible intervals. Stabilisation factor is calculated based on decomposition of green tea, and is assumed to be consistent across tea types (Keuskamp et al., 2013). See also Table S5.2.
Figure S5.5: Relationships between decomposition rate (k), measured environmental variables (a-c), and gridded climate data (d-f) for summer tea incubations, as opposed to summer mass loss in main text (Fig 5.3). k represents the rate of loss of labile material, and thus short-term decomposition dynamics and biogeochemical cycling. Points indicate individual tea bag replicates across all sites. Lines indicate hierarchical Bayesian model fit with 95% credible intervals. Decomposition rate is calculated based on decomposition of rooibos tea, and is assumed to be consistent across tea types (Keuskamp et al., 2013). See also Table S5.2.
Figure S5.6: Within-grid cell relationships mirror among-site relationships between environmental variables and mass loss, but with greater variability. Within-grid cell relationships between summer decomposition (mass loss) and measured environmental variables, as opposed to among sites (Figure regions (Fig 5.3). Environmental and decomposition variables are standardised within 0.25 x 0.25-degree resolution grid cells using mean zero, unit variance scaling. Points indicate individual tea bag replicates. Lines indicate hierarchical Bayesian model fit with 95% credible intervals. Colours indicate tea type (red = rooibos tea, green = green tea). See also Table S5.3.
Figure S5.7: Soil moisture does not influence the relationships between soil temperature and mass loss, but decomposition is higher at wetter versus drier sites at any given temperature. Relationships between summer decomposition (mass loss), (a) measured soil temperature and soil moisture, and (b) gridded temperature (CHELSA) and soil moisture (ESA). Models incorporate the interaction between soil temperature and soil moisture. Lines indicate predicted decomposition at upper (dark) and lower (light) quartiles of soil moisture, representing wet and dry sites respectively, based on hierarchical Bayesian model fit with 95% credible intervals. Points indicate individual tea bag replicates. Colours indicate tea type (red = rooibos tea, green = green tea). See also Table S5.4.
Figure S5.8: Mass loss of tea types stabilises after approximately 30 days and does not converge after two years of burial. Mass remaining over time of rooibos and green tea over time at warm and cold tundra sites at the Kluane Lake location (see Table S5.1). (a) Mass remaining at the warm experimental site, with tea extracted every two days over a two-month summer period; (b) mass remaining at the warm experimental site with summer, one-year and two-year incubation lengths; and (c) mass remaining at the cold experimental site with summer, two-month, one-year, and two-year incubation lengths.
Figure S5.9: Mass loss of buried tea bags is significantly greater than tea placed on the ground surface for green tea but not or rooibos tea. Teabags were incubated in a common site (Kluane Lake, see Table S5.1) and were either buried at 5cm depth directly in the soil (grey) or placed within a litterbed and covered in a local litter medium (white), following protocols outlined in Cornelissen et al (2007). Teabags were incubated for one year, though the time periods of incubation differed between the two treatment types (buried: June – June, surface: August – August). Stars indicate significance (***, $P < 0.001$, ns, $P > 0.05$).
Figure S5.10: Site-measured environmental variables align with gridded climate variables for temperature but not moisture. Relationships between site-measured environmental variables, and gridded climate data for all tea bag sites with available data. Lines indicate Bayesian hierarchical model fit and 95% credible intervals. See also Table S5.

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term warming restructures Arctic tundra without changing net soil carbon storage.
S6. Supporting information for Chapter 6: ‘Tundra vegetation change does not alter community litter decomposability’

Below are all supplementary tables and figures supporting the analyses set out in ‘Tundra vegetation change does not alter community litter decomposability’.

S6.1 Supplementary Tables

Table S6.1: Litter collection locations. New sites added by this study are indicated by an asterisk. All other sites are presented in Cornelissen et al. (2007).

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>MAT (°C)</th>
<th>No of species sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tibet HGM (Tibet)</td>
<td>37.62</td>
<td>101.20</td>
<td>0.7</td>
<td>8</td>
</tr>
<tr>
<td>Tibet LGM (Tibet)</td>
<td>37.62</td>
<td>101.20</td>
<td>0.7</td>
<td>6</td>
</tr>
<tr>
<td>Tibet HGSH (Tibet)</td>
<td>37.62</td>
<td>101.20</td>
<td>0.7</td>
<td>7</td>
</tr>
<tr>
<td>Tibet LGSH (Tibet)</td>
<td>37.62</td>
<td>101.20</td>
<td>0.7</td>
<td>11</td>
</tr>
<tr>
<td>Wyoming ungrazed (USA)</td>
<td>41.33</td>
<td>-106.28</td>
<td>-0.7</td>
<td>1</td>
</tr>
<tr>
<td>Wyoming grazed (USA)</td>
<td>41.33</td>
<td>-106.28</td>
<td>-0.7</td>
<td>1</td>
</tr>
<tr>
<td>Italy E.-Vaccinietum (Italy)</td>
<td>44.13</td>
<td>10.58</td>
<td>3.6</td>
<td>2</td>
</tr>
<tr>
<td>Italy V.-Hypericetum (Italy)</td>
<td>44.13</td>
<td>10.58</td>
<td>3.6</td>
<td>2</td>
</tr>
<tr>
<td>Finse 1 (Norway)</td>
<td>60.60</td>
<td>7.53</td>
<td>-1.2</td>
<td>3</td>
</tr>
<tr>
<td>Finse 2 (Norway)</td>
<td>60.60</td>
<td>7.53</td>
<td>-1.2</td>
<td>2</td>
</tr>
<tr>
<td>*Kluane Plateau (Canada)</td>
<td>60.96</td>
<td>-138.41</td>
<td>-6.6</td>
<td>3</td>
</tr>
<tr>
<td>*Pika Camp (Canada)</td>
<td>61.21</td>
<td>-138.28</td>
<td>-7.6</td>
<td>12</td>
</tr>
<tr>
<td>Ruby Range (Canada)</td>
<td>61.21</td>
<td>-138.28</td>
<td>-7.6</td>
<td>4</td>
</tr>
<tr>
<td>Thingvellir (Iceland)</td>
<td>64.28</td>
<td>-21.08</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Auokuluheioi (Iceland)</td>
<td>65.27</td>
<td>-20.25</td>
<td>1.6</td>
<td>5</td>
</tr>
<tr>
<td>Latnja jaure Meadow (Sweden)</td>
<td>68.21</td>
<td>18.29</td>
<td>-1.9</td>
<td>9</td>
</tr>
<tr>
<td>Latnja sedge meadow (Sweden)</td>
<td>68.21</td>
<td>18.29</td>
<td>-1.9</td>
<td>1</td>
</tr>
<tr>
<td>Sloahtta (Sweden)</td>
<td>68.21</td>
<td>18.29</td>
<td>-1.9</td>
<td>1</td>
</tr>
<tr>
<td>Stordalen peat bog (Sweden)</td>
<td>68.33</td>
<td>19.00</td>
<td>-1.8</td>
<td>3</td>
</tr>
<tr>
<td>Stordalen woodland (Sweden)</td>
<td>68.33</td>
<td>19.00</td>
<td>-1.8</td>
<td>2</td>
</tr>
<tr>
<td>Paddus (Sweden)</td>
<td>68.35</td>
<td>18.82</td>
<td>-0.2</td>
<td>5</td>
</tr>
<tr>
<td>Paddus 1996 (Sweden)</td>
<td>68.35</td>
<td>18.82</td>
<td>-0.2</td>
<td>1</td>
</tr>
<tr>
<td>DART Paddus (Sweden)</td>
<td>68.35</td>
<td>18.82</td>
<td>-0.2</td>
<td>2</td>
</tr>
<tr>
<td>Abisko birch stools (Sweden)</td>
<td>68.35</td>
<td>18.82</td>
<td>-0.2</td>
<td>1</td>
</tr>
<tr>
<td>Abisko Sheffield site (Sweden)</td>
<td>68.35</td>
<td>18.82</td>
<td>-0.2</td>
<td>4</td>
</tr>
<tr>
<td>Abisko (Sweden)</td>
<td>68.35</td>
<td>18.82</td>
<td>-0.2</td>
<td>3</td>
</tr>
<tr>
<td>Latnja dry heath (Sweden)</td>
<td>68.37</td>
<td>18.46</td>
<td>-3.4</td>
<td>5</td>
</tr>
<tr>
<td>Caucasus (Russia)</td>
<td>68.37</td>
<td>18.67</td>
<td>-4</td>
<td>6</td>
</tr>
<tr>
<td>Toolik Tussock (USA)</td>
<td>68.63</td>
<td>-149.60</td>
<td>-11.3</td>
<td>1</td>
</tr>
<tr>
<td>Kilpisärvi high site (Finland)</td>
<td>69.02</td>
<td>20.83</td>
<td>-2</td>
<td>2</td>
</tr>
<tr>
<td>Kilpisjärvi low site (Finland)</td>
<td>69.02</td>
<td>20.83</td>
<td>-2</td>
<td>1</td>
</tr>
<tr>
<td>*Qikiqtaruk (Canada)</td>
<td>69.57</td>
<td>-138.90</td>
<td>-11.2</td>
<td>16</td>
</tr>
<tr>
<td>Isdammnen (Svalbard, Norway)</td>
<td>78.20</td>
<td>15.72</td>
<td>-7.6</td>
<td>4</td>
</tr>
<tr>
<td>Adventalen (Svalbard, Norway)</td>
<td>78.28</td>
<td>16.00</td>
<td>-8.8</td>
<td>3</td>
</tr>
<tr>
<td>Ny Alesund (Svalbard, Norway)</td>
<td>78.93</td>
<td>11.83</td>
<td>-5.4</td>
<td>1</td>
</tr>
</tbody>
</table>
Table S6.2: Correlation matrix for the six significant trait predictors of leaf decomposition. Combinations of traits with a Pearson’s correlation coefficient greater than 0.6 (red) were not included in the same model.

<table>
<thead>
<tr>
<th></th>
<th>LDMC</th>
<th>Leaf nitrogen</th>
<th>Leaf carbon</th>
<th>Leaf area</th>
<th>Leaf dry mass</th>
<th>Leaf fresh mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf nitrogen</td>
<td>-0.57</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf carbon</td>
<td>0.33</td>
<td>-0.21</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf area</td>
<td>-0.51</td>
<td>0.50</td>
<td>-0.10</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf dry mass</td>
<td>-0.48</td>
<td>0.45</td>
<td>-0.21</td>
<td>0.87</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Leaf fresh mass</td>
<td>-0.50</td>
<td>0.44</td>
<td>-0.24</td>
<td>0.81</td>
<td>0.92</td>
<td>-</td>
</tr>
</tbody>
</table>
**Table S6.3:** Comparison of R2 and AIC scores for models of litter decomposability. The model used in the main analysis (LDMC + leaf nitrogen + leaf area; indicated by * in table) was selected to maximise different aspects of trait expression while maintaining i) high R2 and ii) a low AIC score. We also ran results with multiple alternative models, but this did not alter results. The final model and any additional models tested are highlighted in bold. Highly correlated variables (Table S1) were not included in the same model. Note that trait data is not available for all species and so sample sizes differ among models.

<table>
<thead>
<tr>
<th>Model</th>
<th>R2 (marginal)</th>
<th>R2 (conditional)</th>
<th>AIC Score</th>
<th>No. species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Single variable models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf nitrogen</td>
<td>0.20</td>
<td>0.91</td>
<td>-1884</td>
<td>47</td>
</tr>
<tr>
<td>Leaf carbon</td>
<td>0.18</td>
<td>0.92</td>
<td>-1724</td>
<td>40</td>
</tr>
<tr>
<td>Leaf fresh mass</td>
<td>0.17</td>
<td>0.90</td>
<td>-1711</td>
<td>40</td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.20</td>
<td>0.90</td>
<td>-1659</td>
<td>44</td>
</tr>
<tr>
<td>LDMC</td>
<td>0.36</td>
<td>0.89</td>
<td>-1652</td>
<td>43</td>
</tr>
<tr>
<td>Leaf dry mass</td>
<td>0.15</td>
<td>0.90</td>
<td>-1634</td>
<td>42</td>
</tr>
<tr>
<td><strong>Best two-variable models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LDMC + leaf area</td>
<td>0.41</td>
<td>0.90</td>
<td>-1650</td>
<td>43</td>
</tr>
<tr>
<td>LDMC + leaf dry mass</td>
<td>0.41</td>
<td>0.90</td>
<td>-1626</td>
<td>41</td>
</tr>
<tr>
<td>LDMC + leaf fresh mass</td>
<td>0.39</td>
<td>0.90</td>
<td>-1622</td>
<td>40</td>
</tr>
<tr>
<td>LDMC + leaf nitrogen</td>
<td>0.33</td>
<td>0.90</td>
<td>-1578</td>
<td>41</td>
</tr>
<tr>
<td>LDMC + leaf carbon</td>
<td>0.34</td>
<td>0.90</td>
<td>-1436</td>
<td>35</td>
</tr>
<tr>
<td><strong>Best three-variable models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*LDMC + leaf nitrogen + leaf area</td>
<td>0.40</td>
<td>0.90</td>
<td>-1576</td>
<td>41</td>
</tr>
<tr>
<td>LDMC + leaf carbon + leaf area</td>
<td>0.43</td>
<td>0.90</td>
<td>-1433</td>
<td>35</td>
</tr>
<tr>
<td>LDMC + leaf nitrogen + leaf dry mass</td>
<td>0.40</td>
<td>0.90</td>
<td>-1553</td>
<td>41</td>
</tr>
<tr>
<td>LDMC + leaf nitrogen + leaf fresh mass</td>
<td>0.38</td>
<td>0.90</td>
<td>-1549</td>
<td>41</td>
</tr>
<tr>
<td>LDMC + leaf nitrogen + leaf carbon</td>
<td>0.36</td>
<td>0.90</td>
<td>-1432</td>
<td>41</td>
</tr>
<tr>
<td>LDMC + leaf carbon + leaf fresh mass</td>
<td>0.41</td>
<td>0.90</td>
<td>-1408</td>
<td>35</td>
</tr>
<tr>
<td>LDMC + leaf carbon + leaf dry mass</td>
<td>0.42</td>
<td>0.90</td>
<td>-1404</td>
<td>35</td>
</tr>
<tr>
<td><strong>Four-variable model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LDMC + leaf nitrogen + leaf carbon + leaf area</td>
<td>0.42</td>
<td>0.90</td>
<td>-1429</td>
<td>35</td>
</tr>
</tbody>
</table>
**Table S6.4:** Comparison of R2 and AIC scores for models of stem decomposability.
The model used in the main analysis (LDMC only, indicated by * in table) was selected to maximise different aspects of trait expression while maintaining i) high R2 and ii) a low AIC score. Only the LDMC model was significant. We also ran results with alternative models, but this did not alter results. The final model and any additional models tested are highlighted in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>R2 (marginal)</th>
<th>R2 (conditional)</th>
<th>AIC Score</th>
<th>No. species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Single variable models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>LDMC</em></td>
<td>0.26</td>
<td>0.73</td>
<td>-222</td>
<td>6</td>
</tr>
<tr>
<td>Stem specific density</td>
<td>0.01</td>
<td>0.75</td>
<td>-222</td>
<td>6</td>
</tr>
<tr>
<td>Leaf phosphorous</td>
<td>0.22</td>
<td>0.73</td>
<td>-221</td>
<td>6</td>
</tr>
<tr>
<td>SLA</td>
<td>0.03</td>
<td>0.75</td>
<td>-220</td>
<td>6</td>
</tr>
<tr>
<td>Leaf nitrogen</td>
<td>0.00</td>
<td>0.75</td>
<td>-220</td>
<td>6</td>
</tr>
<tr>
<td>C:N ratio</td>
<td>0.24</td>
<td>0.80</td>
<td>-160</td>
<td>5</td>
</tr>
<tr>
<td>Leaf carbon</td>
<td>0.32</td>
<td>0.81</td>
<td>-137</td>
<td>4</td>
</tr>
<tr>
<td>δ15 nitrogen</td>
<td>0.28</td>
<td>0.86</td>
<td>-113</td>
<td>3</td>
</tr>
<tr>
<td><strong>Best two-variable models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LDMC + Stem specific density</td>
<td>0.24</td>
<td>0.76</td>
<td>-220</td>
<td>6</td>
</tr>
<tr>
<td>LDMC + leaf phosphorous</td>
<td>0.25</td>
<td>0.75</td>
<td>-218</td>
<td>6</td>
</tr>
<tr>
<td>LDMC + SLA</td>
<td>0.29</td>
<td>0.75</td>
<td>-218</td>
<td>6</td>
</tr>
<tr>
<td>LDMC + leaf nitrogen</td>
<td>0.24</td>
<td>0.75</td>
<td>-218</td>
<td>6</td>
</tr>
<tr>
<td>LDMC + leaf carbon</td>
<td>0.35</td>
<td>0.83</td>
<td>-136</td>
<td>4</td>
</tr>
<tr>
<td>LDMC + δ15 nitrogen</td>
<td>0.11</td>
<td>0.96</td>
<td>-112</td>
<td>3</td>
</tr>
</tbody>
</table>
**Table S6.5** Model outputs for relationships between measured environmental variables and gridded environmental variables. **Bold rows designate relationships (slope parameter) for which the credible interval does not cross zero (i.e., the relationship is “significant”).** Sample size indicates number of sites available to test relationships. Effective sample size indicates number of convergent model runs.

<table>
<thead>
<tr>
<th>Environmental Variable</th>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>97.5%</th>
<th>Sample size</th>
<th>Effective Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Change over space</td>
<td>Intercept</td>
<td>0.506</td>
<td>0.008</td>
<td>0.489</td>
<td>0.522</td>
<td>4,575</td>
<td>9,330</td>
</tr>
<tr>
<td>Change over space</td>
<td>Temperature Slope</td>
<td>0.012</td>
<td>0.003</td>
<td>0.005</td>
<td>0.019</td>
<td>4,575</td>
<td>9,756</td>
</tr>
<tr>
<td>Change over space</td>
<td>Moisture Slope</td>
<td>0.069</td>
<td>0.011</td>
<td>0.048</td>
<td>0.091</td>
<td>4,575</td>
<td>4,064</td>
</tr>
<tr>
<td>Change over space</td>
<td>Temperature x moisture interaction</td>
<td>0.016</td>
<td>0.004</td>
<td>0.008</td>
<td>0.024</td>
<td>4,575</td>
<td>5,571</td>
</tr>
<tr>
<td>Change over time</td>
<td>Intercept</td>
<td>0.375</td>
<td>0.027</td>
<td>0.323</td>
<td>0.428</td>
<td>4,575</td>
<td>404</td>
</tr>
<tr>
<td>Change over time</td>
<td>Temperature Slope</td>
<td>9.03e-04</td>
<td>6.77e-04</td>
<td>-3.75e-04</td>
<td>2.26e-03</td>
<td>4,575</td>
<td>15,000</td>
</tr>
<tr>
<td>Change over time</td>
<td>Moisture Slope</td>
<td>0.064</td>
<td>0.014</td>
<td>0.036</td>
<td>0.090</td>
<td>4,575</td>
<td>364</td>
</tr>
<tr>
<td>Change over time</td>
<td>Temperature x moisture interaction</td>
<td>-3.98e-04</td>
<td>3.47e-04</td>
<td>-1.10e-03</td>
<td>2.74e-04</td>
<td>4,575</td>
<td>15,000</td>
</tr>
<tr>
<td>Change with warming</td>
<td>Intercept</td>
<td>1.25e-05</td>
<td>1.28e-04</td>
<td>-2.40e-04</td>
<td>2.68e-04</td>
<td>4,575</td>
<td>710</td>
</tr>
<tr>
<td>Change with warming</td>
<td>Temperature Slope</td>
<td>1.33e-03</td>
<td>2.70e-03</td>
<td>-3.97e-03</td>
<td>6.54e-03</td>
<td>4,575</td>
<td>266</td>
</tr>
<tr>
<td>Change with warming</td>
<td>Moisture Slope</td>
<td>-1.61e-04</td>
<td>2.50e-04</td>
<td>-6.52e-04</td>
<td>3.35e-04</td>
<td>4,575</td>
<td>610</td>
</tr>
<tr>
<td>Change with warming</td>
<td>Temperature x moisture interaction</td>
<td>3.47e-03</td>
<td>5.45e-03</td>
<td>-6.95e-03</td>
<td>1.43e-02</td>
<td>4,575</td>
<td>457</td>
</tr>
</tbody>
</table>
S6.2 Supplementary Figures

Figure S6.1: Relationship between leaf two-year mass loss and twelve plant traits for tundra species. Points indicate sample mass loss, coloured by decomposition site (red = Abisko, orange = Kluane, blue = Latnjajure). Lines indicate linear mixed model fit (bold = \( P < 0.05 \), solid = \( P < 0.1 \), dashed, \( P > 0.1 \)) with decomposition site as a fixed effect and species and origin site as random effects. Shaded areas represent 95% confidence intervals. Bold titles indicate traits used final leaf decomposition model.
Figure S6.2: Relationship between stem two-year mass loss and eight plant traits for tundra species. Points indicate mass loss of samples. All stem samples were decomposed at the Kluane site. Lines indicate linear mixed model fit (bold = $P < 0.05$, solid = $P < 0.1$, dashed, $P > 0.1$) with decomposition site as a fixed effect and species and origin site as random effects with fixed slopes. Shaded areas represent 95% confidence intervals. Bold titles indicate traits used in final decomposition model.
Figure S6.3: Two year mass loss shows no significant relationship with trait collection site characteristics within species. Relationship between mass loss and a) latitude (slope = -1.3% °N, $P = 0.28$), b) mean annual temperature (slope = 2.0% °C$^{-1}$, $P = 0.10$), c) summer temperature (slope = -1.7% °C$^{-1}$, $P = 0.18$), and d) winter temperature (slope = -1.0% °C$^{-1}$, $P = 0.09$). All variables are scaled within species. Grey lines indicate species-specific linear slopes. Black lines represent linear mixed model fit with decomposition site as a fixed effect and origin site as a random effect with random slopes. Errors represent 95% confidence intervals.
Figure S6.4: Standardised effect sizes of wood decomposition-trait relationships for 8 plant traits. Symbols indicate model significance (• = P < 0.1) with significant traits coloured red.
Figure S6.5: Change in community weighted decomposability a) over space and b) over time is not significantly affected by the assumed proportion of woody inputs (from 0% to 50% of annual litter inputs) entering the litter pool for shrub species. Colours indicate categorical moisture values (blue = wet, red = dry). Dashed line at 10% indicates model used in main text.