Impacts of climate change on carbon and nutrient cycling in oceanic-alpine ecosystems

Rosanne C. Broyd

For Uncle Freddie

Alba nam beanntan ard… Talamh alainn nan daoine

~

I see Scotland of the high mountains… The beautiful soil of the people

- C. MacDonald & R. MacDonald

Declaration

This thesis has not been submitted in support of an application for another degree at this or any other university. It is the result of my own work and includes nothing that is the outcome of work done in collaboration except where specifically indicated. Many of the ideas in this thesis were the product of discussions with my supervisors: Dr Andrea Britton and Dr Andy Taylor (The James Hutton Institute), Prof Nick Ostle (Lancaster University), and Dr Rob Mills (University of York).

This thesis word length is 25,573 (excluding table legends, figure captions, and reference lists), and therefore does not exceed the permitted maximum.

Statement of Authorship

This thesis has been prepared in the alternative format, as a set of three papers presented in Chapters 2 – 4, with some intended for submission to peer-reviewed journals. These chapters have co-authors in addition to my supervisory team. Please find below details of these publications with information regarding my contributions using the CRediT taxonomy, as certified by the signatures of all co-authors. Chapters 1 and 5 are introductory and discussion chapters and are not intended for submission.

Chapter 2

Broyd, Rosanne C., Robert T.E. Mills, Andy F.S. Taylor, Jennifer Michel, José G. van Paassen, Nicholas J. Ostle, and Andrea J. Britton. Variations in snow cover, vegetation communities, and soil carbon pools across topographies and elevation in oceanic-alpine ecosystems. *In preparation.*

RCB was responsible for Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, and Writing – review & editing.

Chapter 3

Broyd, Rosanne C., Andrea J. Britton, Andy F. S. Taylor, Nicholas J. Ostle, Zander Lee, Alex Muxworthy, and Robert T. E. Mills. Drought resilience of ecosystem respiration in *Nardus* snowbeds and *Racomitrium* heath. *Not intended for submission.*

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Chapter 4

Broyd, Rosanne C. Andy F.S. Taylor, Sheila Gibbs, Robert T.E. Mills, Nicholas J. Ostle, Sara Aguado Saiz, and Andrea J. Britton. Impacts of drought and storm events on carbon and nitrogen fluxes in contrasting oceanic-alpine ecosystems. *In preparation.*

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Yours sincerely,

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Abstract

Mountains are global reservoirs of biodiversity, water, and soil carbon (C), but are warming at greater than average rates, with reducing snow cover and changing rainfall regimes. These changes may alter biogeochemical cycling, impacting the fate of soil C. For oceanic-alpine ecosystems, there is limited knowledge about basic attributes and functioning, particularly responses to environmental change. This thesis aimed to improve understanding of C cycling in these ecosystems and potential impacts of climate change. I conducted surveys and experiments across snow melt gradients, elevations, and contrasting habitats. Survey of vegetation and soils in the Cairngorm Mountains showed that snow cover duration, elevation, and topography (snow-collecting vs snow-shedding sites) drove vegetation community composition. However, differences in vegetation were not reflected by C pool size in the upper 15 cm organic topsoil. In laboratory experiments, I examined effects of drought and rewetting intensity on C and nitrogen (N) cycling. Gas fluxes differed between plant communities and drought generally reduced ecosystem respiration rates. Rewetting led to a pulse in ecosystem respiration rates in *Nardus* snowbeds, but the nature of rewetting did not determine the size of the gas flux. Total leachate losses of C and all forms of N were greater following high intensity rewetting (storm). Drought reduced total losses of C and some forms of N, but increased total nitrate losses. Nitrate losses were greatest when storm followed drought. Large losses of nitrate due to dry periods and heavy rain events could acidify soils and lead to eutrophication of surface waters, potentially impacting ecosystem functioning. I conclude that oceanic-alpine ecosystems hold significant carbon stocks and are resilient to drought events, but it will be important to evaluate the functions of soil microbial communities, including the source of C mineralised following rewetting events, as soil microorganisms determine the relative accumulation and release of soil C and N through soil-atmosphere exchange.

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Abbreviations and acronyms

°	degree (unit for slope and aspect)
°	degree (unit latitude and longitude)
°C	degree Celsius (unit of temperature)
'	minute (unit latitude and longitude)
ANOVA	analysis of variance (statistical test)
asl	above sea level
Bd	bulk density
C	control (treatment)
C	carbon
C_{conc}	carbon concentration
C_{pool}	carbon pool
C:N	carbon to nitrogen ratio
$CaCl_2\ 2H_2O$	calcium chloride dihydrate
$CHCl_3$	chloroform
cm	centimetre (unit of length)
cm^3	cubic centimetre (unit of volume)
CH_4	methane
CO_2	carbon dioxide
D	soil depth
D	drought (treatment)
DOC	dissolved organic carbon
DOC:TDN	dissolved organic carbon to total dissolved nitrogen ratio
DON	dissolved organic nitrogen
EH	Empetrum heath

ER	ecosystem respiration
F	effect size (statistics)
g	gram (unit of mass)
GAMM	generalised additive mixed model (statistics)
GP	gross photosynthesis
hr	hour (unit of time)
K_2SO_4	potassium sulphate
KCl	potassium chloride
kg	kilogram (unit of mass)
KH_2PO_4	potassium dihydrogenphosphate
km	kilometre (unit of length)
l	litre (unit of volume)
LME	linear mixed effect (statistics)
M	molar mass (SI-unit)
m	metre (unit of length)
m^2	square metre (unit of area)
MBC	microbial biomass carbon
MBC:N	microbial biomass carbon to nitrogen ratio
MBN	microbial biomass nitrogen
mg	milligram (unit of mass)
MgCl	magnesium chloride
ml	millilitre (unit of volume)
mm	millimetre (unit of length)
N	nitrogen
N	north (geographic direction)

N_{conc}	nitrogen concentration
N_{pool}	nitrogen pool
Na_2SO_4	sodium sulphate
NaCl	sodium chloride
NEE	net ecosystem exchange
NH_4-N	nitrogen in the form of ammonium
NH_4+	ammonium
NH_4NO_3	ammonium nitrate
NMDS	non-metric multidimensional scaling (ordination technique)
NO_3-	nitrate
NO_3-N	nitrogen in the form of nitrate
NPP	net primary production
NS	*Nardus* snowbed
p	probability value
PCoA	principal coordinate analysis (ordination technique)
PFG	plant functional group
pH	potential for hydrogen
ppm	parts per million (concentration)
R^2	correlation coefficient
RH	Racomitrium heath
RL	resilience (index)
RR	response ratio
RS	resistance (index)
S	storm (treatment)
s.e.	standard error

SOC	soil organic carbon
t	effect size (statistics)
TDN	total dissolved nitrogen
W	West (geographic direction)
μg	microgram (unit of mass)
μM	micromoles (unit of molar mass)

1 Introduction

Globally, carbon (C) is cycled between the atmosphere, biosphere, hydrosphere, and geosphere. Carbon is removed from the atmosphere via photosynthesis and is fixed as organic compounds either in plant biomass or as plant-derived inputs into the soil. Soil is the largest terrestrial C store, and is estimated to contain 1462-1548 Pg C and 2376-2456 Pg C in the top one and two metres of soil, respectively (Batjes 1996). Autotrophic respiration and decomposition of organic matter return C from the soil to the atmosphere as carbon dioxide (CO_2) or methane (CH_4) depending on environmental conditions, primarily the availability of oxygen. Carbon dioxide is the main form of C during the atmospheric phase of the cycle and, as a greenhouse gas, is a driver of anthropogenic climate change.

Since the start of the Industrial Revolution in the 18th century human activity has released vast quantities of CO_2, increasing atmospheric concentrations by 48%, from 277 ppm in 1750 to 410 ppm in 2019 (Friedlingstein et al. 2020). The anthropogenic increase in atmospheric CO_2 concentrations has resulted in warming of mean global surface temperatures by 0.85 °C between 1880 and 2012 (IPCC 2013). Understanding the impacts of this rapid climate warming on C cycling in terrestrial ecosystems is of paramount importance to global society.

1.1 Soil carbon store

Soils are the primary terrestrial C store; cold and wet northern ecosystems in particular contain large pools of soil C, estimated to represent almost a third of the global soil C stocks (Post et al. 1982, Gorham 1991). The climate in these biomes limits decomposition rates and promotes C accumulation (Hobbie et al. 2000). Estimates of soil C pools above the treeline in the European Alps and Pyrenees range from up to 5 kg C m⁻

[2] in non-vegetated soils (Pintaldi et al. 2021), and 5-38 kg C m^{-2} under vegetation (Garcia-Pausas et al. 2007, Leifeld et al. 2009, Djukic et al. 2010), to up to 53 kg C m^{-2} in permafrost soils of the Tibetan Plateau (Genxu et al. 2002).

The potential for release of soil C in response to warming is dependent on initial soil C stock, with greater losses originating from soils with initially larger C stocks (Crowther et al. 2016) suggesting that the large C stores of northern biomes and alpine ecosystems will be a source of warming induced by soil C losses. Carbon stocks in soil organic matter (SOM) are a balance between inputs (net primary productivity (NPP)) and outputs (gaseous effluxes and leachates; Davidson and Janssens 2006). Factors affecting NPP include climate, hydrology and plant species composition, while substrate quantity and quality, temperature and soil moisture conditions including drought, flooding and freezing events are among the factors influencing decomposition rates and leachate losses (Hobbie 1996, Davidson and Janssens 2006).

1.2 Heterogenous alpine ecosystems

Alpine ecosystems are estimated to cover < 3% of total land area outside Antarctica (Körner et al. 2011, Testolin et al. 2020), yet are highly biodiverse due to their topographical complexity, supporting around 10,000 plant species (Körner 2003). Topography, climate, elevation, and latitude interact to create varying microclimates and snow cover dynamics in mountain systems. Differences in depth and duration of snow cover drive differences in soil temperature and moisture, availability of nutrients, and plant phenology and growing season length across small spatial scales (Stanton et al. 1994, Zhang 2005, Björk and Molau 2007, Wipf 2010, Ford et al. 2013, Choler 2018). This variation in snow cover depth and duration, and the resulting micro-climate conditions, also promotes differences in plant community composition with varying function and taxonomy (Figure 1.1; Rodwell 1991, 1992, Nagy and Grabherr 2009, Carlson et al. 2015).
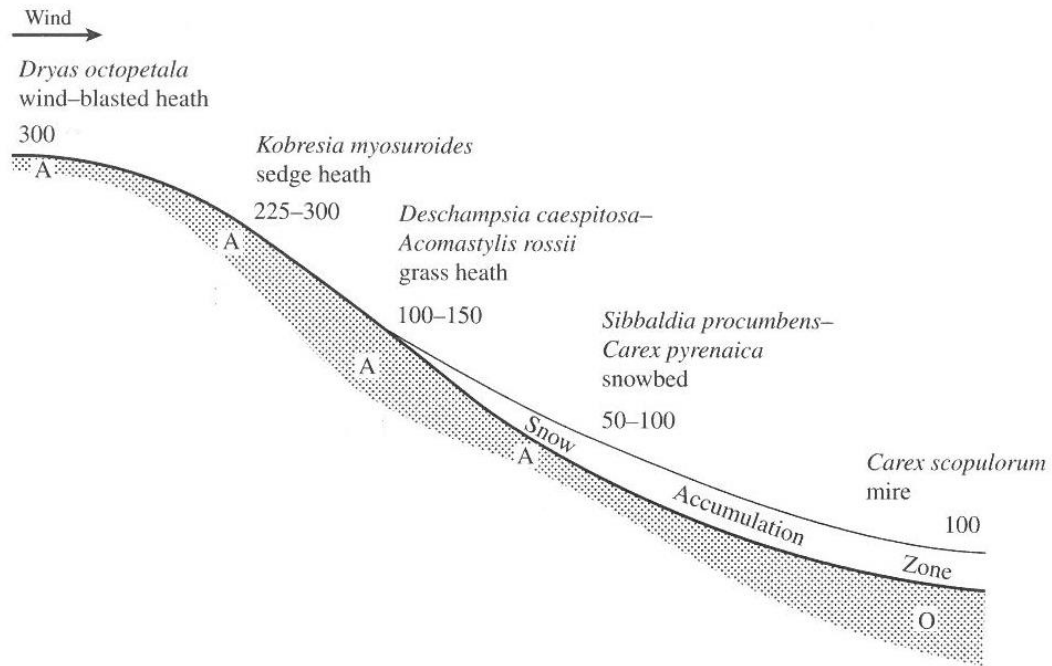
Figure 1.1. Vegetation communities along a snow cover duration gradient in the Colorado Rocky Mountains. Numbers are duration of days per year without snow cover. Development of alpine soil profile in relation to slope, snow cover, and vegetation are also included; thickness of horizons A (mineral horizon with incorporated humified organic matter) and O (organic soil, peat) are not based on measurements (from Nagy and Grabherr 2009).

Plants in arctic and northern alpine ecosystems can be assigned to plant functional groups (PFGs) based on their role in ecosystem processes, and response to changing environmental conditions (Chapin et al. 1996, Dormann and Woodin 2002, Dorrepaal 2007, Strimbeck et al. 2019). The dynamics of C and N cycling vary between PFGs in terms of rates of C uptake via photosynthesis, the quality and quantity of inputs into soil, the presence or absence of roots or rhizoids, and associations with soil microbial communities (Chapin et al. 1996, De Deyn et al. 2008).

Graminoid and forb dominated communities have higher productivity and decomposition rates than evergreen dwarf-shrub or bryophyte dominated communities, where C turnover is limited by the quality of plant inputs (Hobbie 1996, Ward et al. 2009, Quin et al. 2015, Sørensen et al. 2018). The chemical composition of organic inputs to soil primarily determines the rate of decomposition; labile low molecular weight fractions

degrade at a faster rate than the more recalcitrant fractions (Bardgett 2005). The quantity and quality of plant-derived soil inputs drive soil microbial community composition and activity (Zinger et al. 2011).

Seasonal changes in plant activity and plant inputs to soil are reflected in seasonal dynamics in soil microbial community size, composition, and activity, including the breakdown and turnover of C (Figure 1.2; Bardgett et al. 2005). Alpine soil microbial communities show strong seasonality in terms of biomass and community structure, with associated shifts in microbial functioning and biogeochemical pools and fluxes (Björk et al. 2008, Puissant et al. 2015, Gavazov et al. 2017, Broadbent et al. 2021). Soil microbial communities are fungal dominated during snow cover in winter, with an increase in bacterial abundance during the plant growing season in the summer months (Lipson et al. 2002, Schadt et al. 2003, Lipson and Schmidt 2004). Substrate use patterns of soil microbial communities may shift from N-rich material in frozen soils to C-rich material in thawed soil (Schimel et al. 2004).

Plant community composition can be used as a predictor of soil C pools (Hollingsworth et al. 2008). Seasonally snow-covered oceanic-alpine ecosystems have been predicted to be important at an international scale as large stores of soil C (Jones et al. 2005). However, soil C pools in oceanic-alpine soil are very variable, both within and between studies. When sampling 970-1300 m above sea level (asl) on the Cairngorm Plateau, soil C pools of 0.7-12.8 kg C m^{-2} have been reported (Grieve 2000). At lower elevations of 794-908 m asl along an oceanic-alpine toposequence, soil C pools were 13.25 $\pm$ 1.52 kg C m^{-2} and 9.94 $\pm$ 3.98 kg C m^{-2} (mean $\pm$ s.e.) in alpine *Calluna* heath and *Racomitrium* heath, respectively, but increased to 24.86 $\pm$ 1.86 kg C m^{-2} in *Nardus* snowbed, where the majority was old C stored in the organic soil horizon, making it vulnerable to mineralization. (Britton et al. 2011, Mills n.d.). This study suggests that snowbeds could

contain valuable C pools but the relationship between snow cover, vegetation community, and soil C pools is still to be properly explored.
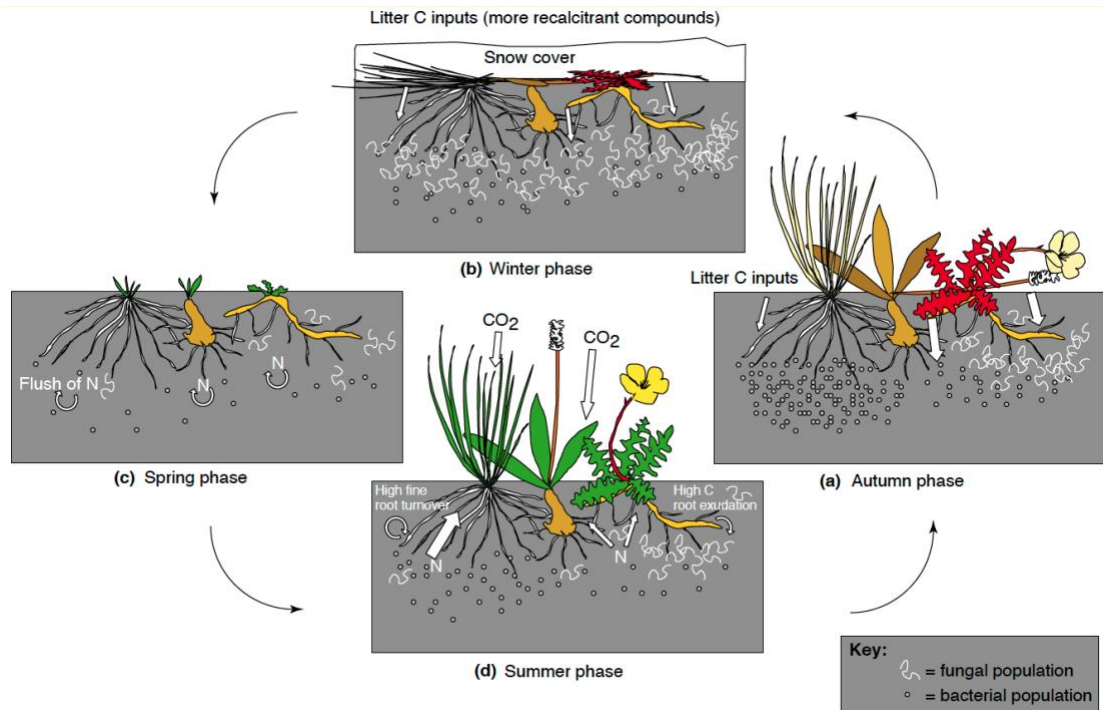
Figure 1.2. Seasonal dynamics of plant and soil microbial activity. (a) In autumn, senescing plants provide a pulse of labile C which supports microbial growth; (b) in winter, the microbial community, particularly fungi, degrade recalcitrant polyphenolic compounds and the C and N in this plant litter promotes further growth of the microbial biomass; (c) in spring, rapid changes in microclimate with snow melt and depletion of labile C compounds results in turnover of the microbial community and release of labile N from microbial biomass (bacterial and fungal) available for plant uptake; (d) in summer plant uptake of microbial N supports plant growth and uptake of C via photosynthesis, plant-derived C inputs to soil are either mineralised by microbes or sequestered as soil C (from Bardgett et al. 2005).

1.3 Global change

Alpine, arctic, and boreal ecosystems are among the most rapidly changing ecosystems on the planet, experiencing greater than average increases in temperature due to arctic amplification and elevation dependent warming (Serreze and Barry 2011, Pepin et al. 2015). Combined effects of nitrogen (N) deposition, grazing, and climate change have led to increased shrub and graminoid cover, reduced moss and lichen cover, and a decline in biodiversity (Bassin et al. 2007, Britton et al. 2009, Armitage et al. 2012, Weijers et al.

2018, Scharnagl et al. 2019). Belowground, reduced snow cover and earlier snowmelt have been found to advance the seasonal transition of winter through snowmelt to spring, triggering reduced microbial biomass, and transitions in microbial community composition and functioning in alpine grassland soil microbial communities (Broadbent et al. 2021). Such shifts in vegetation and microbial communities and changes in plant-microbial interactions as a result of global change are likely to impact biogeochemical cycles and ecosystem function (Wookey et al. 2009, Classen et al. 2015).

1.3.1 Climate change

Mountain areas are particularly vulnerable to climate change and predictions are for these biomes to warm at a greater than average rate (Pepin et al. 2015, Hock et al. 2019, IPCC 2019). In recent decades there has been a decrease of snow cover extent, depth, and duration in mountain regions globally, particularly at lower elevations (loosely defined as areas below the 0°C isotherm – corresponding to approximately 2000 m elevation in Central Europe and 1000 m elevation in Scandinavia; Hock et al. 2019, IPCC 2019). During the cold seasons at higher elevations, where temperatures remain well below 0°C, there has been little change in snow cover dynamics. However, where temperatures are close to 0°C during the cold season at lower elevations, there has been an increase in precipitation falling as rain and a decrease in that falling as snow; a decreased snowpack, and earlier snowmelt in response to warming (Stewart 2009). In low elevation mountain systems in Scotland, there has been a reduction in duration of snow cover of more than 52 days (Rivington et al. 2019). This is equivalent to a more than 30% decrease since the 1960s (Barnett et al. 2006). Concomitantly the intensity and number of days of heavy rain ($\geq$ 10 mm) has increased both annually and particularly in winter since the 1960s and summer precipitation has decreased by more than 18% in some parts of Scotland between 1914 and 2004 (Barnett et al. 2006).

Overall, spring snow cover extent in the northern hemisphere is predicted to decline by a further 7-25% by 2100 depending on the representative concentration pathway used (IPCC 2013). In Scotland, minimum temperatures are expected to rise, with a greater increase occurring in winter than in summer months, resulting in a predicted decline in snowfall of 50% by the 2080s under the UKCIP02, medium high scenario (Barnett et al. 2006). Despite winter months being predicted to be wetter with increased intensity of rainfall (Barnett et al. 2006), reduced snow cover and earlier snow melt will likely result in soil drying in ecosystems previously irrigated by snowpack melt water (IPCC 2019). Summer months are also expected to be drier, interspersed with rainfall events of increased intensity (Barnett et al. 2006).

Research into the responses of alpine ecosystems to climatic changes often occurs at continental alpine locations, such as the Rocky Mountains, European Alps, Pyrenees, and Tibetan Plateau (Verrall and Pickering 2020), with less research concerning oceanic-alpine ecosystems. Oceanic-alpine habitats have been recognised as valuable environments for ecosystem service supply such as C storage, support of biodiversity, and regulation of water (Helliwell et al. 1998, Britton et al. 2011). Warming and subsequent changes in snow cover and precipitation regimes could impact ecosystem function and C stores in mountain soils (Wookey et al. 2009, Classen et al. 2015). In the UK, ~ 40% of all soil C is stored in mountain, moorland, and heath ecosystems, which may contain more than 20 kg C m^{-2} in the top metre of soil (Bradley et al. 2005, van der Wal et al. 2011). However, little is known about the basic attributes or functioning of oceanic-alpine habitats or their response to a changing climate, including the effects of reducing snow cover and changing precipitation regimes.

1.3.1.1 Warming temperatures

Warming manipulations in arctic tundra soils have resulted in increased respiration rates and stimulated enzyme activity (Grogan and Chapin 2000, Phillips et al. 2019, Finderup Nielsen et al. 2019). In mountain ecosystems there have been changes to plant community composition as species range limits shift across Europe; species richness has increased along with the presence of warm-adapted species (Gottfried et al. 2012, Steinbauer et al. 2018). Expansion of generalist vascular plant species into snowbeds has been witnessed in the Alps (Matteodo et al. 2016, Liberati et al. 2019), Rockies (Scharnagl et al. 2019), Scandinavia (Sandvik and Odland 2014), the Western Carpathians (Palaj and Kollár 2019), and Scotland (Britton et al. 2009). Vascular plant expansion into alpine moss dominated communities impacts belowground processes and biogeochemical cycling via shifts in soil microbial community composition and possible changes in extracellular enzyme potential (Bueno de Mesquita et al. 2017). While the effects of warming on C fluxes and pools have been investigated in alpine meadow and alpine steppe in the Tibetan Plateau (Chen et al. 2020), and C fluxes and microbial substrate use at the alpine treeline (Hagedorn et al. 2010, Streit et al. 2014), the effect of warming on C dynamics, particularly microbial function, in alpine ecosystems is still to be explored.

1.3.1.2 Snow cover change

Timing and depth of snow cover influences the relationship between air and soil temperatures. Deep snow decouples soil and air temperatures, with soils under deep snow (greater than 40 cm depth) having higher average temperatures and more spatially and temporally consistent temperatures during winter, but cooler soils in spring, than those under shallow snow (Walker et al. 1999, Larsen et al. 2007a, Elberling 2007, Nobrega and Grogan 2007, Buckeridge and Grogan 2008, Wipf et al. 2015).

Decomposition and respiration rates can be used as proxies for microbial activity. Winter CO_2 flux has been found to be greater under deep snow than under ambient or shallow snow cover in alpine and arctic tundra (Walker et al. 1999, Nobrega and Grogan 2007, Rogers et al. 2011). Similarly, winter decomposition rates were greater in alpine habitats with naturally or experimentally deeper snow cover than those with naturally shallower or ambient snow cover (Britton et al. 2011, Wipf et al. 2015). However, the relationships between snow depth and respiration rates are complicated by the variable litter qualities associated with plants in different habitats along snow cover gradients which contribute to the changes in respiration (Elberling 2007). Increased snow depth is not always associated with an increase in ecosystem respiration and gas fluxes. Carbon dioxide production rates in mesic birch hummock tundra were unaffected by snow depth manipulations; although CH_4 effluxes varied with snow depth, soils under ambient (control) snow conditions produced CH_4, while soils under the deeper snow regimes switched to consumption of CH_4 (Buckeridge et al. 2010). Snow removal studies have rarely been caried out under field conditions due to the feasibility challenges associated with maintaining the treatment. However, a one year study in an alpine bog found no impacts from either snow removal or snow addition on ecosystem respiration rates but this was conjectured to be because of anomalously high spring temperatures during the experiment and an absence of freeze thaw events (Bombonato and Gerdol 2012).

1.3.1.3 Freeze-thaw

Changes to snow conditions during spring are likely to have greater effects than changes during winter, as snow cover during shoulder seasons determines soil temperatures and therefore regulates biological activity and ecosystem functioning (Olsson et al. 2003). Shallow or absent snow cover in spring exposes soil to air temperature fluctuations and freeze-thaw events (Robroek et al. 2013). Under freeze-thaw incubations, pulses of

respiration have been observed during the thaw phase from arctic tundra and alpine soils (Schimel and Clein 1996, Grogan et al. 2004, Wipf et al. 2015), although the amount of CO_2 released during thaw decreased with successive cycles (Schimel and Clein 1996, Larsen et al. 2002, Wipf et al. 2015). The pulse of CO_2 during thaw may be attributed to increased availability of dissolved organic carbon (DOC) to microbes (Wipf et al. 2015); freezing disrupts soil aggregates and induces microbial and root cell death, causing cell lysis and release of organic substrates which can be metabolised by surviving microbes (Schimel and Clein 1996, Larsen et al. 2002). Microbial biomass has been seen to decline after single or multiple freeze-thaw events (Larsen et al. 2002, Grogan et al. 2004, Larsen et al. 2007a) and this has been associated with the increase in DOC (Grogan et al. 2004). In the field however, experimental manipulation of freeze-thaw cycles using open-top chambers (OTCs) found that increasing frequency of freeze-thaw cycles did not affect ecosystem respiration or gross ecosystem photosynthesis over three years relative to controls; net ecosystem exchange decreased only in May, but significant respiration and photosynthesis rates occurred during the non-growing season (October to May) accounting for at least 22% and up to 19% of annual respiration and photosynthesis, respectively (Larsen et al. 2007b). This shows the importance of considering ecosystem functions and responses to climatic disturbance during the cold season and at transitional times, in addition to the growing season.

1.3.1.4 Precipitation change

In the alpine and arctic systems, spatial variation in hydrology and soil moisture strongly influence C cycling (Sjögersten et al. 2006, Knowles et al. 2015). In both alpine and arctic areas, many regions have undergone changes in the patterns of both precipitation and snowmelt which are affecting and altering the hydrology (IPCC 2014). It is predicted that warming will alter rates of snowmelt and therefore water supply on both global and

local scales (Hock et al. 2019, IPCC 2019, Rivington et al. 2019). This, coupled with reduced precipitation and warmer temperatures which cause an increase in rates of evapotranspiration, results in soils drying (Sherwood and Fu 2014). Drought in alpine habitats has been shown to be associated with reductions in gas fluxes, gross primary production and DOC fluxes in leachate (Johnson et al. 2011, Zhang et al. 2019). Additionally, pulses of respiration and N mineralization have been observed following rewetting of dry soil (Birch 1958, Kim et al. 2012). Intensity of rewetting (i.e. the intensity of rainfall events) is likely to be an important factor in determining whether C is mobilised and available to be mineralised by microbes after rewetting of dry soil (Schimel 2018). Given the predictions for increased frequency of drought periods and more intense periods of rainfall (Barnett et al. 2006, Collins et al. 2013, Met Office 2019) it is important to understand how both of these changes might impact on C and nutrient cycling in alpine ecosystems.

1.4 Thesis overview

1.4.1 Thesis aims and objectives

In general, there is still limited knowledge about many of the basic attributes and functioning of oceanic-alpine ecosystems, particularly responses to climatic change. The overarching aim of this thesis was to improve understanding of C cycling in oceanic-alpine ecosystems and the consequences of climate change on these C dynamics. My research aimed to improve knowledge of C cycling in oceanic-alpine habitats by examining relationships between snow cover, vegetation, soil C pools, and decomposition dynamics, and by exploring how changing rainfall patterns may impact on these relationships. The project is reported in three data chapters:

Relationships between snow cover duration, vegetation community composition and topsoil C pools are explored in Chapter 2. For this study, I surveyed oceanic-alpine vegetation and soils in snowbed and non-snowbed topographies at sites of various elevations. Snow cover duration was estimated from soil temperature data collected over two cold seasons.

In Chapter 3 I tested the resistance and resilience of contrasting oceanic-alpine ecosystems to a drought-rewetting event; where resistance is the amount of change caused by a disturbance, and resilience being the ability of a system to return to pre-disturbance levels (Pimm 1984, Orwin and Wardle 2004). I conducted a manipulative experiment measuring ecosystem respiration rates in *Nardus* snowbed and *Racomitrium* heath mesocosms subjected to a 37-day drought period. The influence of other environmental variables which could potentially affect respiration rates (air temperature, vegetation community composition and biomass, and soil C pool) was also explored.

Finally, in Chapter 4 I examined the influence of precipitation extremes, including the nature of rewetting after a drought, on C and N fluxes in contrasting oceanic-alpine ecosystems. I conducted a factorial manipulative experiment consisting of drought and storm events and measured gas and leachate fluxes of C and N in *Nardus* snowbed and *Empetrum* heath mesocosms.

1.4.2 Thesis structure

This thesis is submitted in the alternative format, with data chapters (Chapters 2-4) presented as manuscripts, two of which (Chapters 2 and 4) are intended for submission in peer-reviewed journals. Chapter 5 is a synthesis of key findings from Chapters 2-4, drawing general conclusions and highlighting areas for future research. References and supplementary information for each manuscript are included at the end of each chapter.

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2 Elevation, topography, and snow cover regulate vegetation communities in oceanic-alpine ecosystems

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2.1 Abstract

Alpine ecosystems are diverse in terms of vegetation communities and climatic regimes. They are also important reservoirs of soil carbon. Changing snow cover regimes may alter carbon dynamics in these plant-soil systems, impacting the fate of soil carbon. We surveyed and sampled vegetation and soil within and outwith snowbeds and along an elevation gradient to quantify variability in snow cover regimes, vegetation, soil carbon and microbial communities. Snow cover duration was longer, and snow melt later, within snowbed topographies and with increasing elevation. Elevation, topography, and snow cover regime were important factors in determining vegetation community composition

and aboveground biomass. However, the differences in vegetation between topographies and elevation were not reflected in the upper 15 cm organic topsoil carbon pool, microbial biomass or activity. Low-elevation mountain systems are expected to be particularly impacted by climatic change; these systems are already experiencing annual variability of snow cover and an expansion of shrubs. It will be important to determine the relationships between snow cover, vegetation community and ecosystem carbon pool when considering the soil store to a greater depth, in order to understand how C pools vary across mountain landscapes and predict how these C stores may be impacted by climate change.

Keywords: alpine heath; elevation gradient; mountain; snow cover; snowbed; soil carbon; topography; vegetation community.

2.2 Introduction

Northern biomes are large carbon (C) stores; the cold, wet climate limits decomposition rates and promotes soil C accumulation (Hobbie et al. 2000). Seasonally snow-covered mountain ecosystems are predicted to be large stores of soil C (Jones et al. 2005). Mountain systems are particularly vulnerable to climate change, and are predicted to experience greater than average increases in temperature via elevation dependent warming (Pepin et al. 2015, Hock et al. 2019), which may impact ecosystem function and carbon stores in mountain soils (Wookey et al. 2009, Classen et al. 2015). In the UK, ~ 40% of all soil C is stored in mountain, moorland, and heath ecosystems and may contain > 20 kg C m^{-2} in the top metre of soil (Bradley et al. 2005, van der Wal et al. 2011).

Alpine landscapes are topographically complex creating varying snow cover regimes. Gradients of snow cover duration and depth are associated with variation in plant community composition (Rodwell 1991, 1992, Nagy and Grabherr 2009), through the regulating effects of moisture, temperature, nutrients, light availability and length of the

growing season. Snow cover (> 40 cm deep) buffers the soil from fluctuating air temperatures and can prevent freezing (Walker et al. 1999, Elberling 2007, Larsen et al. 2007a, Nobrega and Grogan 2007, Buckeridge and Grogan 2008). Snow cover regulates plant phenology and growth (Wipf 2010), and snow pack is a source of water and nutrients during snowmelt (Brooks and Williams 1999). Variation in snow cover depth and duration, and resulting micro-climate conditions promotes differences in plant community composition of varying function and taxonomy (Carlson et al. 2015). In the UK, the alpine zone is at lower elevations than in continental systems due the UK's oceanic climate with high wind speeds and rainfall. This oceanic climate strongly influences alpine plant communities found in the UK, which comprise both arctic and alpine species. In Scotland, alpine ecosystems range from heath communities on shallow soils on slopes and exposed summits, to snowbed communities in sheltered topographic hollows with deeper organic soils where snow cover accumulates and persists after melt-out on more exposed slopes (Britton et al. 2011). Within snowbed topographies, vegetation traits and species change along a gradient of snow cover duration (Komac et al. 2015).

Plant community composition impacts C dynamics through various pathways. Plant functional groups (PFGs) have different traits in C cycling such as rates of C uptake via photosynthesis, the quality and quantity of inputs into soil, the presence or absence of roots or rhizoids, and associations with soil microbial communities (Chapin et al. 1996, De Deyn et al. 2008). Communities are often dominated by dwarf-shrubs, graminoids, or bryophytes, which have different litter qualities (Hobbie 1996, Aerts 2006, Lang et al. 2009). The quantity and quality of plant-derived soil inputs drive soil microbial community composition (Zinger et al. 2011). As snowbeds contain graminoids as well as mosses, the prevalence of less recalcitrant graminoid material in snowbed vegetation compared to shrub dominated non-snowbed communities could promote greater microbial biomass and stimulate microbial activity.

Plant community composition, in boreal forests, can be used as a predictor of soil C pools (Hollingsworth et al. 2008). Globally, soil C pools in temperate non-forested wet systems are estimated to be > 13 kg soil C m^{-2}, and > 20 kg C m^{-2} soil in oceanic-alpine regions of Scotland (Bradley et al. 2005, De Deyn et al. 2008). However, a study of soil C pools along a toposequence in Scotland found the largest soil C pool (25 kg C m^{-2}) in an early melting snowbed, but soil pools of less than 14 kg C m^{-2} in alpine and *Racomitrium* heaths (Britton et al. 2011). The early melting snowbed also contained a greater amount of old C (based on mean residence time of ^{14}C) when compared with other alpine ecosystems (Mills n.d.). However, these data were based on one study site in the Cairngorms, Scotland, and did not consider the variability in snow cover regimes or the diversity of oceanic-alpine ecosystems across the UK.

In the northern hemisphere, spring (March – April) snow cover extent has decreased by 7.2% over 90 years between 1922 and 2012, and it is expected to decline by a further 7 to 25% by 2100 (Collins et al. 2013). Mountain areas are expected to be particularly impacted by changing climate due to elevation-dependent warming (Pepin et al. 2015). Globally around 78% of mountain areas show a decline in snow cover duration or area between 2000 and 2018 (Notarnicola 2020). Low-elevation mountain systems are particularly vulnerable as these systems already experience more variable snow cover annually and proportions of cold season precipitation are increasingly falling as rain (Stewart 2009). In the low-elevation mountain systems in Scotland, duration of snow cover has declined by more than 52 days, equivalent to more than 30% decrease, since the 1960s (Barnett et al. 2006, Rivington et al. 2019). The decline in snow fall, areas covered by snow, and snow cover duration in the Scottish mountains are predicted to continue and accelerate (Barnett et al. 2006, Rivington et al. 2019). Changes in snow cover regime may alter rates of ecosystem process and in turn affect the size of soil C pools. Deeper snowpack can enhance ecosystem respiration during the cold season (Nobrega and Grogan 2007).

However, reduced insulation under a shallower snowpack can result in freeze-thaw cycles, which can also enhance ecosystem respiration rates and dissolved organic carbon concentration in leachate (Wipf et al. 2015).

In order to predict effects of climate change on C storage in mountain landscapes, it is important to understand how C pools vary across the heterogeneous landscape and how this relates to environmental drivers. Firstly though, it is important to evaluate whether snow cover is a good proxy, at smaller spatial scales, for soil C pools and vegetation communities. In this study, we examined how snow cover duration, plant community composition, and soil C and N pools varied with topographic position and elevation in an oceanic-alpine mountain system. We hypothesised that differences in snow cover duration, and associated variation in microclimate between topographic hollows (within snowbed) and surrounding areas (non-snowbed) and along elevation gradients would result in:

1. Different plant communities, in terms of species composition, biomass and PFGs, between snowbed and non-snowbed topographies, and between elevations.

We also hypothesised that the characteristics of the plant communities found in these contrasting topographies, along with the different snow cover regimes would result in:

2. Greater organic topsoil C pools in snowbeds compared with non-snowbed topographies,

3. Greater microbial biomass and activity, measured as soil respiration, in snowbed than in non-snowbed topographies.

2.3 Methods

2.3.1 Study area

The study area was located in the eastern Cairngorm mountains, Scottish Highlands. The climate in this region is oceanic, with cold winters and cool wet summers.

Mean annual precipitation is > 850 mm, with mean daily minimum and maximin air temperatures of -1.96 ºC and 13.93 ºC in January and July, respectively, at 750 m elevation; climate data were recorded between 2003-2018 from an automatic weather station (latitude, 57.07025°N; longitude, 3.34909°W) ranging from 0.4-4.3 km from study sites.

Alpine plant communities are present above 650 m elevation, and are underlain by alpine and subalpine podzols; plant communities include: dwarf shrub heaths with *Calluna vulgaris* or *Empetrum nigrum*, and *Cladonia* sp.; *Racomitrium* heath; grass-, sedge- or rush-heaths with *Nardus stricta*, *Carex bigelowii* or *Juncus trifidus*; *Nardus* snowbeds; and bryophyte snowbeds with *Polytrichum sexangulare* and *Kiaeria starkei* (Rodwell 1991, 1992). At lower elevations, vegetation is rotationally burned as part of management for grouse shooting. The study area is managed for red deer stalking; mean herbivore densities (2000-2016) are estimated to be 7-9 red deer km^{-2} (Albon et al. 2017). Four sampling sites were selected along an elevation gradient of 676 m to 1018 m above sea level (asl; Figure 2.1a; Table 2.1). Sites were chosen based on accessibility. At each site areas of snowbed and non-snowbed habitat were identified, based on topography. We assumed that topographic hollows indicated that snow would accumulate and snow cover would persist for longer within the hollow than on surrounding areas.

Table 2.1. Site location and characteristics.

	Latitude, longitude	Elevation (m asl)	Aspect (°)	Slope (°)
1.	57.09214°N, 3.40520°W	1018	81	19
2.	57.09674°N, 3.40026°W	990	79	18
3.	57.07097°N, 3.34228°W	705	182	13
4.	57.07046°N, 3.38025°W	676	110	22

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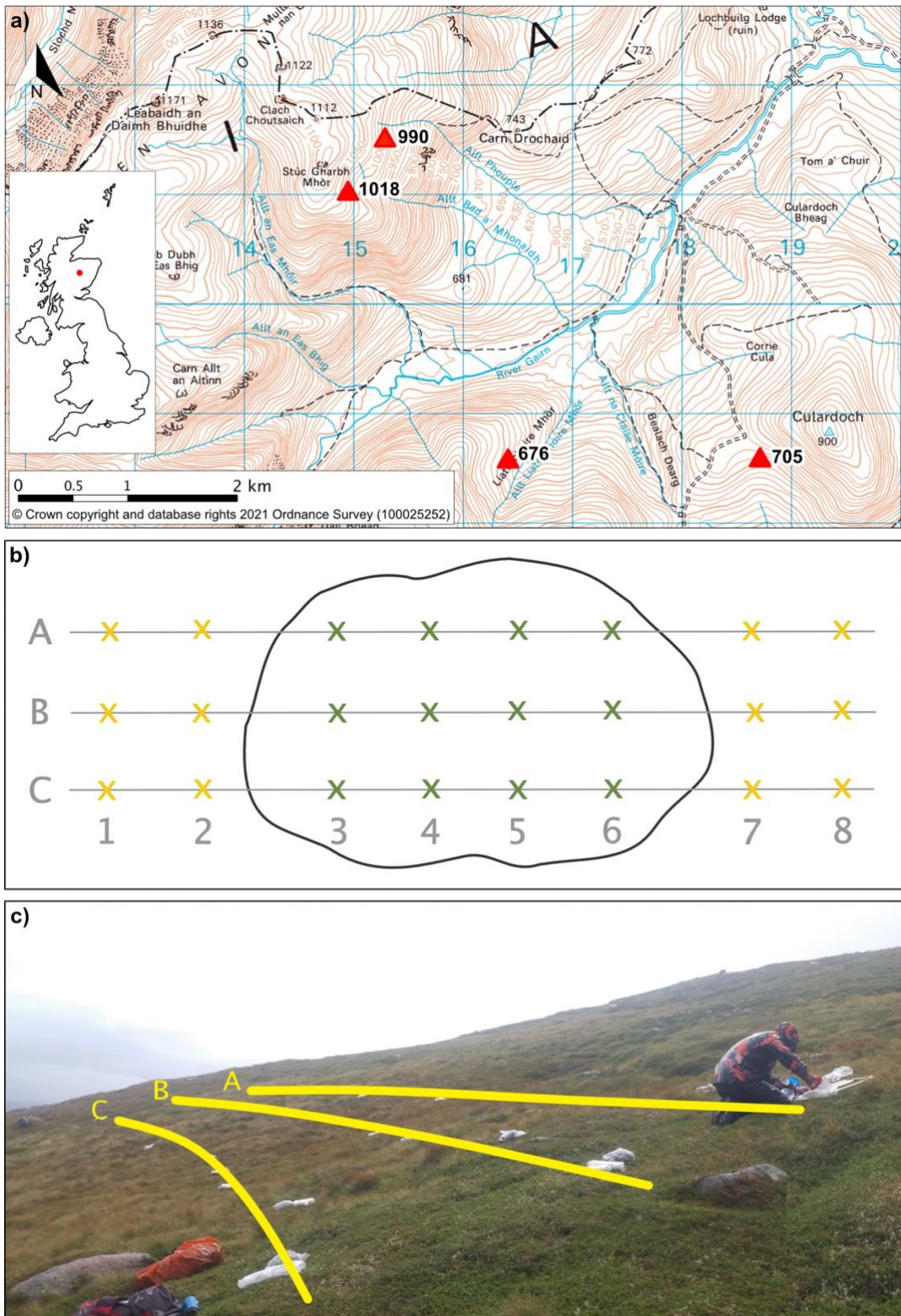
Figure 2.1. (a) Location of study area (red circle) within the UK, and study sites (red triangles) within the Cairngorms. See Table 2.1 for site locations and characteristics. (b) set-up at each site: black outline represents snowbed topography, horizontal grey lines represent transects (labelled A, B, C), crosses are survey and sample plots where yellow represents non-snowbed and green snowbed ecosystems. (c) sampling in the field, with yellow lines showing transects contouring across the slope.

2.3.2 Sampling

At each site, a horizontal transect was established through the centre of the snowbed, running across the main slope (Figure 2.1b). A second and third transect were then established above and below the central transect, equidistant between the central transect and the snowbed boundary. Eight 50 cm by 50 cm plots were positioned along each transect; four within the snowbed and 2 out with the snowbed on either side, plots were not placed in transitional areas where microtopography changed, in order to focus on the two contrasting topographies. Plots within and outwith the snowbed were equally distributed and distances between plots ranged from 4 m to 40 m depending on the length of transect, due to the varying sizes of snowbeds. At each plot, we recorded location (latitude and longitude), elevation (m asl), slope (°), and aspect (°), using handheld GPS (Garmin GPSmap 62s, Olathe, KS, USA), clinometer, and compass, respectively.

2.3.3 Vegetation and soil sampling

Vegetation communities were described by listing the vascular, bryophyte and lichen species present in each 50 cm by 50 cm plot. Bare ground was recorded if present in the plots; bryophytes and lichens growing exclusively on rocks were excluded and these areas were also recorded as bare ground, as species exclusively associated with rocks can form distinct communities separate from soil.

Vegetation biomass was collected around peak biomass, between 4 July 2017 and 3 August 2017. Within each plot, a 20 cm by 20 cm quadrat was placed in the bottom left corner, and all aboveground biomass was harvested, by clipping to the soil surface, removing vegetation but leaving litter. When bryophytes were harvested, biomass was clipped to remove the photosynthetically active part of the bryophytes. Aboveground vegetation biomass was oven dried at 60°C for a minimum of 48 hours and total mass

recorded. Aboveground biomass was sorted to PFG for 10 minutes before the mass of sorted material was recorded and the proportion (%) of sorted biomass calculated; any biomass remaining after 10 minutes was allocated to unsorted. PGFs were defined as evergreen shrubs, deciduous shrubs, graminoids, forbs, seedless vascular (pteridophytes), *Sphagnum* mosses, other bryophytes, and lichens for predicting their role in the C cycle (Chapin et al. 1996, Dorrepaal 2007). Bryophytes were separated into *Sphagnum* mosses and other bryophytes as *Sphagnum* productivity is greater than that of feather mosses (Turetsky et al. 2010).

Soil cores were collected for determination of soil bulk density, and soil C and N stocks in the top 15 cm of the organic horizon. One soil core (5 cm diameter, 15 cm deep) was collected from each of the 20 cm by 20 cm quadrats used for the biomass harvest. If the depth of the soil organic horizon exceeded the length of the core (15 cm) then horizon depth was determined using a screw auger to a maximum depth of ≥110 cm. Samples were stored at 4°C prior to analysis.

Soil cores were sectioned into organic and mineral horizons and the mineral horizon was discarded. Bulk density of the organic horizon was calculated from the dry mass and volume of organic soil in the core excluding stones. The organic soil was homogenised by hand for 10 minutes and then sieved to 4mm to remove large debris. Debris was sorted into roots and stones before the mass of stones was recorded, and volume of stones measured by water displacement. Soil was split into fresh sub-samples for determination of soil moisture, soil pH, microbial biomass, and soil respiration, and freeze-dried sub-samples for quantifying total soil C and N.

An aliquot of 5 ± 0.5 g fresh soil was weighed, oven dried at 60°C for 48 hours and the mass of the dry soil recorded. Moisture content of the aliquot was used to calculate dry mass of the organic soil. Organic soil bulk density was then calculated as the dry mass of soil divided by the soil volume excluding stones.

Total soil C and N content in the upper organic horizon, to a maximum depth of 15 cm (referred to as top organic horizon C and N content), were analysed on 30 ± 1 mg subsamples of ground, freeze-dried soil samples by high temperature combustion gas chromatography (Elementar Vario El III C/N analyser; Stockport, UK). The soil C pool (kg m^{-2}) in the upper 15 cm (max) of the organic horizon (hereafter referred to as top organic horizon C pool) was then calculated as the product of C content, bulk density and horizon thickness.

Soil pH in H_2O was determined on aliquots of fresh soil using a pH meter (Mettler Toledo InLab Versatile Pro, Columbus, OH, USA), in a 1: 2.5 soil: water slurry. 25 ml MilliQ water was added to 10 g soil; the solution was agitated for 30 minutes on an orbital shaker at 120 rpm and left to settle for 12 hours. Measurements of pH were then taken in the solution.

Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were measured by fumigation-extraction of fresh soil. Forty ml of 0.5 M K_2SO_4 was added to paired 5.0 ± 0.5 g lightly homogenised fresh soil subsamples, 0.5 ml $CHCl_3$ was added to fumigated samples. Samples were shaken at 100 rpm for 30 minutes, centrifuged at 2000 rpm for 5 minutes, filtered through Whatman 42® (GE Healthcare, Chicago, IL, USA) filter paper, sparged for 20 minutes to remove chloroform, and stored at -20°C before analysis. Sample extracts were diluted with MilliQ water at a ratio of 1:8 extract:MilliQ water prior to analysis for total organic C and total N on a TOC-L combustion analyser coupled with a TNM-L unit (Shimadzu Corp, Kyoto, Japan). MBC and MBN were calculated as the difference between C and N recovered from fumigated and non-fumigated samples.

Soil basal respiration was measured on fresh soil incubated at 10°C for 24 hours. We used 10°C rather than 25°C, as we considered the lower temperature to be more realistic for alpine systems. Lightly homogenised fresh soil, 5 ± 0.5 g, was measured into

50 mL conical centrifuge tube and left to equilibrate at 10°C. After 24 hours, soil microbial respiration was measured using an infrared gas analyser (Li-8100; LI-COR Biosciences, Lincoln, NE, USA) for 1 minute with a 15 second deadband.

2.3.4 Soil temperature and snow cover regime

Eight soil temperature loggers (iButton® DS1922L, Maxim Integrated, San Jose, CA, USA) were installed at each site; four were randomly allocated to plots within the snowbed and four to plots in non-snowbed topographies. Loggers were installed at 2 cm depth below the soil surface, 30 cm to the right of the biomass harvest, to avoid potential effects of reduced insulation without vegetation cover. Soil temperature (± 0.5°C accuracy) was recorded every 2 hours from 1 October 2017 to 2 July 2019. Following retrieval, soil temperature data were used to estimate snow cover duration. Days with mean 24 hr soil temperatures < 2.5 °C and standard deviation < 0.2 were classed as snow days (Schmid et al. 2012). We then calculated total days of snow cover, the longest duration of continuous snow cover (days), and the date of last snow melt (day of year) for each winter season.

2.3.5 Statistical analyses

All statistical analyses were carried out in R version 3.6.2, and multivariate analyses were performed using vegan: Community Ecology Package (Oksanen et al. 2018). To determine the effects of topography and elevation on snow cover duration, aboveground biomass, soil depth and nutrients, microbial biomass, or soil microbial respiration, linear mixed effects models (LMEs) were used with topography and elevation and their interaction as fixed effects, and nested topography within site as a random effect (lmer function; Bates et al. 2014). Post-hoc pairwise comparisons were conducted with the emmeans package (Lenth et al. 2019) to identify statistically different means between

elevations and topographies. Elevation was included in models as a factor based on site mean elevation rather than a continuous variable to make allowance for GPS accuracy at plot-level within sites, and limited site replicates. The significance of individual terms was tested using AIC values, as terms were sequentially dropped from the model. The final model was tested against the null model using an ANOVA, reported as significant at $p < 0.05$, and the model fit was visually assessed using diagnostic plots. When models did not satisfy assumptions of normality, data were log-transformed. Kruskal-Wallis tests were used when residuals were not normally distributed and could not be normalised by log-transformation.

The effects of topographic position (snowbed or non-snowbed topographies) and elevation on vegetation community composition (species present) were determined by permutational multivariate analysis of variance with 9,999 permutations (PerMANOVA; adonis function). Although using plot-based species presence does not account for pseudo-replication within sites, it allows us to examine variation within as well as between snowbeds. We used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity to represent plant communities (metaMDS function). A stable three-dimensional solution with stress scores < 0.2 and $r^2 > 0.95$ was used for subsequent analysis. We used vector fitting to the NMDS ordination (envfit function) with 99,999 permutations and significance set to < 0.05, to determine the effects of topographic position (snowbed vs non-snowbed habitat), elevation, mean snow cover, aspect, slope, organic horizon depth, soil moisture and soil pH on vegetation community composition. Mean metrics of snow cover regimes were calculated as vegetation community composition is likely to be a product of long-term snow cover trends not annual variation.

2.4 Results

Snow cover regimes varied with topographic position and elevation, although the amount of variation depended on the metric of snow cover regime used and the winter season considered (Figure 2.2). During the 2018-19 winter, the model which best explained longest continuous snow cover duration included topography and site, but not the interaction between these (Table 2.2). Total snow cover duration and day of final snowmelt for both the 2017-18 and the 2018-19 winters were best explained by models which included topography, site, and the interaction between these factors (Table 2.2). When topography and site explained snow cover duration and snow melt, snow cover duration was greater and snow melt was later within snowbeds and at higher elevation sites. When the interaction term was included in the final model this indicated that the response was not consistent across sites; there was a particularly marked difference between snowbed and non-snowbed topographies at the site at 705 m elevation.
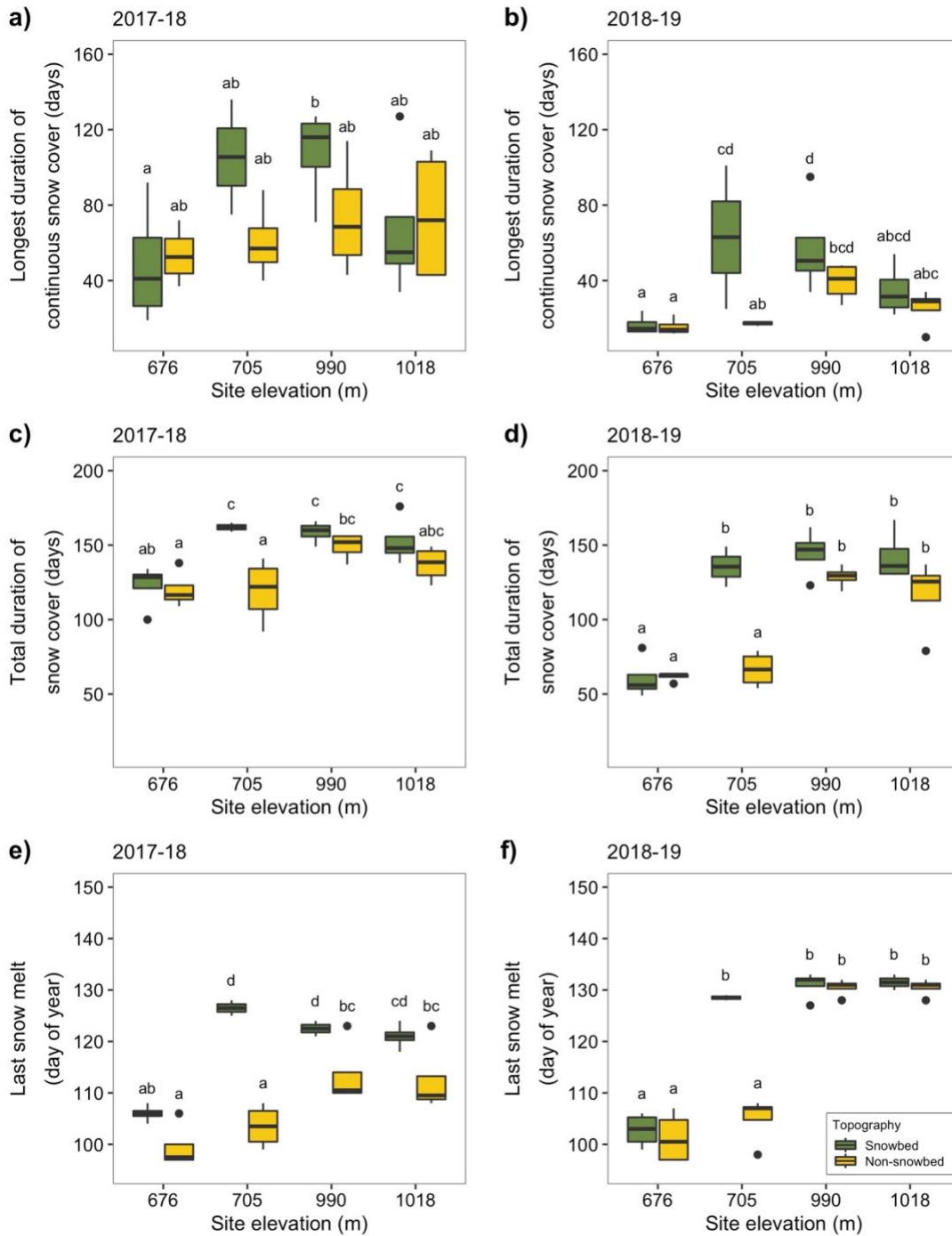
Figure 2.2. Duration of snow cover for (a, c, e) 2017-18 winter and (b, d, f) 2018-19 winter seasons; (a, b) longest duration of continuous snow cover, (c, d) total days of snow cover, and (e, f) last snow melt as day of year. Colours represent ecosystem. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5(IQR)$ or greater than $Q_3 + 1.5(IQR)$. Letters on top of boxplots indicate statistical difference.

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Table 2.2. Summary of linear mixed effects models to explain snow cover regime, vegetation, and soil characteristics. When the final model was not significantly different to the null model, the model including topography, site, and interaction term is shown. For each parameter included, effect size (F) and p value are shown, along with the overall model summary statistic comparing the final model to the null model (X^2 and p values). When null model was best fitting model, model with interaction term is included in the table. Bold values represent parameters and models significant at $p < 0.05$.

| | | Model parameters | | | | | | Model summary | |
| | | Topography | | Elevation | | Interaction | | | |
		F	p	F	p	F	p	X^2	p
Snow cover	Continuous snow cover 2017-18 (days)	1.10	0.304	3.67	**0.023**	1.75	0.178	12.04	0.099
	Continuous snow cover 2018-19 (days)	7.78	**0.009**	10.27	**< 0.001**			15.60	**0.004**
	Total snow cover 2017-18 (days)	15.41	**< 0.001**	10.62	**< 0.001**	3.25	**0.035**	22.39	**0.002**
	Total snow cover 2018-19 (days)	30.50	**< 0.001**	53.87	**< 0.001**	7.79	**< 0.001**	32.02	**< 0.001**
	Snow melt 2017-18 (DOY)	69.96	**< 0.001**	29.00	**< 0.001**	5.84	**0.004**	31.38	**< 0.001**
	Snow melt 2018-19 (DOY)	35.94	**< 0.001**	173.57	**< 0.001**	21.08	**< 0.001**	39.42	**< 0.001**
Vegetation community	Total aboveground biomass (kg m^{-2})	115.19	**< 0.001**	9.39	**< 0.001**	3.39	**0.021**	31.27	**< 0.001**
Soil	Top organic horizon soil C pool (kg C m^{-2})	0.40	0.530	2.30	0.082	1.72	0.168	11.13	0.133
	Organic soil horizon depth (cm)			65.12	**< 0.001**			19.40	**< 0.001**
	Top organic soil horizon C content (%)			16.08	**< 0.001**			13.24	**0.004**
	Top organic soil horizon N content (%)	7.08	**0.009**	10.25	**< 0.001**			17.18	**0.002**
	Top organic soil C:N ratio	21.43	**< 0.001**	3.05	**0.033**			13.32	**0.010**
Microbial biomass	MBC (µg C g^{-1} dry soil)			4.37	**0.037**			7.63	0.054
	MBN (µg N g^{-1} dry soil)	1.56	0.215	2.20	0.095	2.37	0.076	12.80	0.077
	Microbial biomass C:N ratio			4.09	**0.010**			8.20	**0.042**
Soil respiration	Soil respiration (µg C g^{-1} dry soil hr^{-1})	0.14	0.714	0.22	0.880	0.73	0.539	3.02	0.884
	Soil respiration (µg C µg^{-1} MBC hr^{-1})			8.49	**< 0.001**			11.28	**0.010**

Vegetation community composition differed between snowbed and non-snowbed topographies ($F_{1,92}$ = 24.73, p < 0.001), between sites ($F_{1,92}$ = 36.63, p < 0.001), and with the interaction between the two ($F_{1,92}$ = 8.52, p < 0.001; Figure 2.3). The difference between snowbed and non-snowbed plant communities was particularly apparent at higher elevations. Tight clustering of non-snowbed plant communities at higher elevations suggested a relatively uniform species composition while within snowbed communities were more variable. At lower elevation, snowbed and non-snowbed communities were still separated but there was a greater degree of overlap. Different species of shrubs were present at different elevations, with *Vaccinium oxycoccus* only present at higher elevations and *Calluna vulgaris* at lower elevations (Table 2.3). Environmental factors found to be significantly associated with community composition included snow cover regime, elevation, aspect, organic horizon depth, soil moisture, and soil pH.
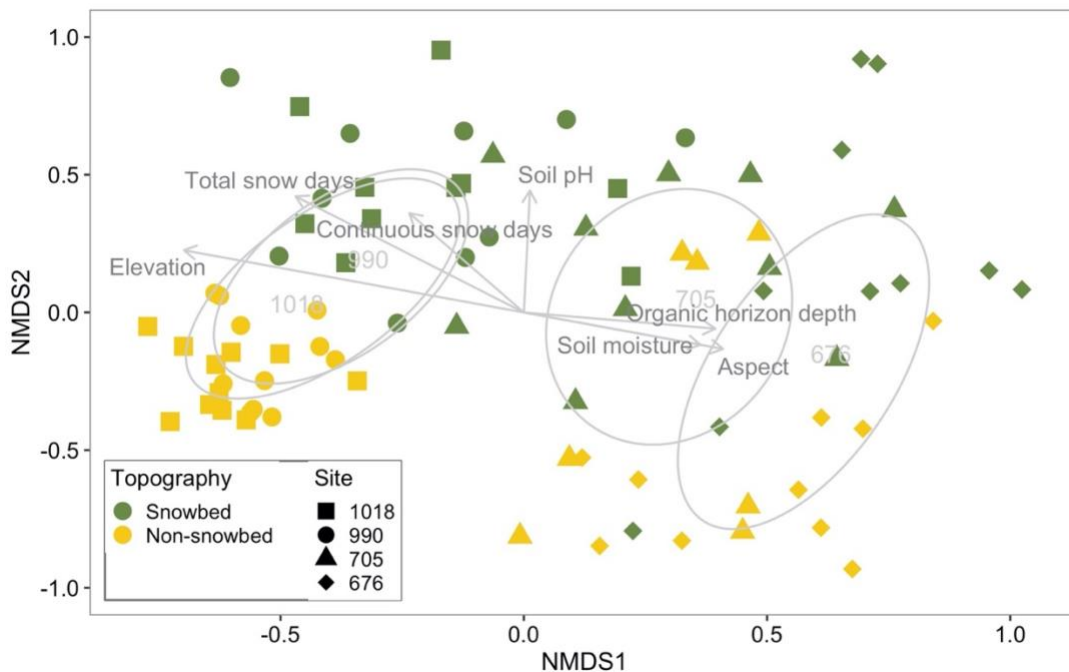
Figure 2.3. Plant community composition of snowbed and non-snowbed ecosystems. Each symbol represents a surveyed plot based on vegetation species present. Shapes represent the four different sites of 1019, 990, 705, and 676 elevation (m above sea level). Colours represent ecosystem. Arrows are environmental drivers found to influence community composition significant at p < 0.05.

Table 2.3. Vegetation species only present at low or high elevation, and in snowbed or non-snowbed topographies.

	Snowbed	Non-snowbed	Snowbed and non-snowbed
High elevation sites (1018 and/or 990)	*Juncus trifidus* *Alchemilla alpina* *Gnaphalium supinum* *Diphasiastrum alpinum*		*Vaccinium oxycoccus* *Epilobium brunnescens* *Lycopodiopsida sp.* *Racomitrium lanuginosum* *Cetraria islandica*
Low elevation sites (705 and/or 676)	*Deschampsia cespitosa* *Festuca vivipara* *Juncus squarrosus*	*Erica cinera* *Rubus chamaemorus* *Agrostis sp.* *Carex binervis* *Carex echinata* *Viola sp.*	*Calluna vulgaris* *Cornus suecia* *Anthoxanthum odoratum* *Trientalis europaeus* *Blechnum spicant*

Aboveground vegetation biomass was greater in non-snowbed than in snowbed topographies; the model which best explained aboveground biomass included topography, site, and the interaction between these factors (Figure 2.4a; Table 2.2). When the interaction between topography and site was considered, the difference in above ground-biomass between snowbed and non-snowbed topographies was greater with increasing elevation, with lower biomass in snowbed topographies. Abundance of plant functional groups also changed with topography (Figure 2.4b; Table 2.4). Graminoids were also more abundant in snowbeds than non-snowbeds ($X^2 = 47.51$, $p < 0.001$) and there was greater abundance of evergreen shrubs in non-snowbeds than in snowbeds ($X^2 = 58.21$, $p < 0.001$) across all sites. Lichens were more abundant at higher elevation sites than low elevations sites ($X^2 = 58.21$, $p < 0.001$) and in non-snowbed than snowbed topographies ($X^2 = 11.11$, $p < 0.001$). Overall biomass of *Sphagnum* mosses and other bryophytes was not affected by topographic position (*Sphagnum* mosses: $X^2 = 1.07$, $p = 0.302$; other bryophytes: $X^2 = 2.84$, $p = 0.092$). When considering the abundance of all bryophytes (*Sphagnum* mosses and other bryophytes combined), there was greater abundance of bryophytes at the lower elevation sites ($X^2 = 12.47$, $p = 0.006$).
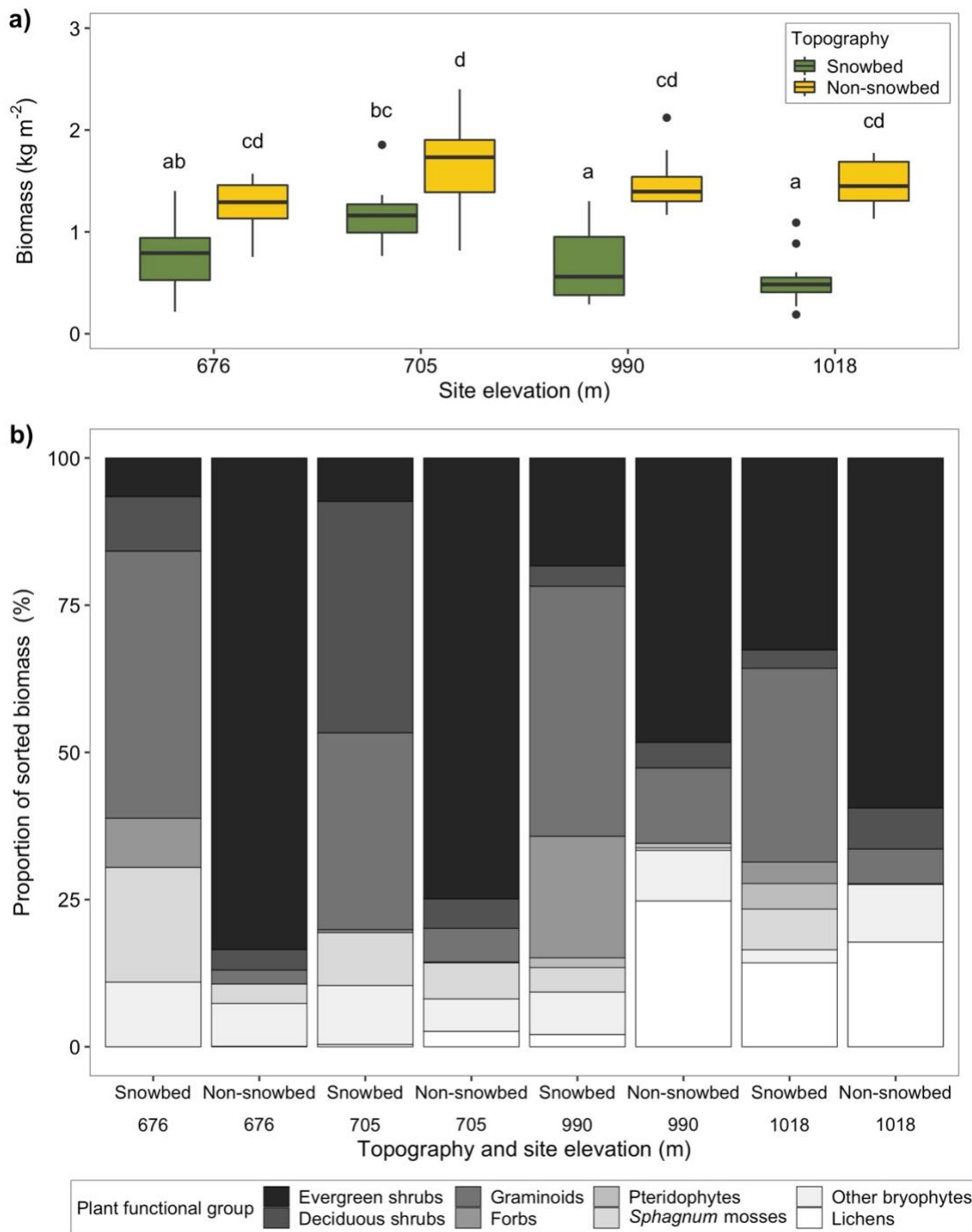
Figure 2.4. (a) Total aboveground vegetation biomass (kg m^{-2}) for snowbed (green) and non-snowbed ecosystems (yellow). Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q$_1$) and 75th (Q$_3$) quartiles, respectively. Difference between Q$_1$ and Q$_3$ is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than Q$_1$ – 1.5(IQR) or greater than Q$_3$ + 1.5(IQR). Letters on top of boxplots indicate statistical difference. (b) Proportion of biomass sorted to plant functional groups. Data are plotted as mean values.

Table 2.4. Biomass sorted to plant functional group (PFG) from snowbed and non-snowbed plots by site. Data shown are mean ± s.e. (n = 12), PFGs within topographies which do not share a letter are significantly different at $p < 0.05$, * indicate significant difference in PFG between topographic positions at that site.

| Site elevation (m) | Plant functional group | Proportion of sorted biomass (%) | | X^2 | p |
		Snowbed	Non-snowbed		
676	Evergreen shrubs	6.55 ± 3.63 a *	83.47 ± 3.07 a *	17.21	< 0.001
	Deciduous shrubs	9.27 ± 4.73 a	3.50 ± 0.85 ab	0.35	0.555
	Graminoids	45.36 ± 8.34 b *	2.38 ± 1.04 bc *	14.17	< 0.001
	Forbs	8.37 ± 4.30 ab *	0.00 ± 0.00 c *	10.06	0.002
	Sphagnum mosses	19.47 ± 7.81 ab	3.28 ± 1.81 bc	1.68	0.195
	Other bryophytes	10.99 ± 3.74 ab	7.28 ± 2.28 ab	0.06	0.805
	Lichens	0.00 ± 0.00 a	0.09 ± 0.09 c	1.92	0.166
	X^2	39.74	69.23		
	p	< 0.001	< 0.001		
705	Evergreen shrubs	7.37 ± 4.12 abc *	74.86 ± 5.39 d *	16.48	< 0.001
	Deciduous shrubs	39.31 ± 7.97 a *	5.03 ± 2.83 abc *	7.48	0.006
	Graminoids	33.42 ± 7.91 a *	5.70 ± 3.31 acd *	11.60	< 0.001
	Forbs	0.50 ± 0.19 bc	0.14 ± 0.11 ab	1.66	0.197
	Sphagnum mosses	8.98 ± 6.00 bc	6.13 ± 3.27 abc	0.00	0.945
	Other bryophytes	10.02 ± 2.75 ac	5.50 ± 2.08 cd	3.20	0.073
	Lichens	0.40 ± 0.40 b	2.63 ± 1.68 abc	2.14	0.143
	X^2	55.13	58.85		
	p	< 0.001	< 0.001		
990	Evergreen shrubs	18.31 ± 4.16 ac *	48.29 ± 3.76 c *	12.41	< 0.001
	Deciduous shrubs	3.50 ± 1.86 ab	4.35 ± 1.23 ab	2.85	0.092
	Graminoids	42.43 ± 6.84 c *	12.80 ± 3.11 bc *	10.83	< 0.001
	Forbs	20.66 ± 5.44 ac *	0.02 ± 0.02 a *	11.45	< 0.001
	Pteridophytes	1.64 ± 0.89 ab	0.76 ± 0.76 a	1.91	0.167
	Sphagnum mosses	4.15 ± 4.15 b	0.41 ± 0.30 a	0.25	0.616
	Other bryophytes	7.21 ± 3.32 ab	8.59 ± 2.77 b	1.79	0.181
	Lichens	2.10 ± 1.23 ab *	24.78 ± 4.95 bc *	12.24	< 0.001
	X^2	44.50	76.18		
	p	< 0.001	< 0.001		
1018	Evergreen shrubs	32.57 ± 6.51 a *	59.42 ± 4.69 a *	8.67	0.003
	Deciduous shrubs	3.15 ± 1.08 ab *	6.99 ± 0.82 ab *	5.61	0.018
	Graminoids	32.91 ± 6.38 a *	5.88 ± 1.15 b *	15.41	< 0.001
	Forbs	3.64 ± 1.86 b	0.08 ± 0.05 c	2.28	0.131
	Pteridophytes	4.34 ± 4.32 b	0.00 ± 0.00 c	2.09	0.149
	Sphagnum mosses	6.90 ± 4.49 b	0.03 ± 0.03 c	1.44	0.230
	Other bryophytes	2.22 ± 1.85 b *	9.80 ± 3.48 b *	11.49	< 0.001
	Lichens	14.26 ± 5.65 ab	17.79 ± 2.86 ab	2.44	0.118
	X^2	47.08	84.54		
	p	< 0.001	< 0.001		

The C pool in the top 15 cm of the organic horizon was not explained by topography, site, or the interaction between these factors (Figure 2.5a; Table 2.2). Organic horizon depth was best explained by a model including site alone, with deeper organic soils found at the two lower elevation sites (Figure 2.5b, Table 2.2). Soil C content was also best explained by the model containing site (Figure 2.6a, Table 2.2) and followed the same pattern as organic horizon depth, with greater organic soil C content at the two lower elevation sites than at the two higher elevation sites. Overall soil N content was greater in snowbeds than in non-snowbed topographies and declined with elevation (Figure 2.6b, Table 2.2). Soil C:N ratio (Figure 2.6c) was consistently greater in non-snowbed than in snowbed topographies; the model which best explained soil C:N ratio included topography and site without the interaction term, declining with increased elevation (Table 2.2).

Microbial biomass carbon and nitrogen were unaffected by topography or elevation (Figure 2.7; Table 2.2). However, microbial biomass C:N ratio (Figure 2.7c) was best explained by the model including site alone (Table 2.2).

Soil respiration per unit dry soil mass was unaffected by topography, site, or the interaction between these factors (Figure 2.8a; Table 2.2). When expressing soil respiration as per unit MBC (Figure 2.8b), respiration rates were unaffected by topography but were greater at the two higher elevation sites compared to the two lower elevations sites; the model which best explained soil respiration per unit MBC included site alone (Table 2.2).
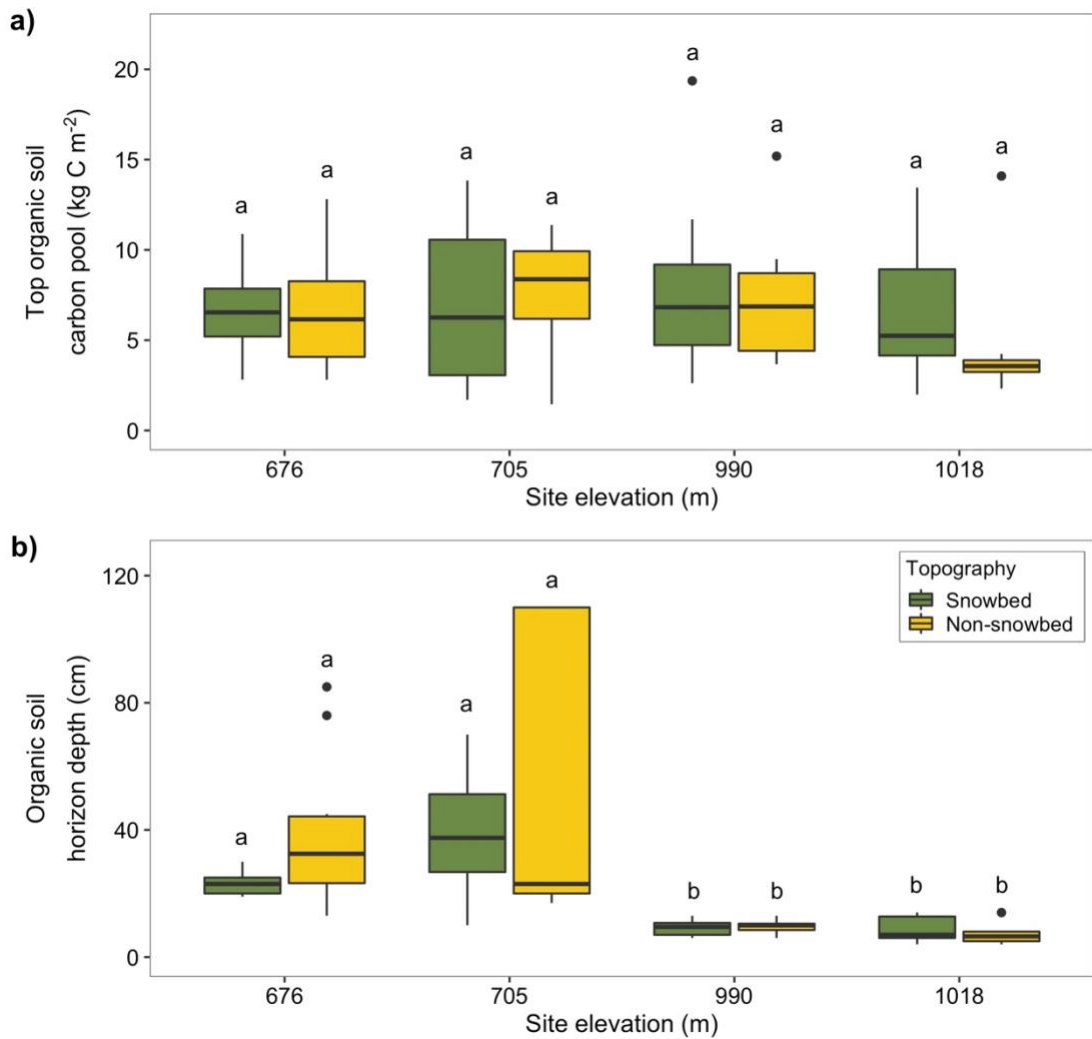
Figure 2.5. (a) Soil carbon (kg C m^{-2}) in the upper 15 cm of the organic horizon, and (b) organic horizon depth to a maximum depth of 110 cm. Colours represent ecosystem. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q$_1$) and 75th (Q$_3$) quartiles, respectively. Difference between Q$_1$ and Q$_3$ is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than Q$_1$ − 1.5(IQR) or greater than Q$_3$ + 1.5(IQR). Letters on top of boxplots indicate statistical difference.
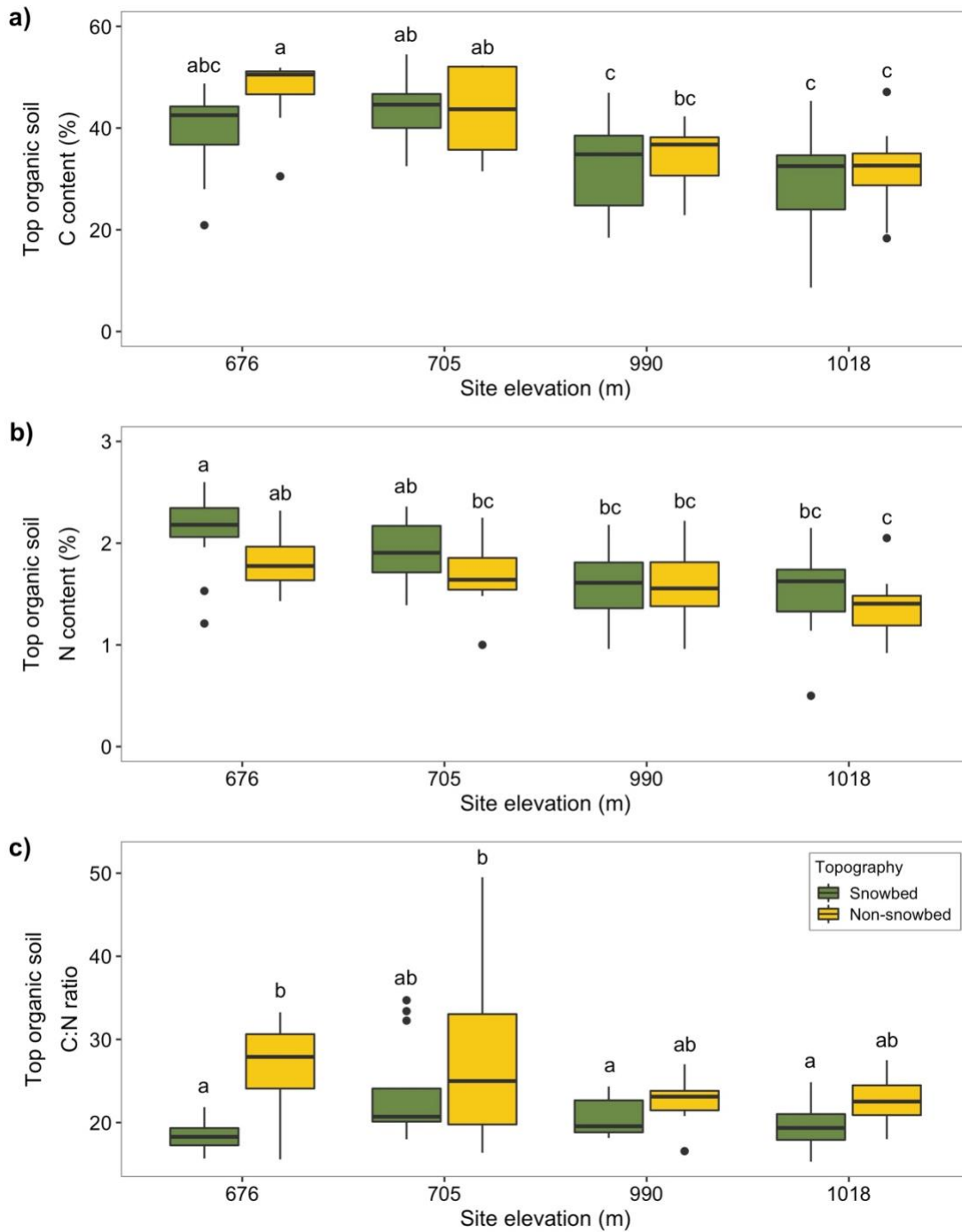
Figure 2.6. Top organic soil (a) carbon content (%), (b) nitrogen content (%), and (c) C:N ratio. Colours represent ecosystem. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5(IQR)$ or greater than $Q_3 + 1.5(IQR)$. Letters on top of boxplots indicate statistical difference.
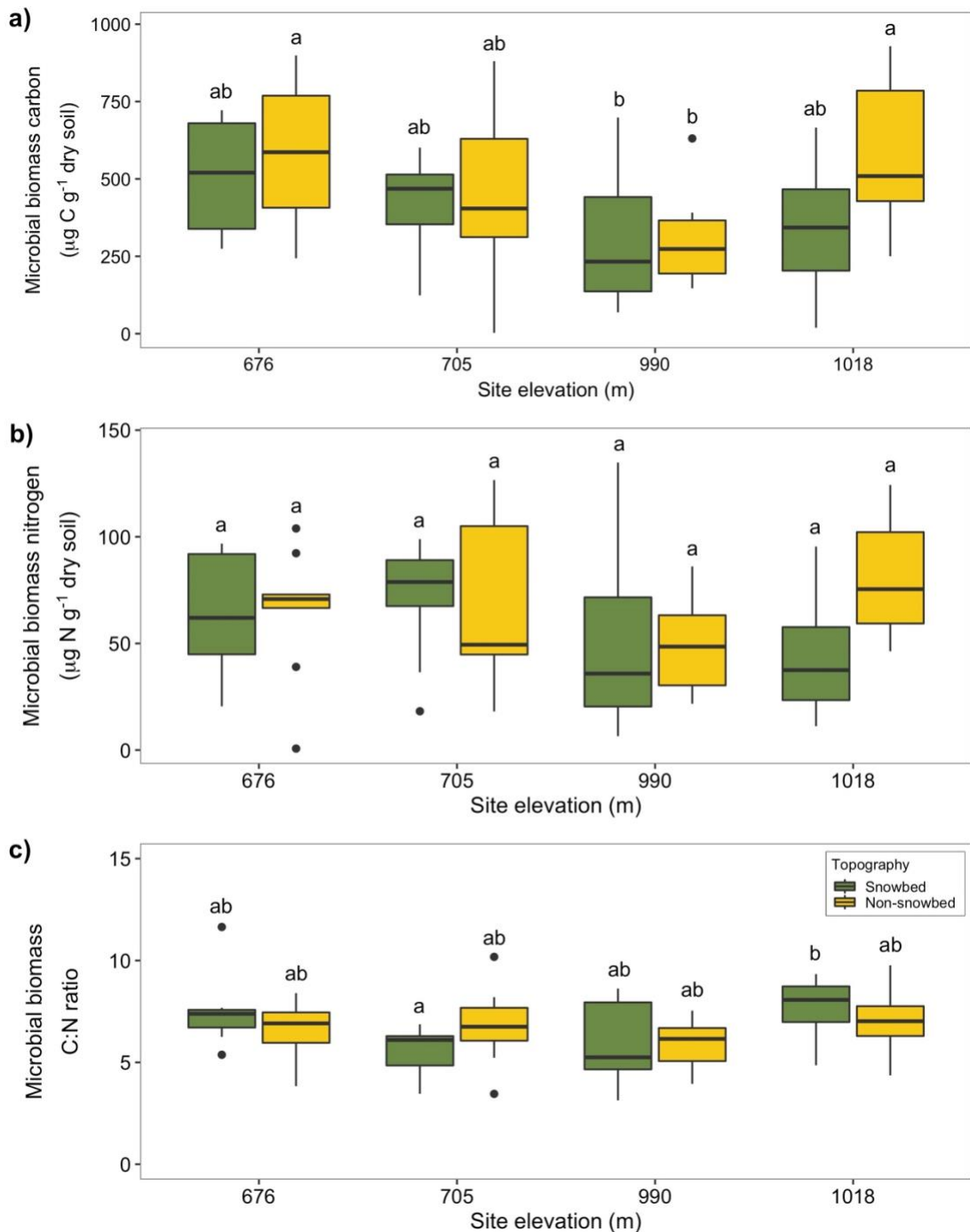
Figure 2.7. Microbial biomass (a) carbon (µg C g⁻¹ dry soil), (b) nitrogen (µg N g⁻¹ dry soil), and (c) C:N ratio. Colours represent ecosystem. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5(IQR)$ or greater than $Q_3 + 1.5(IQR)$. Letters on top of boxplots indicate statistical difference.
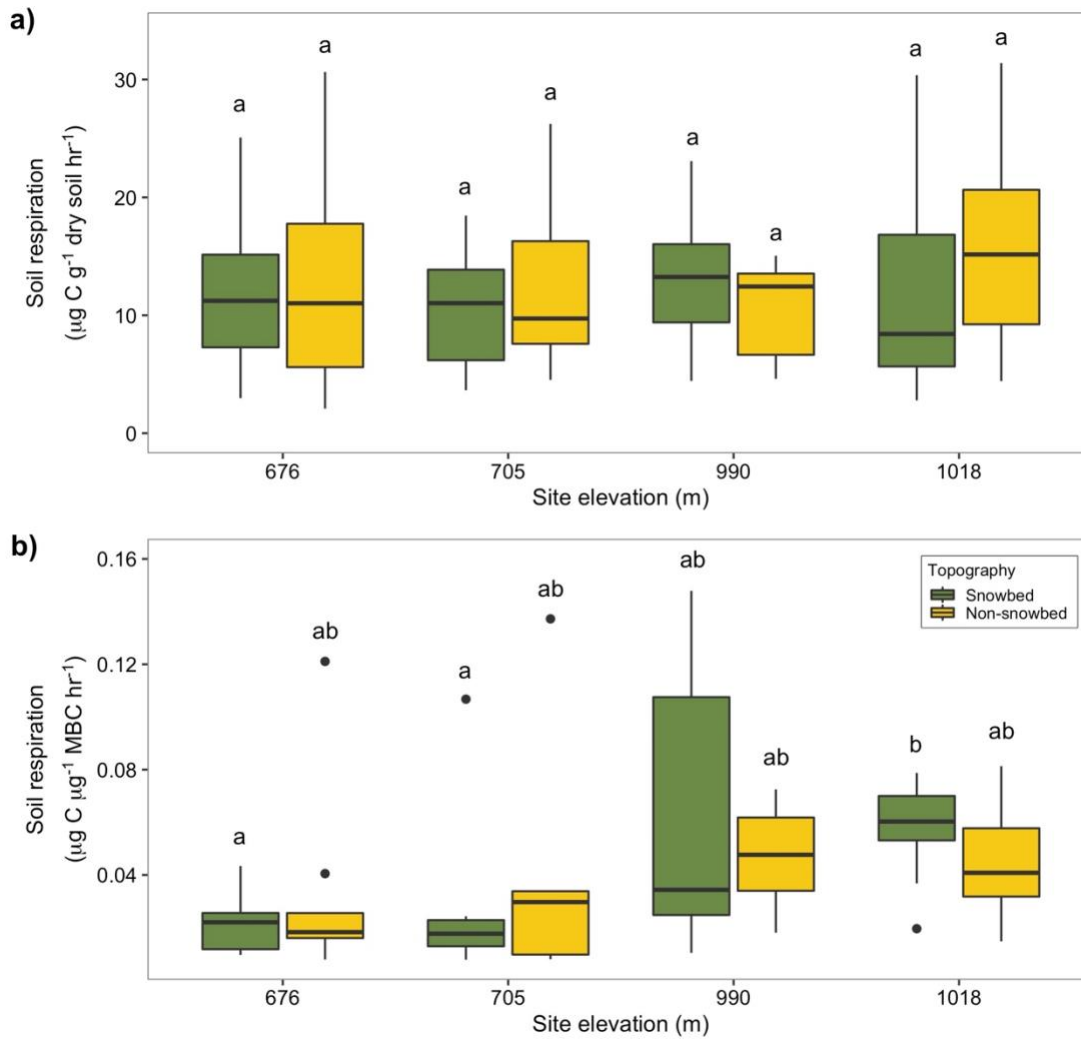
Figure 2.8. Soil respiration (a) per unit soil (µg C g^{-1} dry soil hr^{-1}) and (b) per unit microbial biomass carbon (µg C µg^{-1} MBC hr^{-1}). Colours represent ecosystem. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q$_1$) and 75th (Q$_3$) quartiles, respectively. Difference between Q$_1$ and Q$_3$ is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than Q$_1$ − 1.5(IQR) or greater than Q$_3$ + 1.5(IQR). Letters on top of boxplots indicate statistical difference.

2.5 Discussion

Snow cover regime was a product of elevation and topography, which in turn drove vegetation community composition and regulated some, but not all, soil and microbial properties we considered.

Our study showed clear differences in snow cover duration and melt date with topographic position and elevation (Figure 2.2) resulting in shorter plant growing season in snowbeds and at higher elevations. Total days of snow cover were on average 22 days

greater in snowbed than non-snowbed topographies, and snow melt was on average 9 days later in snowbed than non-snowbed topographies, increasing up to 56 more days of total snow cover and 23 days later snow melt at 705 m elevation. Snow cover duration for these low elevation snowbeds is shorter than late-melting snowbeds > 3200 m asl in the Colorado Rockies with > 290 days of snow cover (Walker et al. 1993). Total days of snow cover was 46 days greater at the highest compared to lowest elevation site, with snowmelt 21 days later. Differences in duration of snow cover varied between years; there was greater snow cover duration in 2017-18 than 2018-19, but in the winter with less snow cover (2018-19) the effect of topography and elevation on snow cover regime were greater with larger differences in total days of snow cover between high and low elevation sites, and snowbed and non-snowbed topographies. Air temperature is the main driver of snow cover duration, regulating snow onset and melt (Notarnicola 2020). Snow cover duration varies annually, with greater variation at low elevations near the snow line systems such as in the Scottish Highlands than at high elevations (Hammond et al. 2018). In Scotland, total days of snow cover have varied from approximately 40 to 120 days at 600 m elevation to 110 to 190 days at 1060 m elevation between 1954 and 2003 (Trivedi et al. 2007).

Mean metrics of snow cover regime were important in determining vegetation community composition (Figure 2.3); vegetation community composition varied along gradients of snow cover duration as has been previously observed along microclimatic gradients (Carlson et al. 2015, Choler 2018). Communities differed between snowbed and non-snowbed topographies, and along the elevation gradient, as was hypothesised. Snow cover duration in late-melting snowbed community *Sibbaldia procumbens – Carex pyrenaica* in the Rockies ranges from 265 to 315 days of snow cover (Nagy and Grabherr 2009), and in five distinct snowbank vegetation communities in New Zealand, also dominated by forbs and graminoids, snow cover duration ranges from 143 to 199 days (Talbot et al. 1992),

while snow cover duration in the graminoid dominated snowbeds in this study was shorter at 121 days.

Communities differed both in terms of the total amount of above ground biomass present and in the functional type composition of the biomass (Figure 2.4). Total aboveground vegetation biomass was greater in non-snowbed than snowbed topographies, and the difference was greater at higher elevation sites, indicating the effects of topography and snow cover could be more important with increasing elevation. Low and high elevation sites were sampled in this study across an elevation range of 342 m; it would be worth establishing sites at mid elevations to quantify the relationship between snow cover, plant communities, and ecosystem pools. Over an elevation range of 114 m, three distinct plant communities with contrasting carbon pools have been identified (Britton et al. 2011). Snowbed communities were dominated by graminoids, while non-snowbed communities were dominated by evergreen shrubs, as seen previously with shrub dominance in alpine heath, and *Nardus stricta* and moss dominance in snowbeds (Britton et al. 2011); although we are aware that PFGs may be over or under represented when considering the proportion of biomass sorted. Such differences in functional composition of the vegetation would be expected to impact on the development of soil C pools through differences in the quantity and quality of plant-inputs, as litter or root exudates, into soil (De Deyn et al. 2008). Shrubs produce recalcitrant litter with high C:N and lignin content and low quality carbon leading to slow decomposition rates and promoting soil C storage (Hobbie 1996). Graminoid litter has lower lignin content and decomposes at a faster rate than evergreen shrubs (Hobbie 1996, Dorrepaal 2007), forb litter is more labile with lower lignin content, lower C:N ratio and faster decomposition rates still (Dorrepaal et al. 2005). Overall, vascular plant dominated communities have increased C inputs with root exudate inputs resulting in faster cycling of labile C, while mosses contribute to slow cycling of stable C (Bueno de Mesquita et al. 2017, Zeh et al. 2019). Combined biomass of *Sphagnum* mosses

and other bryophytes was greater at low elevation sites. *Sphagnum* mosses in particular, with their high C:N ratio, high concentration of recalcitrant C compounds and slow decomposition rate would be expected to contribute to larger soil C pools at lower elevations (Hobbie 1996, Dorrepaal et al. 2005, Aerts 2006, Dorrepaal 2007, Lang et al. 2009).

Top 15 cm organic soil C pools did not differ between snowbed and non-snowbeds topographies, or across sites, in contrast to our hypothesis. This may be due to our limited sampling effort of the organic soil up to 15 cm depth, which only captured the whole organic horizon at the upper two sites. Both soil C content (%) and depth of the organic horizon increased with decreasing elevation and was > 1.1 m depth in plots at the lower two sites, indicating there could be differences in organic soil C pools across elevation gradients. Top 15 cm organic soil C pools observed in this study ranged from 6.62 – 7.66 kg C m^{-2} in snowbeds to 4.27 – 7.87 kg C m^{-2} in non-snowbeds. However, previous work has found greater soil C pools in oceanic-alpine snowbeds (24.86 kg m^{-2}) and alpine heath (13.25 kg m^{-2}) when sampling the full soil profile including organic and mineral soil horizons (Britton et al. 2011). Although, when considering topsoil (0-10 cm) C stocks, our results are similar to other alpine communities: acidic grasslands (5.35 ± 0.39 kg SOC m^{-2}), alpine meadows (4.86 ± 1.74 kg SOC m^{-2}), and mesic calcareous grasslands (6.97 ± 1.99 kg SOC m^{-2}; Saenger et al. 2015).

Both soil carbon and nitrogen contents declined with increasing elevation, but the proportional change was not equal, resulting in a decline in C:N ratio with elevation also. Soil nitrogen content (%) was greater in snowbed than non-snowbed topographies, although this was likely driven by the lowest elevation site, suggesting there could be an input of N from snow melt (Hiltbrunner et al. 2005) or N release via graminoid litter decomposition (Hobbie 1996).

Differences in plant communities, and soil C and soil N content across topographies and elevations would likely result in differences in microbial community, both in biomass and composition. Both microbial biomass carbon and nitrogen were unaffected by topography or elevation, in contrast to our hypothesis. Microbial biomass carbon ranged between 308.45 and 507.36 μg C g^{-1} dry soil in snowbeds and between 299.54 and 577.91 μg C g^{-1} dry soil in non-snowbed soils, similar to values previously reported in alpine meadow soils (Lipson et al. 2000), but up to several orders of magnitude lower compared to MBC previously observed in subalpine grassland and boreal soils, and peatland (Allison et al. 2008, Puissant et al. 2015, Basińska et al. 2020). Similarly, soil respiration rates were not consistent. When expressing soil respiration per unit of dry soil there was no effect of elevation or topography on respiration rates, but when expressing soil respiration per unit MBC, there were greater respiration rates from higher elevation sites. Sampling in one season may not capture variation in microbial biomass and activity. During our summer sampling campaign, topographic microclimate variability may have been at a minimum, likely contributing to no effect of topography on soil respiration rates, while elevational-derived effects on temperature, may have impacted microbial activity (Löffler et al. 2008) .

The alpine landscape is heterogenous; plant community composition is driven by snow cover duration, topography and elevation but this is not reflected in the top 15 cm organic soil C pool. Given the greater soil C content and depth of the organic soil horizon at lower elevations, if we were to consider the entire horizon when sampling soil and calculating C pool, it is likely there would be an elevation effect, as we would expect with the lower elevation sites containing greater moss biomass. However most soil ecology research considers soil up to 21 ± 26 (mean ± SD) cm deep and most soil biology research considers the top 18 ± 23 (mean ± SD) cm soil depth (Yost and Hartemink 2020), as this is considered the more biologically active part of the soil profile. However here the topsoil does not help our understanding of big ecosystem level differences and ecological

processes. The angle of sampling soil can also impact estimates of SOC stock, as collecting a core 'plumb-vertical' rather than 'orthogonal to slope gradient' can lead to a deeper sample of the soil horizon collected resulting in a miss-estimation of SOC in sloped environments (Prietzel and Wiesmeier 2019).

It is important to consider the temporal dynamics of plant and microbial communities, including the effects of snow cover and melt, and plant-soil interactions, on microbial communities and process (Larsen et al. 2000, Bardgett et al. 2005, Nobrega and Grogan 2007, Britton et al. 2011). Differences in microbial communities and processes between topography and across elevations may be observed when sampling across the year, particularly at transitional times, such as snow melt or across the growing season (Schadt et al. 2003, Lipson and Schmidt 2004, Björk et al. 2008, Löffler et al. 2008, Lazzaro et al. 2015).

The dominant PGF in snowbed and non-snowbed communities have different quantities and quality of plant inputs to soil. Vascular plants are encroaching into snowbeds and have been linked to warming temperatures and reduced snow cover (Britton et al. 2009, Niittynen et al. 2018, 2020, Scharnagl et al. 2019). An increase in shrubs at the expense of non-vascular plants could alter the C cycling dynamics through effects of altered productivity rates, quality and quantity of litter inputs, in turn impacting microbial activity, decomposition rates, and potentially altering the soil C pool (Myers-Smith et al. 2011).

2.6 Conclusions

Snow cover, topography and elevation are major drivers of vegetation community composition in mountain ecosystems, with elevation having the greatest impact. While we expect differences in microclimate and plant communities to result in varying soil C pools, microbial community biomass and activities, this was not observed in the upper 15 cm

organic soil horizon during mid-growing season. Organic horizon depth and C content were greater at lower elevation, suggesting there may be an elevational effect when considering whole soil profiles. Snow cover has declined over recent decades (Barnett et al. 2006, Collins et al. 2013, Rivington et al. 2019) and is likely a factor contributing to the expansion of vascular plants into alpine snowbed communities (Myers-Smith and Hik 2017, Scharnagl et al. 2019). As shrubs increase rates of soil respiration through root exudates (Zeh et al. 2019), it is important we quantify the still unknown variability in oceanic-alpine ecosystem carbon pools in order to predict how snow cover and vegetation change may impact on carbon cycling and storage in mountain soils.

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2.8 Funding

2.9 References

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3 Drought resilience of ecosystem respiration in *Nardus* snowbeds and *Racomitrium* heath

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3.1 Abstract

Climate change is predicted to increase the frequency and duration of droughts in alpine ecosystems, with drought events having the potential to alter carbon dynamics in plant-soil systems. Vegetation community and soil conditions may regulate the response of systems to drought events. We conducted a controlled mesocosm experiment to assess the response of two contrasting oceanic-alpine ecosystems to drought and rewetting: graminoid dominated *Nardus* snowbed and bryophyte dominated *Racomitrium* heath. Ecosystem respiration was measured throughout a 37-day drought and 22-day recovery phase, and the response ratio calculated as the ratio of the ecosystem respiration rate in the droughted mesocosms to that in the control mesocosms to determine if the sensitivity of these ecosystems to drought differed. Ecosystem respiration was greater in *Nardus* snowbed than in *Racomitrium* heath, with vegetation community composition (PCoA ordination axis) a key predictor of rates of ecosystem respiration. Drought suppressed

ecosystem respiration in both ecosystems. Following rewetting, rates of ecosystem respiration increased in both ecosystems and exceeded control levels in *Nardus* snowbeds in a short-term pulse. However, by the end of the recovery phase, ecosystem respiration returned to control levels in *Nardus* snowbeds. The response ratio did not differ between ecosystems. These results demonstrate that both *Nardus* snowbeds and *Racomitrium* heath are responsive to a drought-rewetting cycle and despite a short-term pulse in *Nardus* snowbeds, over a longer period they did not differ in their resilience to these events. Changing plant community composition in alpine ecosystems (including increasing abundance of vascular plants), and the predicted increase in frequency and duration of drought interspersed with rain events, may have implications for the fate of large pools of currently stable soil carbon in *Nardus* snowbeds, depending on the source of carbon mineralised following rewetting events.

Keywords: carbon dioxide; drought; ecosystem respiration; *Nardus* snowbeds; oceanic-alpine; *Racomitrium* heath; resilience; resistance; rewetting.

3.2 Introduction

Water availability is a key factor determining ecosystem functioning, including carbon (C) cycling (Raich and Schlesinger 1992). Mountainous areas are expected to be particularly affected by climatic change due to elevation dependent warming (Pepin et al. 2015). Changing precipitation and snow melt patterns are altering hydrology in many regions (IPCC 2014). Warming is predicted to alter rates of snowmelt and therefore water supply globally and on local scales (Hock et al. 2019, IPCC 2019, Rivington et al. 2019). Snow cover dynamics in mountain systems are very variable and are strongly dependent on geographic location, latitude and elevation. In mountain systems globally, snow cover

depth, extent and duration have decreased over recent decades, particularly at lower elevations (loosely defined as areas below the 0°C isotherm – corresponding to approximately 2000 m elevation in Central Europe and 1000 m elevation in Scandinavia; Hock et al. 2019, IPCC 2019). At higher elevations where temperatures remain well below 0°C during the cold season, there has been little change in snow cover dynamics (Stewart 2009). However at lower elevations where temperatures are close to 0°C during the cold season, there has been an increase in precipitation falling as rain and a decrease falling as snow; a decrease in snowpack, and earlier snowmelt in response to warming (Stewart 2009). Duration of snow cover in low elevation mountain systems in Scotland has changed markedly; days of snow cover have declined by more than 52 days, equivalent to more than 30% decrease since the 1960s (Barnett et al. 2006, Rivington et al. 2019).

Ecosystem responses to changing precipitation and snow cover regimes may be habitat specific; in habitats irrigated by meltwater from snowpack, soils may become saturated at snowmelt, resulting in reduced rates of respiration (Brooks et al. 1996). However, irrigation from meltwater can also maintain base levels of soil moisture (Blankinship et al. 2014), thereby reducing the effects of rainfall events and drought incidence in the summer, thus maintaining ecosystem productivity in habitats irrigated by snowpack meltwater.

Habitats not influenced by snowmelt may be drier all year round and therefore affected by rainfall events to a greater extent. Reduced snow cover and earlier snowmelt could reduce the amount and duration of irrigation and may result in soil drying in habitats previously irrigated by snowpack meltwater (IPCC 2019). This could potentially lead to a reduction in anaerobic conditions and increases in ecosystem respiration in habitats previously saturated by snowpack meltwater. Alternatively there may be decreases in ecosystem respiration in habitats usually dependent on meltwater to maintain summer soil moisture availability.

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Rainfall levels also influence soil moisture availability and thus ecosystem respiration (Zhang et al. 2019). Summer precipitation has decreased by more than 18% in parts of Scotland between 1914 and 2004 (Barnett et al. 2006). In addition, air temperature is predicted to rise, with summer months becoming drier (Barnett et al. 2006). Less precipitation alongside warming temperatures are increasing rates of evapotranspiration, resulting in soil drying (Sherwood and Fu 2014). Ecosystems with drier soils as a result of drought have altered rates of ecosystem carbon fluxes, with ecosystem respiration rates observed to increase or decrease compared to controls, depending on antecedent soil conditions (Sowerby et al. 2008). Ecosystem respiration in an oceanic-alpine snowbed, in a controlled manipulation experiment, was suppressed two days after drought and rewetting compared to a control (Johnson et al. 2011). However, this experiment did not consider the changes in ecosystem respiration during drying or immediately following rewetting. Other studies have shown that after rewetting there are physical changes to soil organic matter (SOM) resulting in its increased availability and resulting in a pulse of CO_2 release (Birch 1958). It has been suggested that soils which rarely experience dry-rewetting events will have a larger pulse of respiration than soils regularly experiencing dry-rewet cycles (Fierer and Schimel 2002). Across multiple dry-rewet events there may be less SOM available, or the microbial community accommodates the rapid change in water potential, reducing microbial cell lysing, and the opportunity for surviving microbes to mineralise available labile substrates (Birch 1958, Van Gestel et al. 1993, Fierer and Schimel 2002, 2003).

Seasonally snow-covered oceanic-alpine ecosystems are predicted to be important at an international scale as large stores of soil carbon (C; Jones et al. 2005). In the UK, ~ 40% of all soil C is stored in mountain, moorland, and heath ecosystems which may contain > 20 kg C m^{-2} in the top metre of soil (Bradley et al. 2005, van der Wal et al. 2011). Alpine landscapes have varied topographies and microclimates and the resulting variation in snow

cover regimes promotes development of heterogeneous plant communities varying in function and taxonomic composition (Carlson et al. 2015). Plant community composition is driven by the duration and depth of snow cover via differences in soil temperature and moisture, availability of nutrients, and the length of the plant growing season across small spatial scales (Stanton et al. 1994, Zhang 2005, Björk and Molau 2007, Ford et al. 2013, Choler 2018). In heterogeneous alpine landscapes, differences in vegetation communities are associated with variations in ecosystem C pools, primarily driven by differences in organic soil C pool, and variability in C fluxes (Sørensen et al. 2018). Carbon fluxes differ between graminoids and bryophytes, with greater rates of ecosystem respiration in graminoid than bryophyte dominated soils (Ward et al. 2009, 2013).

Globally, soil respiration rates are positively correlated with precipitation and net primary productivity (NPP; Raich and Schlesinger 1992). However, changes in climate may alter the balance between NPP and decomposition and therefore impact on soil C storage (Chapin et al. 2009), potentially changing soil from a net C sink to a net C source.

Since low-elevation oceanic-alpine systems can have large pools of soil C (Bradley et al. 2005, Jones et al. 2005, van der Wal et al. 2011) and are particularly sensitive to climatic change (Pepin et al. 2015, Hock et al. 2019, IPCC 2019, Rivington et al. 2019) it is important to understand how the changes in soil moisture regimes resulting from changes in snowpack and precipitation will affect C cycling and soil C stocks. Ecosystem respiration can be used as an indicator of C cycling, reflecting short-term responses of plant metabolism and microbial activity to changing environmental conditions (Ryan and Law 2005), while avoiding destructive sampling for soil microbes during the experiment. The stability of an ecosystem determines its ability to continue functioning under changing conditions and is composed of resistance and resilience (Orwin and Wardle 2004). Resistance is the amount of change caused by a disturbance; resilience being the ability of a system to return to pre-disturbance levels (Pimm 1984, Orwin and Wardle 2004).

Resistance and resilience indices can be used to quantify the stability of different systems and their ability to maintain ecosystem properties and processes under changing conditions (Pimm 1984, Orwin and Wardle 2004).

Racomitrium heath is a moss dominated ecosystem with shallow organic soils found on exposed summits that experience a variable microclimate in terms of soil temperature and moisture (Britton et al. 2011), with plant and soil microbial communities adapted to fluctuating conditions. Early melting *Nardus* snowbeds are graminoid dominated; are highly productive during short growing seasons; have relatively stable microclimates with wetter soils during winter and summer, and are large stores of old C with deep organic soils (Britton et al. 2011, Mills n.d.). *Nardus* snowbeds are sensitive to drought (Johnson et al. 2011), and with precipitation regimes predicted to change (Barnett et al. 2006, Collins et al. 2013) it is important to quantify the resistance and resilience of this system to a drought and rewetting event. We compared the response of early melting *Nardus* snowbeds and contrasting *Racomitrium* heath, to a prolonged drought, with a subsequent rewetting and recovery period. We hypothesised that:

1. *Nardus* snowbeds would have higher rates of ecosystem respiration than *Racomitrium* heath as they have greater NPP rates and are dominated by vascular rather than non-vascular plants.

2. Ecosystem respiration under drought would decrease in the relatively drier *Racomitrium* heath, but in the relatively wetter *Nardus* snowbeds initially increase and then decrease as their soils gradually dry.

3. Ecosystem respiration following rewetting would increase to greater than control levels in both ecosystems, as rewetting dry soil increases the availability of substrates for soil microbes to mineralise.

4. Ecosystem respiration in *Racomitrium* heath would be more resistant and resilient to a drought-rewet cycle than *Nardus* snowbeds, as it is already adapted to a more

variable microclimate, with a soil microbial community that is less sensitive to drought-rewetting.

3.3 Methods

3.3.1 Study area

The study area was located in the Allt a'Mharcaidh catchment (3°50' W, 57°5' N), in the western Cairngorm Mountains, Scottish Highlands. The climate in this region is cool oceanic; mean monthly air temperatures range from -2.0°C in February to 13.6°C in July (at 700 m elevation), and mean annual precipitation is ~1100 mm, with approximately 30% falling as snow during winter (Helliwell et al. 1998, Britton et al. 2011, Rennie et al. 2017). Six sampling areas were selected, three at ~880 m elevation in early-melting *Nardus* snowbeds and three at ~900 m elevation in *Racomitrium* heath areas. *Nardus* snowbed sampling areas were graminoid and forb dominated with peaty podzol/histic podzol soils; *Racomitrium* heath sampling areas were bryophyte dominated (*R. lanuginosum*) with oroarctic podzol/endoskeletic podzol soils (Britton et al. 2011). In each sampling area, we selected three sampling points ≥ 4m apart. Two intact plant-soil mesocosms (10.2 cm diameter, 15 cm deep) were collected per sampling point on 5 June 2018 (n = 36). Mesocosms were collected in PVC pipe sections; vegetation was cut with a knife around the outer edge of the PVC pipe, and then the pipe driven into the soil using a wooden block and hammer until vegetation was flush with the top of the pipe section. A paired baseline soil grab sample (loose sample to 10 cm depth) was collected adjacent to each mesocosm for determination of initial soil moisture (%) and microbial biomass. Mesocosms were removed and wrapped in clingfilm, returned to the laboratory and maintained in the dark at 4°C until the start of the rainfall manipulation study on 6 July 2018.

3.3.2 Rainfall manipulation

The rainfall manipulation experiment was conducted at Hazelrigg Field Station (2° 46' 30" W, 54° 1' 50" N). Mesocosms were maintained outdoors under a clear plastic clad, timber framed shelter which excluded natural rainfall but allowed free flow of air for ventilation. The base of each mesocosm was covered with 20 μm nylon mesh to retain soil but allow free drainage of leachate. Mesocosms were held in 110 mm internal diameter end caps, with holes drilled for leachate to drain, encased in 119 mm internal diameter acrylic tubes. The encased mesocosms were surrounded by potting compost for insulation with the acrylic tubes allowing easy removal of the mesocosms without disturbance of the insulating compost (Figure 3.1). The compost was covered by a thin layer of sand to limit heating of the compost under the sun. Initial soil moisture was not standardised; reducing soil moisture in *Nardus* snowbed soils to that of *Racomitrium* heath soils would have applied a strong drought treatment before starting the experiment. The effects of differing initial and control soil moisture are captured as part of the ecosystem effect and are part of the contrast between these systems. One mesocosm per sampling point was randomly allocated to each of the two treatments: control, or drought. Mesocosms were blocked by treatment (control, or drought) to apply treatments without watering the droughted mesocosms.

Drought and control treatments were chosen based on summer precipitation data from the Cairngorms. During June-August between 2000 and 2015, the longest number of consecutive days without rain recorded in the Allt a'Mharcaidh catchment was 26 days (Rennie et al. 2017), however duration of dry periods are predicted to increase in summer (Collins et al. 2013). Dry spell duration is based on April to September precipitation data collected between 2003 to and 2017 from the Culardoch meteorological station (57° 04' 13" N, 3° 20' 57" W) at 750 m elevation, in the eastern Cairngorms, where a period of 39 days without rain was recorded in 2012. For the present study we selected a drought phase

of 37 days (11 August – 16 September 2018), preceded by a 24-day acclimation and 9-day baseline phases (9 July 2018 to 1 August 2018, and 2 August 2018 to 10 August 2018, respectively), and followed by a 22-day recovery phase, until ecosystem respiration of droughted mesocosms returned to that of control (17 September 2018 to 8 October 2018).

Figure 3.1. (a) Drought manipulation experimental set up of (b) *Nardus* snowbed and (c) *Racomitrium* heath mesocosms.

Watering treatments were also based on Allt a'Mharcaidh precipitation data. The mean daily rainfall was 2.59 mm, the mean number of consecutive days with rain was four, and the mean number of consecutive dry days was three. The volume of water applied in the control treatment was based on the mean daily rainfall in the Allt a'Mharcaidh catchment (2.59 mm) and was calculated as:

$$control\ treatment\ (ml) = \frac{\left(\frac{\pi r^2 \times h}{1000}\right) \times 7}{4}$$

where $r = 51$ mm and $h = 2.59$ mm. Mean daily volume of rain was used to calculate mean weekly volume of rain and divided over four watering days. In the control treatment, mesocosms were watered with 37 ml artificial rain for four days a week (Monday-Thursday). In the drought treatment, mesocosms were also watered during

acclimation, baseline and recovery phases. Artificial rain water was made to the NPK ratio of rain in the Allt a'Mharcaidh catchment (UKEAP: Precip-Net 2018). Artificial rainwater contained NH_4 (9.3 µM l^{-1}), $NaNO_3$ (12.4 µM l^{-1}), PO_4 (0.4 µM l^{-1}), KCl (1.8 µM l^{-1}) and had a pH of 6.2.

Meteorological and soil conditions were recorded throughout the study at 30-minute intervals. Soil moisture (volumetric water content m^3/m^3) and temperature (°C) were recorded based on a stratified random design; paired mesocosms from one sampling point per sampling area were randomly chosen to be instrumented at 5 cm depth from soil surface (n = 12; soil moisture sensors: GS1; soil temperature sensors: RT-1; data loggers: Em5b and Em50; all of METER Group, Inc., Pullman, WA, USA). Air temperature (°C), air pressure (kPa) and relative humidity (%) were recorded under the rainout shelter (humidity, temperature sensor and barometer: VP-4; data logger: Em50; both of METER Group, Inc., Pullman, WA, USA). The rainout shelter meteorological station was damaged in a storm on 19 September 2018. Meteorological data after the storm were estimated based on data from Hazelrigg Field Station meteorological station located around 50 m away from the experiment. Regression equations based on rainout shelter and field station meteorological data from 1 August 2018 to 18 September 2018 (air temperature: R^2 = 0.935, n = 2352, y = -1.52 + 1.14x; air pressure: R^2 = 0.996, n = 2352, y = 0.95 + 0.99x; relative humidity: R^2 = 0.87, n = 2352, y = 21.92 + 0.72x) were used to estimate conditions within the rainout shelter. Daily means were calculated for meteorological and soil conditions used in further analyses.

3.3.3 Ecosystem respiration fluxes

Ecosystem respiration was measured twice per week (on Mondays and Thursdays) during the baseline and drought phases. Following rewetting, measurement frequency was increased to four days per week (Monday, Tuesday, Wednesday, Friday) for the first week

of the recovery phase. In subsequent weeks during the recovery phase ecosystem respiration was measured three days per week (Monday, Wednesday, and Friday). To measure ecosystem respiration, a dark chamber connected to an infrared gas analyser (Li-8100, LI-COR Biosciences, Lincoln, NE, USA) was temporarily sealed to the core for 60 s enclosure time including a 15 s equilibrium phase following a 15 second purge (Mills et al. 2011).

Ecosystem respiration measurements were used to calculate response ratio, and resistance and resilience indices. As *Nardus* snowbed and *Racomitrium* heath are intrinsically different, the response ratio, resistance and resilience indices calculate the magnitude of change. Response ratio and resilience and resistance indices were calculated from the paired mesocosms per sampling point. Response ratio (RR) was calculated as:

$$RR \; at \; t_x = \frac{D_x}{C_x}$$

where D_x represents ecosystem respiration in droughted mesocosms at time x, and C_x represents ecosystem respiration in control mesocosms at time x. A response ratio of 1 indicates that ecosystem respiration of the droughted mesocosm is equal to control; a value greater or less than 1 represents ecosystem respiration of a droughted mesocosm greater or less than that of the control, respectively.

Resistance and resilience indices were calculated based on Orwin and Wardle (2004). The resistance index (RS) was calculated for the drought phase. The resistance index quantifies the amount of change caused by a disturbance and is relative to the control:

$$RS \; at \; t_x = 1 - \frac{2 \times |A_x|}{(C_x + |A_x|)}$$

where $|A_x|$ represents absolute difference in ecosystem respiration between control and droughted mesocosms at time x, and C_x is as above. The resistance index is bounded by +1 and -1. An index of +1 represents maximal resistance with the disturbance having no effect and no change from control. Lower values represent a lack of resistance: an index

value between 0 and 1 indicates respiration values from control soils are more than 2-fold greater than disturbed soils, with an index value of 0 representing a 100% reduction or increase in respiration relative to control, while a negative value indicates respiration rates from disturbed soils are more than 2-fold greater than control soils.

The resilience index (RL) was calculated for the recovery phase. The resilience index represents the ability of a system to recover from a disturbance in relation to the amount of change caused by a disturbance:

$$RL \ at \ t_x = \frac{2 \times |A_0|}{(|A_0| + |A_x|)} - 1$$

where $|A_x|$ is as above and $|A_0|$ is the absolute difference in ecosystem respiration between control and droughted mesocosms at the end of the disturbance, establishing the starting position and status for the system's recovery (the last respiration measurement day during the drought period). The resilience index lies in the range of +1 to -1; an index of +1 represents full recovery to control levels with lower values representing a lower ability to recover. A value of RL = 0 indicates that disturbed mesocosms have not recovered at all or that ecosystem respiration in disturbed soils is still equally different in relation to control but have shifted in the opposite direction. A negative value indicates that disturbed mesocosms have diverged further from control and ecosystem respiration has greatly increased relative to control in a pulse event.

3.3.4 Vegetation and soil

Vegetation community composition was described by visual estimates of species cover per mesocosm on 10 October 2018 before harvest. Mesocosms were stored at 4°C following harvest on 10 October 2018 until destructive sampling between 11 October 2018 and 18 October 2018. Vegetation and soil characteristics were determined following mesocosm harvest. Firstly, fresh mass of intact mesocosms was recorded. As mesocosms

were sampled with vegetation flush to the top of the core, depths of bryophyte and soil layers varied; therefore depth and fresh mass of vegetation (bryophytes) and soil layers were also recorded. Aboveground vegetation biomass (excluding litter layer) was dried at 60°C for at least 48 hours, sorted to plant functional groups (PFGs) for 30 minutes and its mass recorded. Any biomass remaining after 30 minutes was allocated to 'unsorted'. Proportion of PFGs in sorted biomass was calculated. PFGs were defined as: shrubs, graminoids, forbs, pteridophytes, *Sphagnum* mosses, other bryophytes, and lichens (Chapin et al. 1996, Dorrepaal 2007).

Soil was lightly homogenised by hand removing large stones and roots for a standardised 10 minutes per sample. A subsample of 5.0 ± 0.5 g fresh soil was dried at 105°C for 24 hours to determine soil moisture. Soil C and N content (%) were analysed on 30 ± 1 mg subsamples of ground, freeze-dried soil samples by high temperature combustion gas chromatography (Vario El III C/N analyser; Elementar, Stockport, UK). Soil C and N pools were calculated as:

$$C_{pool} = D \times Bd \times C_{conc}$$

$$N_{pool} = D \times Bd \times N_{conc}$$

where D is soil depth (cm), Bd is soil bulk density (g dry soil per cm³), C_{conc} and N_{conc} are soil C and N content (%), and C_{pool} and N_{pool} are soil C and N pools (kg m⁻²), respectively.

Soil microbial biomass C (MBC) and microbial biomass N (MBN) were determined by liquid fumigation-extraction on fresh organic soil adapted from Gregorich et al. (1990). Forty ml of 0.5 M K_2SO_4 was added to paired 5.0 ± 0.5 g lightly homogenised fresh soil subsamples; 0.5 ml $CHCl_3$ was added to fumigated samples. Samples were shaken at 165 rpm for 2 hours, centrifuged at 3000 RPM for 10 minutes, filtered through Whatman 42® (GE Healthcare, Chicago, IL, USA) filter paper, sparged for 20 minutes to remove chloroform, and stored at -20°C until analysis. Sample extracts were diluted with MilliQ

water at a ratio of 1:8 extract:MilliQ water prior to analysis for total organic C and total N on a TOC-L combustion analyser coupled with a TNM-L unit (Shimadzu Corp, Kyoto, Japan). MBC and MBN were calculated as the difference between C and N recovered from fumigated and non-fumigated samples and were expressed as dry-mass specific. MBC and MBN were quantified for the baseline grab soil samples and after mesocosm harvest and were used to calculate microbial biomass C:N ratio.

3.3.5 Statistical analyses

All statistical analyses were conducted in R version 4.0.4. Generalised additive mixed models (GAMMs) with repeated measures were performed using *gamm4* (Wood and Scheipl 2020). Multivariate analyses were performed using *ape* (Paradis et al. 2019) . Results are reported as significant at $p < 0.05$.

The effects of ecosystem type on vegetation community were determined by permutational multivariate analysis of variance with 9,999 permutations (PerMANOVA; adonis function). Although using mesocosm-based species cover does not account for pseudo-replication within sampling areas, it allows an examination of variation within as well as between sampling areas and ecosystems. Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity was used to represent and quantify plant communities (pcoa function). The scores from the first two axes were used for subsequent analysis.

Differences in soil characteristics (C and N content, C:N ratio, depth, soil C and N pools), microbial biomass (C pool, C:N ratio), and aboveground biomass between ecosystems and treatment were determined using ANOVAs with an interaction term. Sampling time (baseline field conditions or experimental harvest) was also included for MBC. Kruskal-Wallis tests were used when residuals were not normally distributed and could not be normalised by transformation.

Diurnal changes in air temperature were quantified using air temperature recorded at 30 minute intervals in a GAMM with day and time of day as non-linear random factors (spline, gamm4 function; Wood and Scheipl 2020). Change in daily mean air temperature over the course of the experiment was determined using a GAMM with day as a non-linear random effect. Change in mean daily mean soil temperature and soil moisture were quantified using a GAMM with treatment and ecosystem as fixed effects, day as a non-linear random effect, unique mesocosm ID (for repeated measures), and nested sampling area and point as random effects.

To determine if drought treatment and ecosystem type had an effect on ecosystem respiration, repeated measures GAMMs were used with treatment, ecosystem and their interaction as fixed effects, day and time as non-linear random effects (spline), unique mesocosm ID (for repeated measures), nested sampling area and point as random effects. Fixed effects were dropped from the model when not significant, in order to reduce the number of parameters in the model. Model fit was visually assessed using diagnostic plots. When model residuals did not satisfy assumptions of normality, data were log or square root transformed. Following rewetting, potential differences in ecosystem respiration rates between ecosystems and treatments on specific days were assessed using an ANOVA with an interaction term.

To determine if meteorological conditions, vegetation, or soil characteristics influenced ecosystem respiration, additional environmental factors – daily mean air temperature, PCoA axes 1 and 2 or total aboveground biomass, and soil C pool – were included as fixed effects in a subsequent model. To avoid overfitting the model, highly correlated variables ($R^2 \leq$ -0.7 and $\geq$ 0.7) were excluded, therefore soil temperature was excluded as this was highly correlated with air temperature ($R^2 = 0.959$, n = 816), C content (%) was excluded as this was highly correlated with PCoA Axis 1 ($R^2 = $ -0.841, n = 33), and soil depth was excluded as this was highly correlated with C pool ($R^2 = 0.754$, n = 33).

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To determine whether response ratio, resistance or resilience indices varied between ecosystems, GAMMs were used with ecosystem as a fixed effect, nested sampling area and point (accounting for sampling design and repeated measures) as random effects, and day as a non-linear random effect.

3.4 Results

Air temperature was variable, peaking mid-afternoon on a diurnal scale ($F = 186.50$, $p < 0.001$). Daily mean air temperature fluctuated over the course of the experiment and overall declined as the season changed from summer to autumn ($F = 61.31$, $p < 0.001$; Figure 3.2). Mean daily mean soil temperature was strongly driven by daily mean air temperature (control mesocosms during drought period: $R^2 = 0.95$, $n = 74$; droughted mesocosms during drought period: $R^2 = 0.95$, $n = 74$); soil temperature followed the trend of air temperature and fluctuated and decreased over time ($F = 233.6$, $p < 0.001$; Figure 3.2). Soil temperature did not differ between *Nardus* snowbed and *Racomitrium* heath mesocosms ($t = -1.43$, $p = 0.154$), but treatment had an effect on soil temperature, with droughted mesocosms being warmer than control ($t = 2.66$, $p = 0.008$). Unfortunately, the soil moisture probes were not installed correctly in the *Racomitrium* heath mesocosms and the data were unusable. In *Nardus* snowbeds, mean daily mean soil moisture was greater in the control than droughted mesocosms ($t = -3.93$, $p < 0.001$; Figure 3.3). At the end of the drought phase, soil moisture was 30-fold greater in the control than droughted mesocosms at 0.396 ± 0.011 compared to 0.013 ± 0.001 volumetric water content m^3/m^3, respectively. Although treatments were based on previously recorded summer precipitation, soil moisture in control *Nardus* snowbed mesocosms increased over the drought and recovery phases ($F = 105.5$, $p < 0.001$), possibly due to the timing of the experiment. Summer in 2018 prior to sampling the mesocosms was particularly warm and dry, therefore initial soil

moisture may have been below average. Additionally, the experiment was conducted over late summer into autumn, when declining temperature and senescing plants would contribute to a decrease in evapotranspiration and we would expect the soils to become wetter. Variability in soil moisture appears to decrease in droughted mesocosms, however this is an artifact of excluding data after rain was driven under the shelter by wind. Soil moisture in droughted mesocosms increased following rewetting but did not return to that of control during the recovery phase.
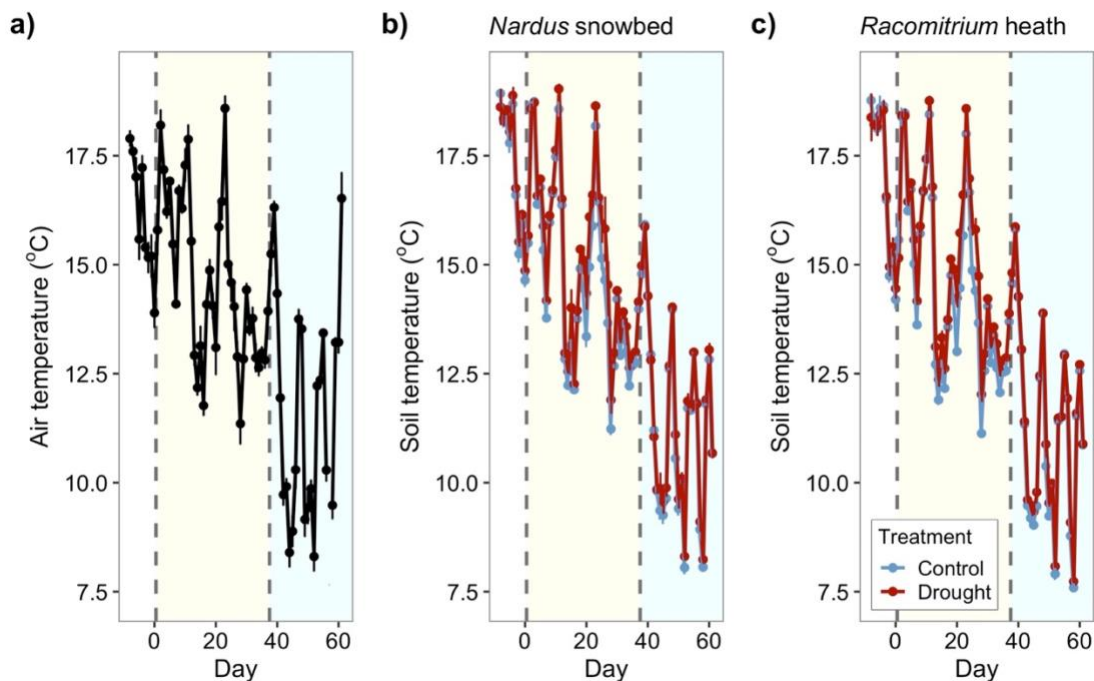
Figure 3.2. (a) Daily mean air temperature, and (b, c) mean daily mean soil temperature (~ 5 cm depth) in (a) *Nardus* snowbed and (b) *Racomitrium* heath mesocosms. Data show control (blue) and drought (red) mesocosms, during baseline (white background), drought (yellow background) and recovery (blue background) phases of the experiment. Data points show daily mean ± s.e (soil temperature n = 3).
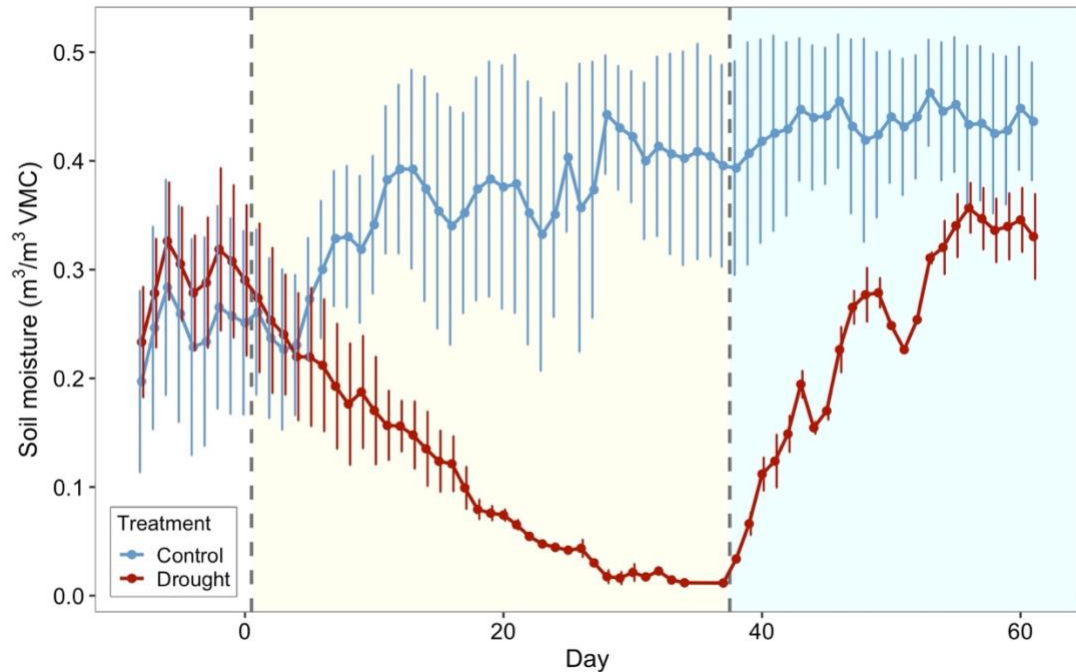
Figure 3.3. Soil moisture in *Nardus* snowbed mesocosms receiving control (blue) and drought (red) treatments. Background colours show experimental phases; baseline (white), drought (yellow) and recovery (blue) phases. Data points are daily mean ± s.e.

Soil C and N contents (%) were greater in *Nardus* snowbed than in *Racomitrium* heath (C content: $F_{1,29}$ = 127.23, p < 0.001; N: $F_{1,30}$ = 142.35, p < 0.001; Figure 3.4). Soil C:N ratio did not differ between *Nardus* snowbed and *Racomitrium* heath or between droughted and control mesocosms within ecosystems ($F_{1,29}$ = 0.00, p = 0.997). Soil depth was greater in *Nardus* snowbed than in *Racomitrium* heath ($F_{1,31}$ = 6.64, p = 0.015). Soil C and N pools were also greater in *Nardus* snowbed than in *Racomitrium* heath (C pool: $F_{1,29}$ = 7.93, p = 0.009; N pool: $F_{1,30}$ = 7.13, p = 0.012).
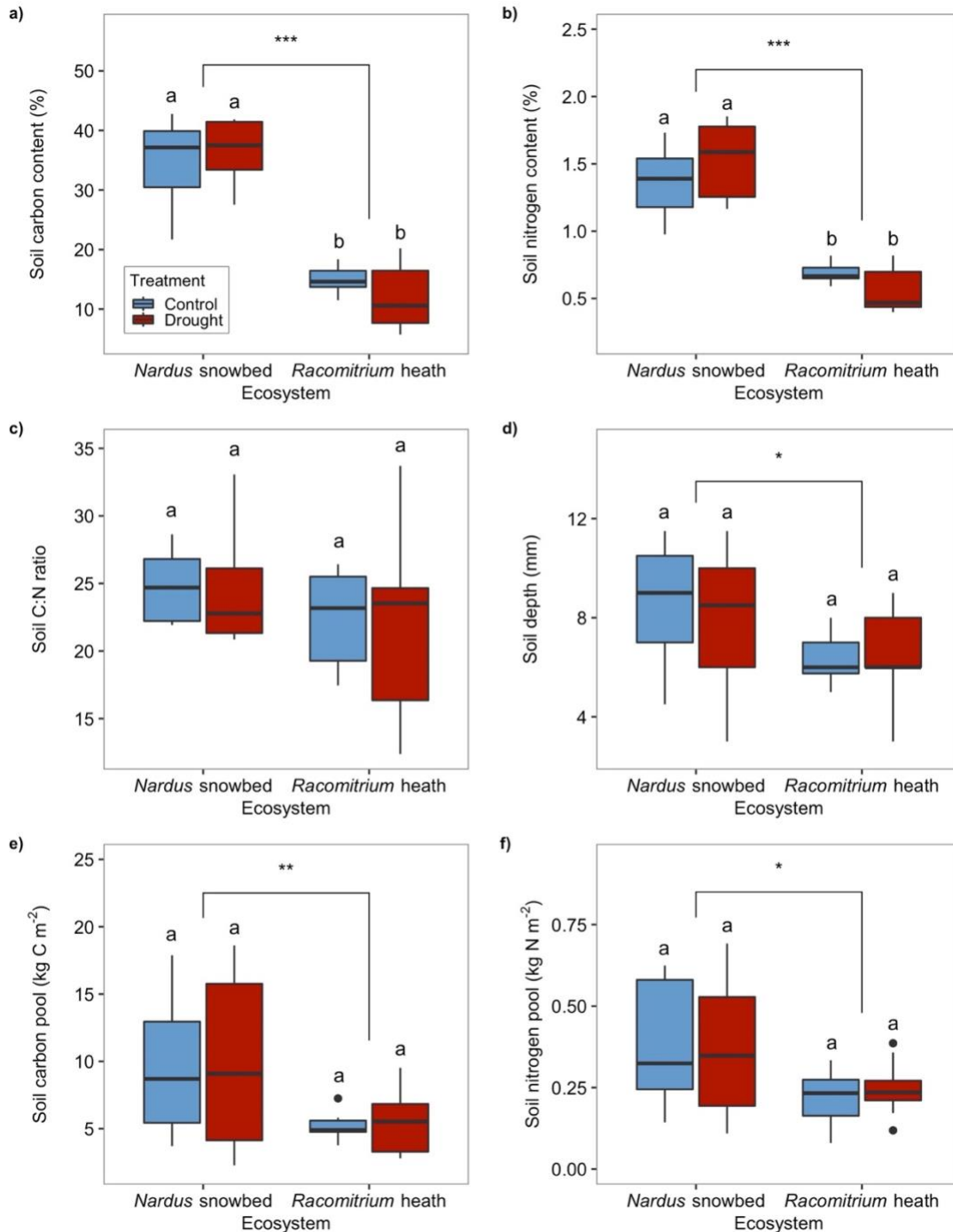
Figure 3.4. (a) Soil carbon content, (b) soil nitrogen content, (c) soil C:N ratio, (d) soil depth, (e) soil carbon pool, and (f) soil nitrogen pool for control (blue) and droughted (red) *Nardus* snowbed and *Racomitrium* heath mesocosms. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5(IQR)$ or greater than $Q_3 + 1.5(IQR)$. Letters on top of boxplots indicate statistical difference. Asterisks indicate significant difference between ecosystems at $p < 0.05$ when ecosystem:treatment interaction term is not considered; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Differences in MBC and microbial biomass C:N ratio between *Nardus* snowbed and *Racomitrium* heath largely followed that of soil C and C:N. Microbial biomass C:N ratios did not differ between *Nardus* snowbed and *Racomitrium* heath ($F_{1,51} = 3.57$, $p = 0.065$; data not shown), or between droughted and control mesocosms within ecosystems at initial field conditions or mesocosm harvest (field: $F_{1,21} = 0.02$, $p = 0.898$; harvest: $F_{1,24} = 1.53$, $p = 0.229$). Microbial biomass carbon was greater in *Nardus* snowbed than *Racomitrium* heath ($F_{1,58} = 32.45$, $p < 0.001$). At experiment harvest, MBC was unaffected by treatment and did not change relative to baseline field samples in both ecosystems (*Nardus* snowbed: $F_{1,26} = 0.04$, $p = 0.852$; *Racomitrium* heath: $F_{1,26} = 2.65$, $p = 0.116$; Figure 3.5).
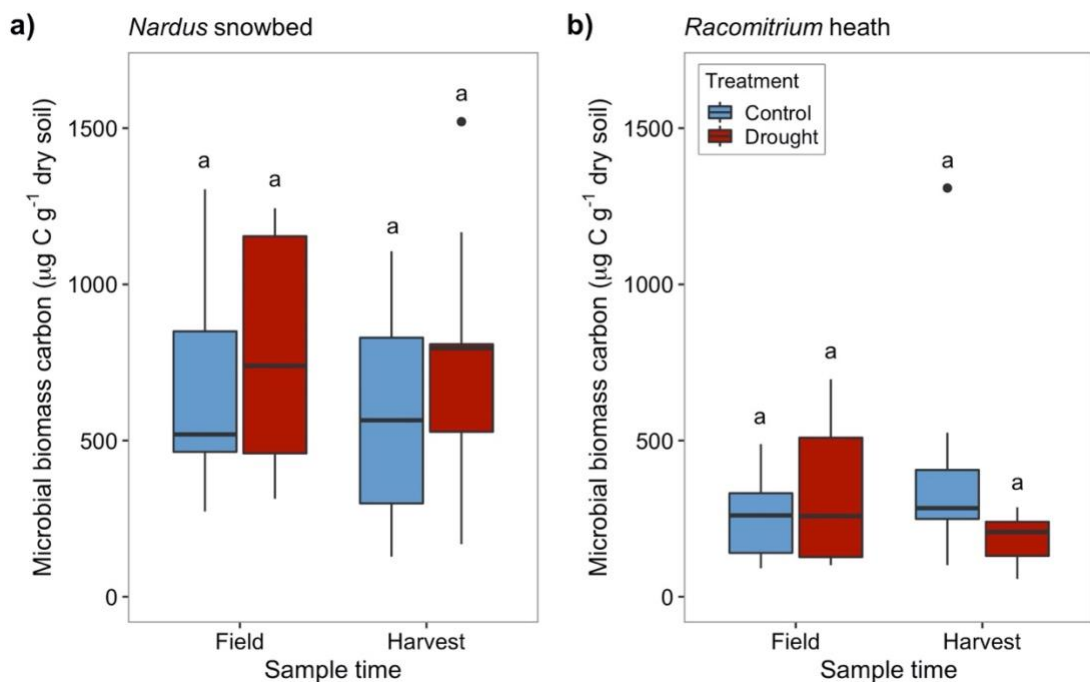
Figure 3.5. Soil microbial biomass carbon in (a) *Nardus* snowbed and (b) *Racomitrium* heath for control (blue) and droughted (red) mesocosms at field conditions and experiment harvest. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5(IQR)$ or greater than $Q_3 + 1.5(IQR)$. Letters on top of boxplots indicate statistical difference.

Vegetation community composition (species percent cover) differed between ecosystems but not between drought and control treatments (ecosystem: $F_{1,33} = 40.80$, $p <$

0.001; treatment: $F_{1,33} = 0.38$, p = 0.752; Figure 3.6). Combined, the first two ordination axes explain 80% of the community composition. Tighter clustering of *Racomitrium* heath relative to *Nardus* snowbed mesocosms indicated there was greater heterogeneity in *Nardus* snowbed plant community composition than that of *Racomitrium* heath. Aboveground biomass differed between ecosystems, with greater plant biomass from *Racomitrium* heath than *Nardus* snowbed ($F_{1,32} = 28.83$, p < 0.001; Figure 3.7a). *Racomitrium* heath was dominated by PFG 'other bryophytes', while *Nardus* snowbed was dominated by graminoids, forbs and 'other bryophytes' (*Nardus* snowbed: $X^2 = 40.48$, p <0.001; *Racomitrium* heath: $X2 = 89.84$, p < 0.001; Figure 3.7b; Table 3.1). Total aboveground plant biomass was unaffected by drought treatment ($F_{1,32} = 0.73$, p = 0.399). Vegetation community composition based PFG aboveground biomass did not differ between treatments within *Nardus* snowbed or *Racomitrium* heath ecosystems either (Table 3.1).
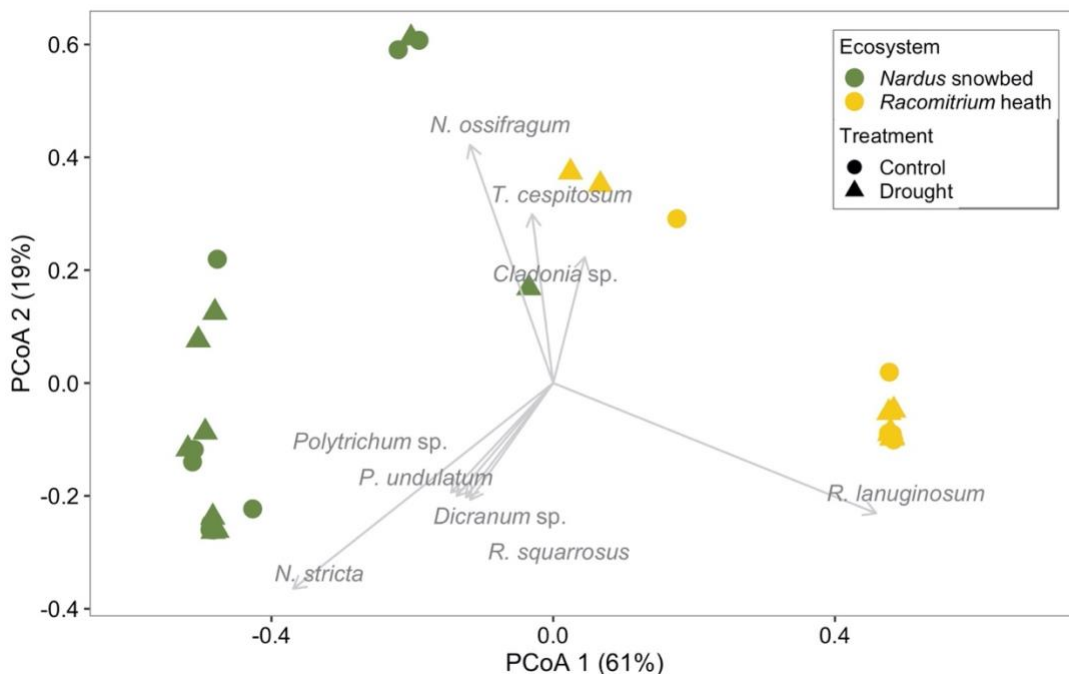
Figure 3.6. Principal coordinate analysis of vegetation community composition based on species percent cover of mesocosms collected from the Allt a'Mharcaidh catchment in the Cairngorm Mountains, Scottish Highlands. Colours represent *Nardus* snowbed and *Racomitrium* heath ecosystems and shapes represent drought and control treatments. Arrows represent species significantly influencing the ordination (p < 0.05).

Table 3.1. Biomass sorted to plant functional group (PFG) from *Nardus* snowbed and *Racomitrium* heath mesocosms. Data shown are mean ± s.e. (n = 18), PFGs within ecosystems which do not share a letter are significantly different at p < 0.05, * indicate significant difference between control and drought treatments.

Ecosystem	Plant functional group	Proportion of sorted biomass (%)		X^2	p
		Control	Drought		
Nardus snowbed	Shrubs	3.74 ± 1.78 b	4.04 ± 2.37 b	0.06	0.802
	Graminoids	38.54 ± 8.05 a	31.08 ± 6.15 a	1.03	0.310
	Forbs	16.36 ± 5.56 ab	26.02 ± 9.43 ab	0.48	0.488
	Pteridophytes	9.45 ± 7.08 b	2.30 ± 2.30 b	0.56	0.455
	Sphagnum mosses	16.04 ± 8.65 ab	16.36 ± 11.16 ab	0.08	0.780
	Other bryophytes	15.62 ± 9.02 ab	19.66 ± 8.80 ab	1.16	0.281
	Lichens	0.25 ± 0.21 b	0.54 ± 0.52 b	0.00	1.000
	X^2	18.19	24.45		
	p	0.006	<0.001		
Racomitrium heath	Shrubs	6.00 ± 5.52 a	0.08 ± 0.08 ab	2.28	0.131
	Graminoids	0.25 ± 0.12 a	0.38 ± 0.37 ab	0.43	0.514
	Other bryophytes	85.30 ± 8.24 b	89.37 ± 8.54 c	0.86	0.353
	Lichens	8.45 ± 6.52 ab	10.17 ± 8.18 bc	0.02	0.894
	X^2	43.37	47.49		
	p	<0.001	<0.001		
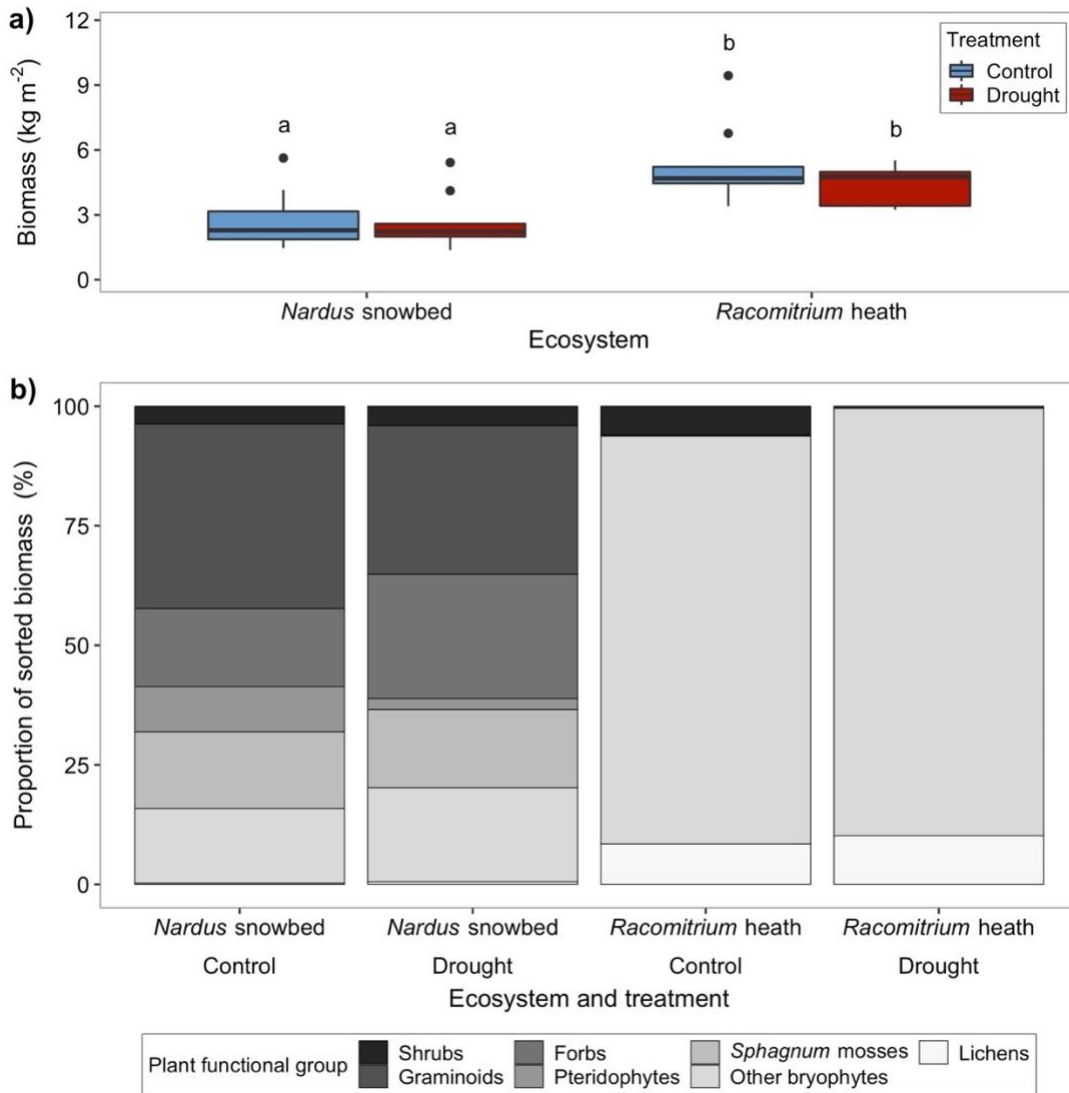
Figure 3.7. (a) Aboveground vegetation biomass (kg m^{-2}) at the end of the experiment for control (blue) and droughted (red) *Nardus* snowbed and *Racomitrium* heath mesocosms. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q$_1$) and 75th (Q$_3$) quartiles, respectively. Difference between Q$_1$ and Q$_3$ is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than Q$_1$ − 1.5(IQR) or greater than Q$_3$ + 1.5(IQR). Letters on top of boxplots indicate statistical difference. (b) Proportion of biomass sorted to plant functional groups. Data are plotted as mean values.

Ecosystem respiration was greater in *Nardus* snowbed than in *Racomitrium* heath and was suppressed by drought in both ecosystems (Figure 3.8; Table 3.2a). Following rewetting on day 38, there was a pulse in ecosystem respiration in *Nardus* snowbeds on day 40 with rates of ecosystem respiration in the droughted treatment greater than in the control treatment, but this was not seen in *Racomitrium* heath (*Nardus* snowbed: F$_{1,10}$ = 5.63, p = 0.039; *Racomitrium* heath: F$_{1,13}$ = 1.24, p = 0.286). Day number and time of day

measurements were taken were important factors driving rates of ecosystem respiration. Rates of respiration were greater in the afternoon, and at the start of the experiment and fluctuated with day as the experiment progressed. Ecosystem respiration was partly explained by air temperature with increased respiration rates under warmer temperatures, although adding this parameter did not improve the overall model (Table 3.2b). Vegetation community composition was an important factor, as substituting ecosystem for PCoA axis 1 resulted in a comparable model where lower PCoA axis 1 values corresponded to greater rates of respiration (Table 3.2c).
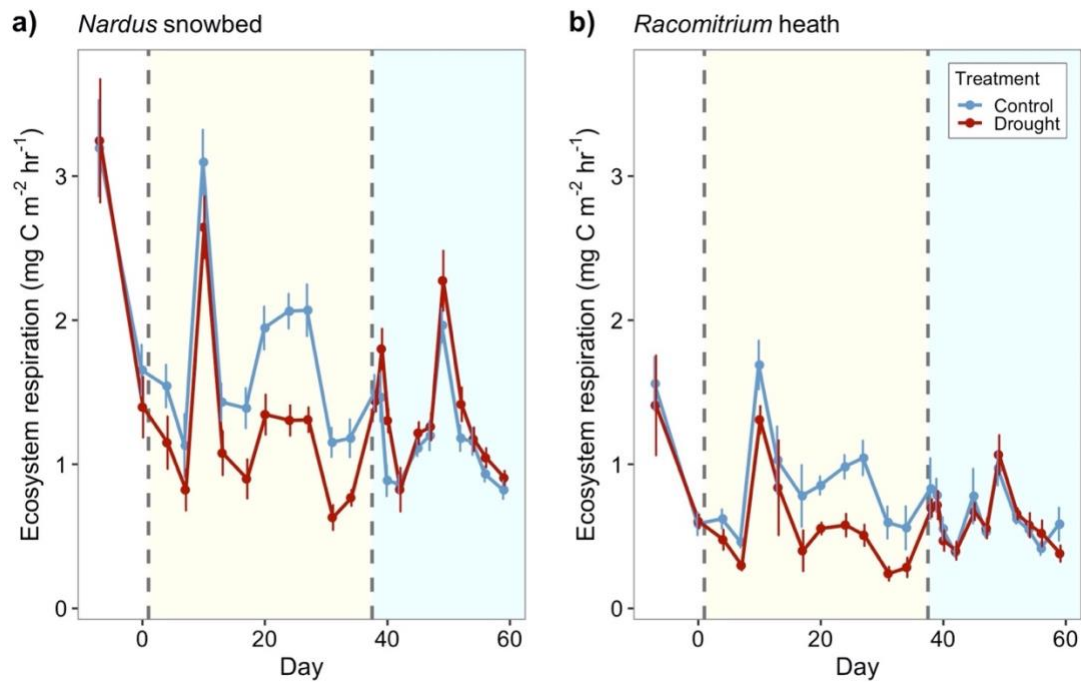
Figure 3.8. Ecosystem respiration in (a) *Nardus* snowbed and (b) *Racomitrium* heath mesocosms. Data show control (blue) and drought (red) mesocosms, during baseline (white background), drought (yellow background) and recovery (blue background) phases of the experiment. Data points show mean ± s.e.

Table 3.2. Summary of models including ecosystem, treatment, and measures of plant community composition, soil characteristics, and environment to explain rates of ecosystem respiration (ER) and response ratio (RR) over the course of baseline, drought and recovery phases in the experiment, and resistance (RS) during drought phase only, and resilience (RL) during recovery phase only in *Nardus* snowbed and *Racomitrium* heath mesocosms. For each parameter included, direction of change (d), effect size statistic (t, F), and p value are shown. Ecosystems are abbreviated to NS (*Nardus* snowbed) and RH (*Racomitrium* heath), treatments are abbreviated to C (control), and D (drought), ↑ represent an increase in model parameter increased rates of gas fluxes, while ↓ represent an increase in model parameter decreased rates of gas fluxes, and dashes indicate no change. Variables marked with * are represented with non-linear terms (spline) and direction of response are not reported. Bold values represent significant model parameters at p < 0.05.

	Response	Model parameters	Direction	Statistic		p	Model AIC
a)	ER	Ecosystem	**SB > RH**	t =	6.91	**< 0.001**	-227.71
		Drought	**D < C**	t =	-3.16	**0.002**	
		Day *		F =	23.90	**< 0.001**	
		Time *		F =	5.81	**< 0.001**	
b)	ER	Ecosystem	**SB > RH**	t =	6.48	**< 0.001**	-221.28
		Drought	**D < C**	t =	-2.84	**0.005**	
		Air temperature	↑	t =	7.93	**< 0.001**	
		Day *		F =	24.93	**< 0.001**	
		Time *		F =	8.60	**< 0.001**	
c)	ER	Drought	**D < C**	t =	-2.99	**0.003**	-221.94
		Air temperature	↑	t =	7.92	**< 0.001**	
		PCoA axis 1	↓	t =	-7.45	**< 0.001**	
		Day *		F =	24.99	**< 0.001**	
		Time *		F =	8.70	**< 0.001**	
d)	RR	Ecosystem	---	t =	0.11	0.916	-119.86
		Day *		F =	14.71	**< 0.001**	
e)	RS	Ecosystem	---	t =	-1.67	0.097	-142.67
		Day *		F =	1.38	0.390	
f)	RL	Ecosystem	---	t =	0.73	0.467	-85.21
		Day *		F =	1.57	0.130	

The response ratio controls intrinsic differences between ecosystems and shows the relative magnitude of change in response to the drought treatments for each ecosystem. Both ecosystems were equally sensitive to drought as response ratios did not differ between *Nardus* snowbed and *Racomitrium* heath (Table 3.2d; Figure 3.9). Response ratio values of < 1 during drought reflect the decline in ecosystem respiration rates. Response ratios returned to close to 1 during the 22-day recovery phase.
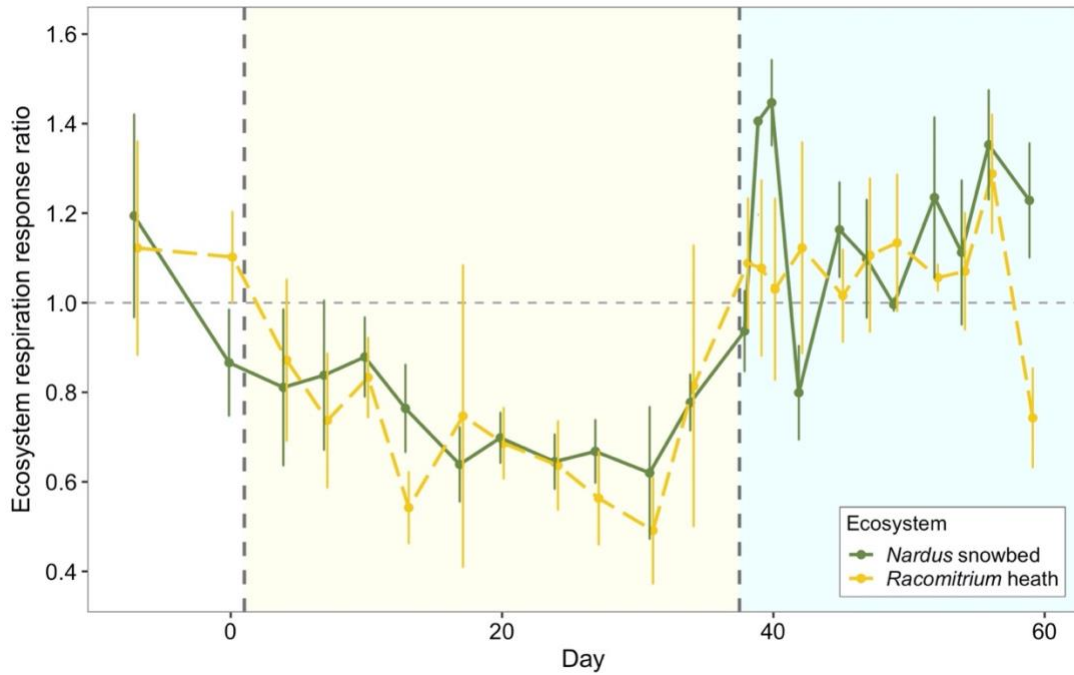
Figure 3.9. Ecosystem respiration in droughted *Nardus* snowbed (green) and *Racomitrium* heath (yellow) mesocosms presented as response ratio during baseline phase (white background), drought (yellow background) and recovery (blue background). Response ratio values of 1 indicate treatment equals control, > 1 indicates treatment is greater than control and < 1 indicates treatment is less than control. Data are plotted as mean ± s.e.

Resistance and resilience indices also show the relative magnitude of change. The sensitivity of both of these oceanic-alpine ecosystems to drought was indicated by the resistance index, with supressed ecosystem respiration in drought versus control reflected in a resistance index of around 0.5 with no difference between ecosystems (Table 3.2e; Figure 3.10). Over the course of the recovery phase, the resilience index did not return to a value close to 1, despite rates of ecosystem respiration in previously droughted mesocosms returning to control levels. The resilience index increased to -0.01 ± 0.09 and 0.19 ± 0.06 (mean ± s.e.) for *Nardus* snowbed and *Racomitrium* heath, respectively, across the 22-day recovery phase, and did not significantly differ between ecosystems (Table 3.2f).
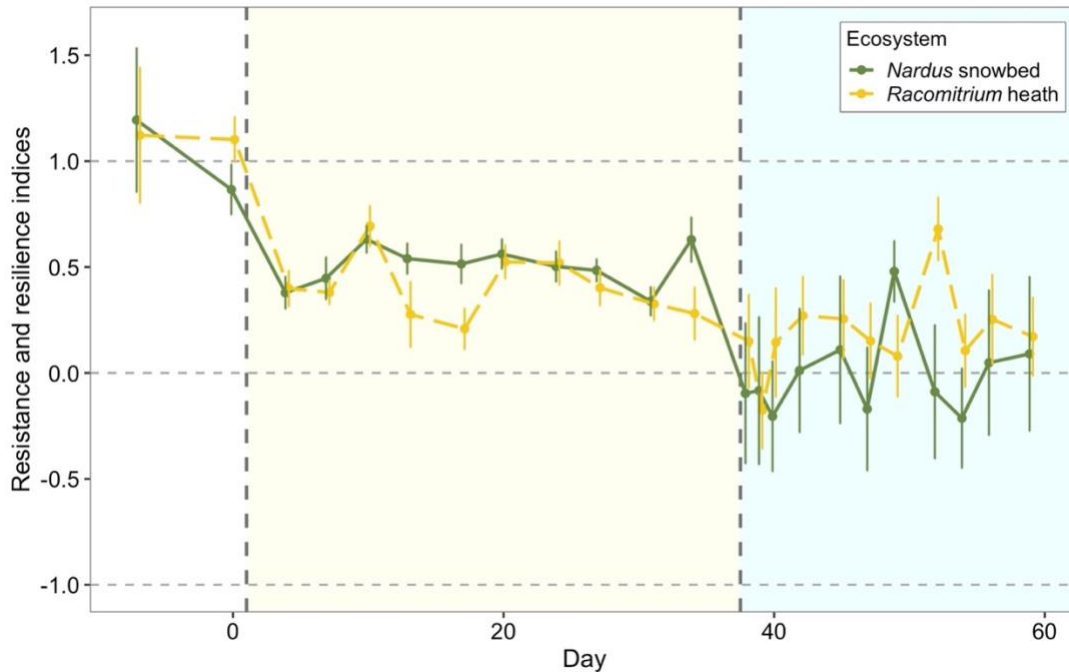
Figure 3.10. Ecosystem respiration in droughted *Nardus* snowbed (green) and *Racomitrium* heath (yellow) mesocosms presented as response ratio during baseline phase (white background), resistance index during drought (yellow background) and resilience index during recovery (blue background). Response ratio values of 1 indicate treatment equals control, > 1 indicates treatment is greater than control and < 1 indicates treatment is less than control. Resistance and resilience indices equal to 1 represent maximal resistance and resilience. Data are plotted as mean ± s.e.

3.5 Discussion

Ecosystem respiration rates were greater in *Nardus* snowbeds than in *Racomitrium* heath, as was hypothesised. Greater ecosystem respiration rates were likely due to the greater abundance of vascular plants, as indicated by the relationship between PCoA axis 1 and rates of ecosystem respiration (Table 3.2c). Positive PCoA axis 1 values were associated with greater abundance of *Racomitrium lanuginosum*, which was reflected with the dominant PFG 'other bryophytes' in *Racomitrium* heath mesocosms. While negative values for PCoA axis 1 were associated with greater abundance of vascular plants, particularly the graminoid *Nardus stricta* and forb *Narthecium ossifragum*, in *Nardus* snowbeds. Vascular plants have greater autotrophic respiration rates than mosses (Ward et al. 2013, Gavazov et al. 2018) and may also enhance microbial respiration through rhizodeposition of recent

photo-assimilate whereas bryophytes lack roots and do not pass carbon to the soil by this route (Johnson et al. 2002, Leake et al. 2006, Walker et al. 2016).

Although soil C pool did not explain differences in respiration rates between ecosystems or individual mesocosms, the difference in the quality of plant detrital inputs to organic *Nardus* snowbed and organo-mineral *Racomitrium* heath soils may contribute to the differences in ecosystem respiration rates between these systems. The effect of vegetation C quality on soil respiration has been shown previously, whereby soils incubated with graminoid litter had greater rates of decomposition and soil respiration than those incubated with moss litter. This has been suggested as a mechanism potentially contributing to the large soil C stores sometimes found in moss dominated systems (Hobbie 1996), but in this experiment there was greater soil C pool in *Nardus* snowbed than in *Racomitrium* heath.

Microbial biomass was not used to explain rates of ecosystem respiration in this experiment as MBC was only sampled at initial field conditions and experimental harvest. Post-harvest MBC suggested that the soil microbial community biomass was unaffected by the drought-rewetting event in either ecosystem. In other studies, microbial community composition and activity has been shown to be affected by drought and in turn to alter respiration rates. In graminoid and forb dominated systems, drought can lead to changes in bacterial and fungal community composition due to changes in plant community composition (de Vries et al. 2018); across a land-use gradient microbial community composition strongly predicted soil respiration rates during a dry-rewet event (Orwin et al. 2016). However, less is known about microbial communities associated with bryophytes (Osono et al. 2012) or the response of bryophytes to dry-rewet events (Slate et al. 2019).

Similarly, soil moisture was not used to explain rates of ecosystem respiration as soil moisture was only determined in both ecosystems at initial field conditions and experimental harvest. Had soil moisture loggers been successfully installed, intrinsic

differences in soil moisture regimes between *Nardus* snowbed and *Racomitrium* heath soils may have helped explain different rates of ecosystem respiration.

Drought supressed ecosystem respiration in both *Nardus* snowbed and *Racomitrium* heath ecosystems. It was hypothesised that ecosystem respiration in *Nardus* snowbeds would initially increase as the soil dried, as has previously been observed when very wet organic soils dry (Strack et al. 2006) and then decrease as the soil moisture declined further. However, in this study, we did not observe any initial increase in ecosystem respiration. It is possible that we may have missed an initial increase in ecosystem respiration in the *Nardus* snowbeds if this occurred within the first 4 days, between measurements. More frequent measurements at the start of the drought period would be required to determine if this was the case. The observed decline in ecosystem respiration and resistance index values of < 1 show that these oceanic-alpine ecosystems are sensitive to drought, as would be expected (Orwin and Wardle 2004, Johnson et al. 2011, Wu et al. 2011, von Buttlar et al. 2018). However, contrary to our initial hypothesis, we found no evidence to suggest that *Nardus* snowbeds and *Racomitrium* heath differed in their resistance to drought.

Ecosystem respiration increased following rewetting in both ecosystems, exceeding control levels in *Nardus* snowbed mesocosms as was hypothesised, but not in *Racomitrium* heath mesocosms. Drought limits microbial activity leading to increased availability of SOM, while rapid rewetting likely leads to microbial cell lysis and increased availability of microbial cytoplasmic solutes, both of which are rapidly mineralised upon rewetting (Birch 1958, Fierer and Schimel 2002, 2003). The increase in respiration is a rapid response known as the 'Birch effect' (Birch 1958). However, the increased rate of ecosystem respiration in this experiment was observed on day 40 only, the third day after rewetting, rather than upon rewetting on day 38 and therefore is likely not the Birch effect. The ecosystem respiration pulse, observed in *Nardus* snowbeds but absent in *Racomitrium* heath, may have been due to the higher abundance of vascular plants in *Nardus* snowbeds and the

dominance of non-vascular plants in *Racomitrium* heath. In vascular plants, under drought, recently plant-assimilated C is preferentially allocated to root stores in osmolyte pools (Hasibeder et al. 2015) and the quality of root exudates may change (de Vries et al. 2019). Thus, upon rewetting in *Nardus* snowbeds, root exudates may stimulate microbial activity and enhance rates of respiration in previously droughted compared to control mesocosms. This response of changed root exudate quality and increased rates of ecosystem respiration in response to drought and rewetting has previously been observed with graminoid and forb temperate grassland species (de Vries et al. 2019).

Contrary to our initial hypothesis, over the full 22-day recovery phase, *Nardus* snowbeds and *Racomitrium* heath did not differ in their resilience to a drought-rewetting event, whether considering the response ratio or the resilience index. Rates of ecosystem respiration in both ecosystem types returned to control levels during the recovery phase. This is reflected in the response ratio, however not in the resilience index. Both response ratio and resilience index are abstractions of ecosystem respiration. However, as ecosystem respiration data were highly variable and day explained a large portion of this variation (Table 3.2), the metrics perform differently. High variability in the initial data subsequently impacts the performance of the resilience index, but as the response ratio is based on ecosystem respiration measurements recorded on the same day, the variability in the data had less of an impact. Variability in environmental conditions likely contributed to variability in ecosystem respiration data. The initial drop in ecosystem respiration during the baseline phase was likely due to the change in soil temperature from 18.31 $\pm$ 0.02°C (mean $\pm$ s.e. across all ecosystems and treatments) on day -7 (3 August 2018), to 14.54 $\pm$ 0.06°C on day 0 (10 August 2018). Air temperature was a driver in rates of ecosystem respiration and the overall decline in air temperature over the course of the experiment probably limited rates of ecosystem respiration as the experiment progressed. In *Nardus* snowbeds, the senescence of vascular plants may have also contributed to the overall

decline in ecosystem respiration rates over the course of the experiment. Working in more controlled conditions would help reduce variability in environmental conditions and thus variability in ecosystem respiration rates when replicates are measured over a period of time.

It is important to disentangle the plant-microbial-soil components of ecosystem respiration, particularly after rewetting, as the origin of heterotrophic respiration has potential implications for soil C pools. Microbial mineralisation of recent plant-assimilated C (Karlowsky et al. 2018) or microbial biomass (Fierer et al. 2003) would lead to fast C cycling and may reduce long-term soil C loss. However, if microbes are mineralising older soil organic C (SOC) then this may result in large losses of, currently stable, long-term soil C pools (Schimel 2018). Root distributions contribute to the supply of SOC at depth (Jobbágy and Jackson 2000), therefore graminoids may increase the distribution of recent plant C inputs along the soil profile in *Nardus* snowbeds as compared with moss dominated *Racomitrium* heath. The addition of recent plant C can also cause a priming effect, potentially leading to the decomposition of older soil C (Fontaine et al. 2007). Furthermore, the release of C as CO_2 following the lifting of drought may be dependent on the nature and intensity of rewetting (Schimel 2018). Greater rates of CO_2 release have been observed from soils rewetted from above (simulated precipitation) than below (simulated groundwater rise; Smith et al. 2017). As it is predicted that there will be longer dry periods interspersed with heavy rain events (Collins et al. 2013), it is important to understand the effects that various drought durations and intensities of rewetting might have on C losses from the soil following drought. The pulse in ecosystem respiration which we observed in *Nardus* snowbeds in our study suggests losses of C may occur when rewetting these C-rich soils. Quantifying the effect of drought and rewetting on C uptake as well as additional effluxes in soil water would provide a more holistic understanding of C dynamics in oceanic-alpine ecosystems and the resilience of their C stocks to global change.

3.6 Conclusion

Nardus snowbeds and *Racomitrium* heath are intrinsically different and contrasting ecosystems in terms of their vegetation community and soil characteristics, and the microclimates these ecosystems experience. Although characterisation of soil conditions was not successfully measured as part of this study, soil moisture may help explain different rates of ecosystem respiration between these contrasting ecosystems. Their dominant PFGs have different traits in the C cycle in not only productivity and respiration, but also the quantity and quality of plant inputs to soil. Differences in vegetation community composition resulted in greater rates of ecosystem respiration in *Nardus* snowbeds than *Racomitrium* heath. Nonetheless these oceanic-alpine ecosystems did not differ in their resistance or resilience to this drought and rewetting event.

Potential changes in alpine plant community composition could alter their net C balance. Across Europe, plant community composition in mountain ecosystems has changed, with increases in species richness and presence of warm-adapted species as range limits shift (Gottfried et al. 2012, Steinbauer et al. 2018). Expansion of generalist vascular plant species into snowbeds has been observed in the Alps (Matteodo et al. 2016, Liberati et al. 2019), Scandinavia (Sandvik and Odland 2014), the Western Carpathians (Palaj and Kollár 2019), and Scotland (Britton et al. 2009). Increasing abundance of vascular plants in *Nardus* snowbeds may lead to greater rates of ecosystem respiration. Ecosystem respiration in *Nardus* snowbeds significantly increased in the short-term following rewetting. Depending on the source of C mobilised during rewetting, and longer-term effects of vegetation community change, drought-rewetting events could potentially lead to losses of currently stable old soil C.

3.7 Acknowledgements

3.8 Funding

3.9 References

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4 Impacts of drought and storm events on carbon and nitrogen fluxes in contrasting oceanic-alpine ecosystems

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4.1 Abstract

Climate change is predicted to increase the frequency of drought and intensity of rainfall. Oceanic-alpine landscapes are potentially large stores of old soil carbon but warmer, drier summers with heavy rain events may alter biogeochemical cycling in these systems. We conducted a controlled factorial mesocosm experiment to determine the impact of drought and storm events, alone and combined, on carbon and nitrogen fluxes in *Nardus* snowbed and *Empetrum* heath, two widespread alpine habitats. Gas and leachate fluxes were measured over a 16-day drought period (+/-), followed by rewetting with a low or high intensity (storm) rainfall event, and a 14-day recovery period. Drought decreased rates of ecosystem respiration, particularly in *Empetrum* heath. Vegetation community composition and biomass drove net ecosystem exchange and gross photosynthesis rates, which were unaffected by treatments. Following rewetting there was

a pulse in ecosystem respiration rates, exceeding control levels in *Nardus* snowbed, but the nature of rewetting did not determine the size of the gas flux. Leachate fluxes were more responsive to drought and storm events; total losses of carbon and all forms of nitrogen were greater following a high intensity (storm) rewetting, while total losses of dissolved organic carbon, total dissolved nitrogen, and dissolved organic nitrogen were lower under drought, and nitrate losses increased under drought. The impact of the storm depended on antecedent conditions, with greatest nitrate losses when the storm was preceded by drought. Large losses of nitrate due to dry periods and heavy rain events could lead to acidification of soils and eutrophication of surface waters potentially impacting ecosystem functioning.

Keywords*:* carbon; drought; dry-rewetting; ecosystem respiration; *Empetrum* heath; gross photosynthesis; leachate; *Nardus* snowbed; net ecosystem exchange; nitrogen.

4.2 Introduction

Precipitation regimes are changing as a result of global change (IPCC 2013). In low elevation mountain systems there has been a decrease in snow pack and earlier snowmelt (Stewart 2009). While summer months have been warmer, drier periods have been interspersed with heavy rain events (Barnett et al. 2006). These drier summers and intense rainfall events are predicted to continue (Barnett et al. 2006, Met Office 2019). Lower precipitation combined with warming temperatures, increases evapotranspiration rates and results in soil drying (Sherwood and Fu 2014). Since water availability is a key driver in ecosystem functioning (Raich and Schlesinger 1992) these changes in moisture regimes have the potential to impact important ecosystem processes.

Alpine landscapes are topographically complex; topography and climate interact, contributing to development of a diverse range of ecosystems with contrasting snow cover regimes and microclimates. Variations in depth and duration of snow cover drive differences in soil temperature and moisture, availability of nutrients, and the length of the plant growing season across small spatial scales (Stanton et al. 1994, Zhang 2005, Björk and Molau 2007, Ford et al. 2013, Choler 2018). These differences in snow cover and microclimate promote development of heterogeneous plant communities varying in function and taxonomic composition (Carlson et al. 2015). Plants in arctic and northern alpine ecosystems can be assigned to plant functional groups (PFGs) based on their role in ecosystem processes, and response to changing environmental conditions (Chapin et al. 1996, Dormann and Woodin 2002, Dorrepaal 2007, Strimbeck et al. 2019). The dynamics of C and N cycling vary between PFGs with higher productivity and decomposition rates in graminoid and forb dominated communities than in the slower growing evergreen dwarf-shrub or bryophyte dominated communities (Hobbie 1996, Ward et al. 2009, Quin et al. 2015, Sørensen et al. 2018).

In heterogeneous alpine landscapes, differences in vegetation communities are associated with variations in ecosystem C pools, primarily driven by differences in the organic soil C pool (Sørensen et al. 2018). Seasonally snow-covered alpine systems can have large pools of soil C (Bradley et al. 2005, Jones et al. 2005, van der Wal et al. 2011), in particular oceanic-alpine snowbeds found in the Scottish Highlands are thought to be large stores of old soil carbon (Britton et al. 2011, Mills n.d.). Early melting *Nardus* snowbeds are graminoid dominated, highly productive during short growing seasons, have deep organic soils, and have relatively stable microclimates with wet soils during winter and summer (Britton et al. 2011). *Empetrum* heaths are dwarf-shrub and lichen dominated ecosystems with shallow organic soils and are found adjacent to *Nardus* snowbeds on more

exposed slopes. As such, we expect the plant and soil microbial communities in *Empetrum* heaths to be better adapted to fluctuating conditions.

Changing precipitation and snowmelt regimes are altering hydrology in many regions (IPCC 2014). Projected changes in climate may impact C cycling in alpine systems through effects of changed water and temperature regimes on microbial and plant activity. In alpine habitats drought has been shown to lead to reductions in gas fluxes, gross primary production and dissolved organic carbon (DOC) in leachate (Johnson et al. 2011, Zhang et al. 2019). Rewetting of dry soil has also been seen to lead to a pulse of respiration and nitrogen mineralisation (Birch 1958, Kim et al. 2012), although the rate and intensity of rewetting could be important factors in determining whether carbon is mobilised and available to be mineralised by microbes (Schimel 2018).

Low-elevation oceanic-alpine systems are particularly sensitive to climatic change (Pepin et al. 2015, Hock et al. 2019, IPCC 2019, Rivington et al. 2019). Warming in low-elevation mountain systems has led to a decrease in winter snowfall, a decrease in snowpack, and earlier snow melt (Stewart 2009), which could result in soil drying in ecosystems previously irrigated by snowpack melt water (IPCC 2019). Duration of snow cover in Scotland has decreased by more than 30% since the 1960s, and summer precipitation has decreased by more than 18% in some parts of Scotland between 1914 and 2004 (Barnett et al. 2006, Rivington et al. 2019). Moisture regimes are likely to vary widely between alpine habitats occupying different topographic locations however, with habitats in ridge top locations being more likely to experience soil drying than those in hollows irrigated by snow melt. As soils which rarely experience dry-rewetting events are expected to have a larger pulse of respiration than soils that regularly experience dry-rewet cycles (Fierer and Schimel 2002), habitats from different topographic locations may thus differ in their resilience to drought.

To explore the effects of drought stress and intensity of rewetting, on C and N fluxes in oceanic-alpine habitats, we conducted an incubation experiment with *Nardus* snowbed and *Empetrum* heath mesocosms. We compared the response of these two contrasting habitats to a prolonged drought followed by either a return to a standard watering regime or a simulated intense rainfall event followed by normal watering. We hypothesised:

1. Oceanic-alpine systems will be sensitive to drought. There will be supressed ecosystem respiration, net ecosystem exchange, gross photosynthesis, and flux of C and N in leachate under drought, followed by increased ecosystem respiration and leachate upon rewetting.

2. That rainfall intensity during rewetting would influence the magnitude of response. We predicted a greater increase in ecosystem respiration, photosynthesis, net ecosystem exchange, and leachate C and N fluxes from the extreme (drought followed by storm) than the mild (drought followed by control) rewetting event; while the storm alone would reduce ecosystem respiration but increase leachate C and N flux.

3. The response would be greater from *Nardus* snowbed than *Empetrum* heath communities; *Nardus* snowbeds will be more sensitive than *Empetrum* heath, as *Empetrum* heath occupies topographic locations where it is frequently exposed to dry-rewet cycles whereas *Nardus* snowbeds experience relatively constant soil moisture conditions.

4.3 Methods

4.3.1 Study sites and sampling

The study area was located in the Allt a'Mharcaidh catchment (3°50' W, 57°5' N), in the western Cairngorm mountains, Scottish Highlands. The climate in this region is cool oceanic; mean monthly air temperatures range from -2.0°C in February to 13.6°C in July (at 700 m elevation), and mean annual precipitation is ~1100 mm, with approximately 30% falling as snow during winter (Helliwell et al. 1998, Britton et al. 2011, Rennie et al. 2017). Mesocosms were collected from a *Nardus* snowbed and an *Empetrum* heath at ~ 880 m elevation on 30 April 2019. *Nardus* snowbed sampling areas were graminoid and forb dominated with peaty podzol/histic podzol soils (Britton et al. 2011), *Empetrum* heath sampling areas were shrub and lichen dominated with shallow podzol soils including an organic layer with high stone content. Six sets of four mesocosms (10 cm dimeter, 15 cm deep) were collected per ecosystem (24 cores in total per ecosystem type). Mesocosms were collected in PVC pipe sections; vegetation was cut with a knife around the outer edge of the PVC pipe, and then the pipe driven into the soil using a wooden block and hammer until vegetation was flush with the top of the core. Paired grab samples of soil to 15 cm depth were collected per set of four mesocosms to determine initial soil moisture content (%) and field microbial biomass. Mesocosms were removed and wrapped in clingfilm and transported to The James Hutton Institute, Aberdeen the following day.

4.3.2 Incubation

Mesocosms were moved into a controlled environment growth room on 1 May 2019, under diurnal cycles of 16 hours light, 8 hours dark, with the light phases including 2 hours of staggered increase and decrease in light intensity starting at 6am and 9pm. Air temperature was set to 7°C during the dark hours and at 11°C during light hours, relative

humidity was set to 90%, although fluctuated. Soil temperature at 2 cm depth was recorded at 2-hourly intervals in 8 mesocosms (one for each ecosystem type and treatment) using soil temperature loggers (iButton® DS1922L, Maxim Integrated, San Jose, CA, USA). Mean daily mean soil temperature ranged from 13.57 ± 0.13°C to 14.29 ± 0.10°C (mean ± s.e.) over the duration of the experiment. Contrasting soil moisture regimes between *Nardus* snowbed and *Empetrum* heath are an important component of ecosystem properties. Initial soil moisture was not standardised as drying *Nardus* snowbed soils or wetting *Empetrum* heath soils to equivalent water content across the ecosystems would impose an additional perturbation. Non-standardisation of soil moisture enabled drought treatment to be applied in the context of two systems with different hydrological regimes and enabled us to observe changes in these ecosystems with contrasting soil conditions more realistic of heterogenous alpine systems. PVC pipes containing the mesocosms were wrapped in foil, and the mesocosm bases were covered in 2 mm nylon mesh and mounted in funnels connected to bottles to collect leachate (Figure 4.1).

Mesocosms were separated into six replicate blocks. Each block contained one set of four *Nardus* snowbed and one set of four *Empetrum* heath mesocosms randomly arranged. One mesocosm per set of four was randomly allocated to each drought/rewetting treatment; these were control x control, control x storm, drought x control, drought x storm. Incubation consisted of five phases: acclimation (1 – 14 May 2019), baseline (15 – 24 May 2019), drought (25 May – 9 June 2019), storm (10 June 2019), and recovery (11 – 24 June 2019). During the acclimation, baseline, and recovery phases all cores received 53 ml artificial rain Monday-Friday, equivalent to 7 mm each day. Although this amount is greater than the mean rainfall of 2.1 mm day^{-1} in May recorded over a 15 year period in the Allt a'Mharcaidh catchment (Rennie et al. 2017), it allows for the higher rates of evapotranspiration in growth rooms and sufficient leachate to be collected. During the drought phase water was withheld from the droughted cores for 16

days. This treatment was based on the duration of droughts previously recorded at the Allt a'Mharcaidh catchment; periods without rain of 14, 17, and 18 days were recorded May-June in 2001 and 2005 (Rennie et al. 2017). During the storm phase cores were re-wetted either with 7 mm of rain in a single dose (control) or with 300 ml, equivalent to 38 mm, applied in three 100 ml doses at 20-minute intervals (storm treatment). Rain chemistry was made using a recipe relevant to northwest Scotland containing $CaCl_2$ $2H_2O$ (7.5 µM l^{-1}), KH_2PO_4 (3.5 µM l^{-1}), Na_2SO_4 (17.5 µM l^{-1}), $MgCl$ $6H_2O$ (20 µM l^{-1}), KCl (4 µM l^{-1}), $NaCl$ (45 µM l^{-1}), NH_4NO_3 (20 µM l^{-1}) and adjusted to pH 4.8 (UK Review Group on Acid Rain 1997).
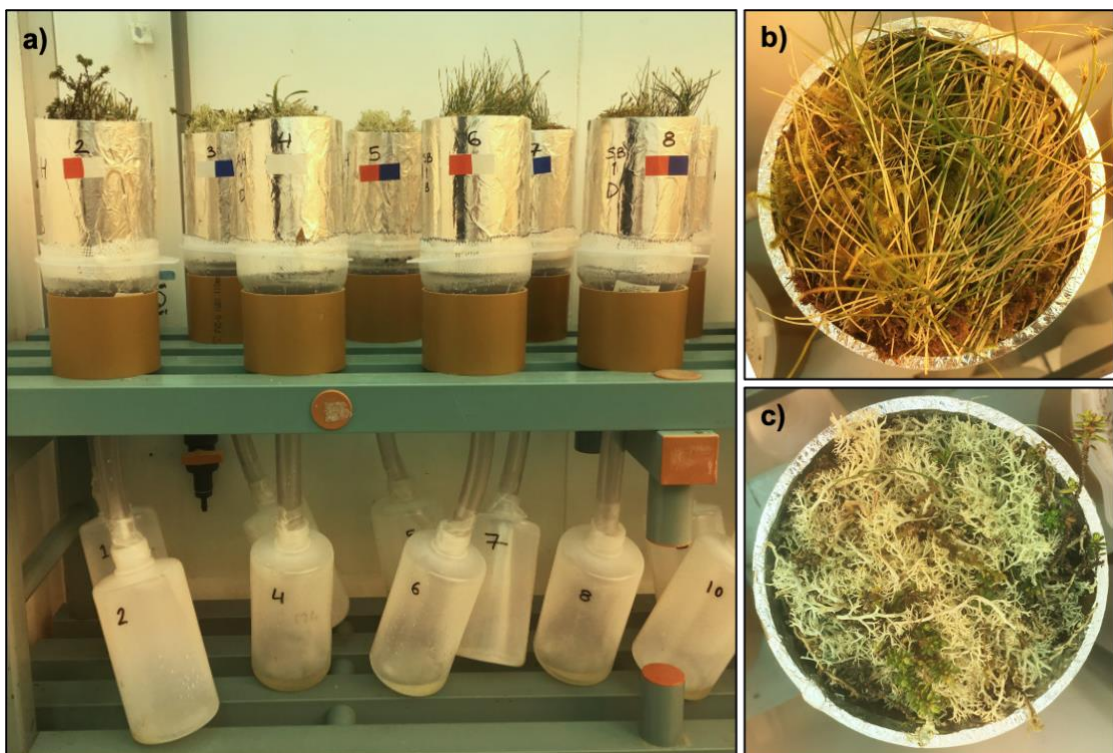
Figure 4.1. (a) Mesocosms mounted in funnels in a controlled environment room. Mesocosms included (b) *Nardus* snowbed and (c) *Empetrum* heath ecosystems.

4.3.3 Gas fluxes

Gas fluxes were measured three times per week (on Mondays, Wednesdays, and Fridays) during baseline and drought phases (17 May – 7 June 2019). Following rewetting, measurement frequency was increased to three times per day for three days (10 – 12 June 2019), decreased to once per day for two days (13 – 14 June 2019), and returned to three times a week for the remainder of the recovery phase (17 – 24 June 2019). Gas fluxes were measured using an EGM-4 infrared gas analyser (IRGA; PP Systems, Amesbury, USA), connected to a clear acrylic chamber over the mesocosms. The chamber had a battery-operated fan inside and two suba-seal gas sampling ports each with a gas line connected to the IRGA. Measurements were taken with and without a blackout cover over the chamber to determine ecosystem respiration and net ecosystem exchange (NEE), respectively. For both ecosystem respiration and NEE measurements, the infrared gas analyser was temporarily sealed to the cores for 60 s enclosure time including a 14 s equilibrium phase following a 14 second purge (Mills et al. 2011). CO_2 concentration (ppm) was used in a linear regression to calculate fluxes ($\mu g\ CO_2\ m^{-2}\ s^{-1}$). Gross photosynthesis rates were calculated as the difference between rates of ecosystem respiration and NEE. Mesocosms were watered by block so that fluxes were measured between 1 to 2 hours after 'rain' events; on days when multiple sets of gas fluxes were measured, mesocosms were watered 1-2 hours before the first set of fluxes.

4.3.4 Leachate fluxes

Leachate was collected prior to watering the mesocosms. Leachate from mesocosms was collected three times per week (on Mondays, Wednesdays, and Fridays) during the baseline phase (15 – 24 May 2019), once a week (on Mondays) during drought (25 May – 10 June 2019), once (on Tuesday) following rewetting (11 June 2019), and on

three further occasions (on Thursday and Mondays) during the recovery phase (12 – 24 June 2019). Leachate samples were stored at 4°C prior to analysis. To calculate nutrient fluxes, leachate volume (ml) was recorded, and the leachate filtered (0.45 µm cellulose acetate filter) to remove particulate matter and select for dissolved components. Concentrations (mg/l) of ammonium (NH_4^+) and nitrate (NO_3^-; Konelab Aqua 20 discrete analyser, Thermo Scientific, MA, USA), total dissolved N (TDN) and dissolved organic C (DOC; Shimadzu TOC-L (CPH/CPN), Kyoto, Japan) were determined. Dissolved organic N (DON) concentrations were calculated as the difference between TDN and dissolved inorganic N concentrations. Daily leachate fluxes were calculated over the course of the experiment, as well as total leachate flux to quantify total nutrient losses.

4.3.5 Relative change in mesocosm moisture content

Mesocosm mass was recorded each day Monday to Friday before the mesocosms were watered. At the end of the experiment the dry mass of the core tube, mesh, stones, soil and vegetation were calculated and used to derive mesocosm water content (mass), and hence percentage moisture content. Relative change in mesocosm moisture content (hereafter referred to as change in moisture content) was calculated in relation to starting moisture content of each core on 13 May 2019.

4.3.6 Vegetation and soil

Vegetation community composition of each mesocosm was measured by visual species cover estimates on 13 May 2019. Mesocosm harvest was undertaken on 25 June 2019, with mesocosms stored at 4°C prior to destructive sampling. Determination of the characteristics of both soil and vegetation followed the harvesting. Firstly, the fresh mass of intact mesocosms was recorded. As mesocosms were sampled with vegetation flush to

the top of the core, depths of bryophyte, lichen, and soil layers varied, therefore depth and fresh mass of vegetation and soil layers were also recorded. Excluding any litter layer, the aboveground vegetation was removed from the mesocosm by clipping at the soil surface and was dried at 60°C for a minimum of 48 hours. Dried biomass was then sorted to plant functional groups (PFGs) for 30 minutes and their mass recorded. After this time any biomass remaining was designated as 'unsorted'. The proportion of PFGs in the sorted biomass was calculated. PFGs were defined as: evergreen shrubs, deciduous shrubs, graminoids, forbs, pteridophytes, bryophytes, and lichens (Chapin et al. 1996, Dorrepaal 2007).

Light homogenisation of soil was achieved by hand including removal of large stones and roots for a standardised 10 minutes per sample. Soil moisture was determined from subsamples of 5.0 ± 0.5 g fresh soil, dried at 105°C for 24 hours. Soil C and N content (%) were measured by high temperature combustion gas chromatography (Vario El lll C/N analyser; Elementar, Stockport, UK) of freeze-dried, ground soil subsamples of 30 ± 1 mg. Soil C and N pools were calculated as:

$$C_{pool} = D \times Bd \times C_{conc}$$

$$N_{pool} = D \times Bd \times N_{conc}$$

where D is soil depth (cm), Bd is soil bulk density (g dry soil per cm^3), C_{conc} and N_{conc} are soil C and N content (%), and C_{pool} and N_{pool} are soil C and N pools (kg m^{-2}), respectively.

The microbial biomass of both C (MBC) and N (MBN) were determined by liquid fumigation-extraction of fresh organic soil samples adapted from Gregorich et al. (1990). Forty ml of 0.5 M K_2SO_4 was added to paired 5.0 ± 0.5 g lightly homogenised fresh soil subsamples, and 0.5 ml $CHCl_3$ was added to fumigated samples. Samples were shaken at 165 rpm for 2 hours, centrifuged at 3000 RPM for 10 minutes, filtered through Whatman 42® (GE Healthcare, Chicago, IL, USA) filter paper, sparged for 20 minutes to remove

chloroform, and stored at -20°C until analysis. Sample extracts were diluted with MilliQ water at a ratio of 1:8 extract:MilliQ water prior to analysis for total organic C and total N on a TOC-L combustion analyser coupled with a TNM-L unit (Shimadzu Corp, Kyoto, Japan). Microbial biomass C and N were calculated as the difference between C and N recovered from fumigated and non-fumigated samples and were expressed as dry-mass specific. Microbial biomass C and N were used to calculate microbial biomass C:N ratio.

4.3.7 Statistical analyses

All statistical analyses were conducted in R version 4.0.4. Generalised additive mixed models (GAMMs) with repeated measures were performed using *gamm4* (Wood and Scheipl 2020). Multivariate analyses were performed using *ape* (Paradis et al. 2019) . Results are reported as significant at $p < 0.05$.

The effects of ecosystem type on vegetation community were determined by permutational multivariate analysis of variance with 9,999 permutations (PerMANOVA; adonis function). Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity was used to represent and quantify plant communities (pcoa function). The scores from the first two axes were used for subsequent analysis.

Differences in soil characteristics (C and N content, C:N, depth, soil C and N pools), microbial biomass (C content, C:N), aboveground biomass, and total leachate fluxes between ecosystems and treatment were determined using ANOVAs with an interaction term. Kruskal-Wallis tests were used when residuals were not normally distributed and could not be normalised by transformation.

Mesocosm moisture content and relative change in mesocosm moisture were analysed with a GAMM with day of study as a non-linear random factor (spline, gamm4 function; Wood and Scheipl 2020). To determine if drought and storm treatments, and ecosystem type affected daily gas and leachate fluxes, repeated measures GAMMs were

used with treatments, ecosystem and their interaction as fixed effects, day of study (and time for gas fluxes only) as non-linear random effects (spline), unique mesocosm ID (for repeated measures) and block as random effects. Additional fixed effects included in the gas fluxes GAMMs were change in moisture, PCoA axes 1 and 2, total aboveground biomass, and soil C pool. Additional fixed effects included in the leachate fluxes GAMMs were change in moisture and either soil C or N pool depending on the nutrient flux in question. Fixed effects were dropped from the model when not significant, in order to reduce the number of parameters. Model fit was visually assessed using diagnostic plots. When model residuals did not satisfy assumptions of normality, data were log transformed.

4.4 Results

Mesocosm moisture content was greater in *Nardus* snowbed (65.89 ± 0.20% (mean ± s.e.)) than *Empetrum* heath mesocosms (47.41 ± 0.38% (mean ± s.e.); t = 8.63, p < 0.001; data not shown). Drought negatively impacted moisture content (t = 9.19, p <0.001; Figure 4.2), with a greater relative decline in *Nardus* snowbed than *Empetrum* heath (t = 3.29, p = 0.001). The effect of drought on moisture content continued into the recovery phase, with lower relative moisture content in previously droughted mesocosms compared with control (t = -4.29, p < 0.001) and a lower relative moisture content in *Nardus* snowbeds than *Empetrum* heath (t = -2.65, 0.008).

Vegetation community composition (species percent cover) differed between ecosystems, but not between treatments (ecosystem: $F_{1,43}$ = 44.64, p <0.001; treatment: $F_{3,43}$ = 0.64, p = 0.794; Figure 4.3). Total aboveground biomass was greater in *Nardus* snowbed than *Empetrum* heath ecosystems (*Nardus* snowbed: 6.61 ± 0.36 kg m^{-2}, *Empetrum* heath: 4.48 ± 0.32 kg m^{-2} (mean ± s.e.); $F_{1,38}$ = 20.27, p < 0.001; Figure 4.4a). *Nardus* snowbed communities were dominated by graminoids, bryophytes, and deciduous shrubs, while

Empetrum heath communities were dominated by lichens and evergreen shrubs (Figure 4.4b; Table 4.1).
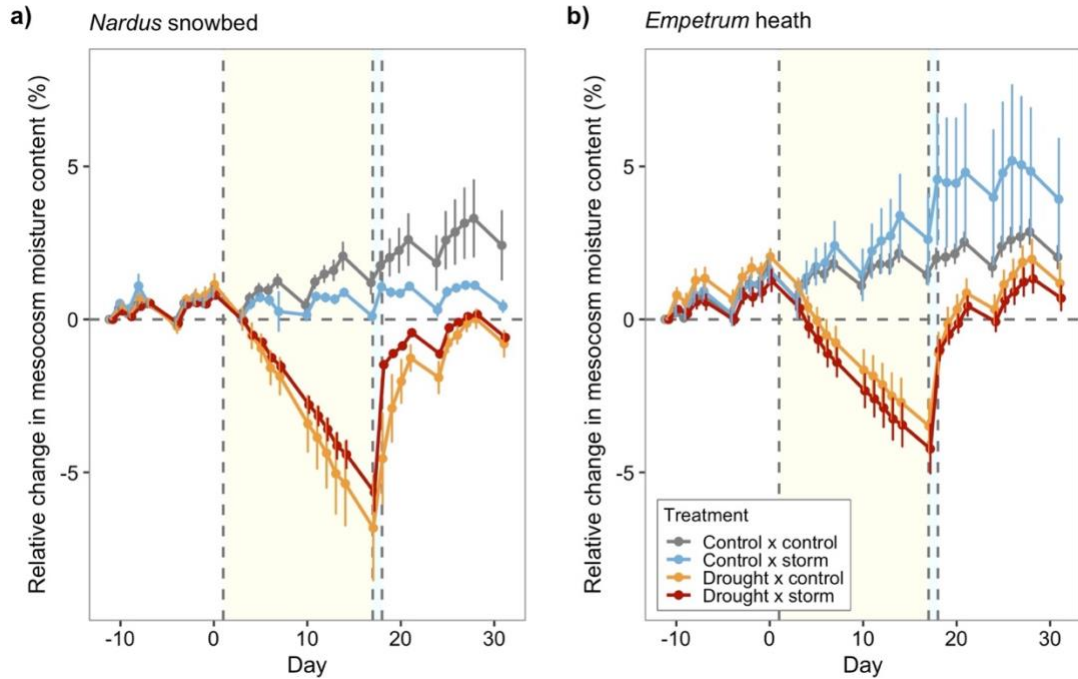
Figure 4.2. Mesocosm moisture content in (a) *Nardus* snowbed and (b) *Empetrum* heath mesocosms. Data show control x control (grey), control x storm (blue), drought x control (orange) and drought x storm (red) mesocosms, during baseline (white background), drought (yellow background), rewetting (blue background) and recovery (white background) phases of the experiment. Data points show mean ± s.e.
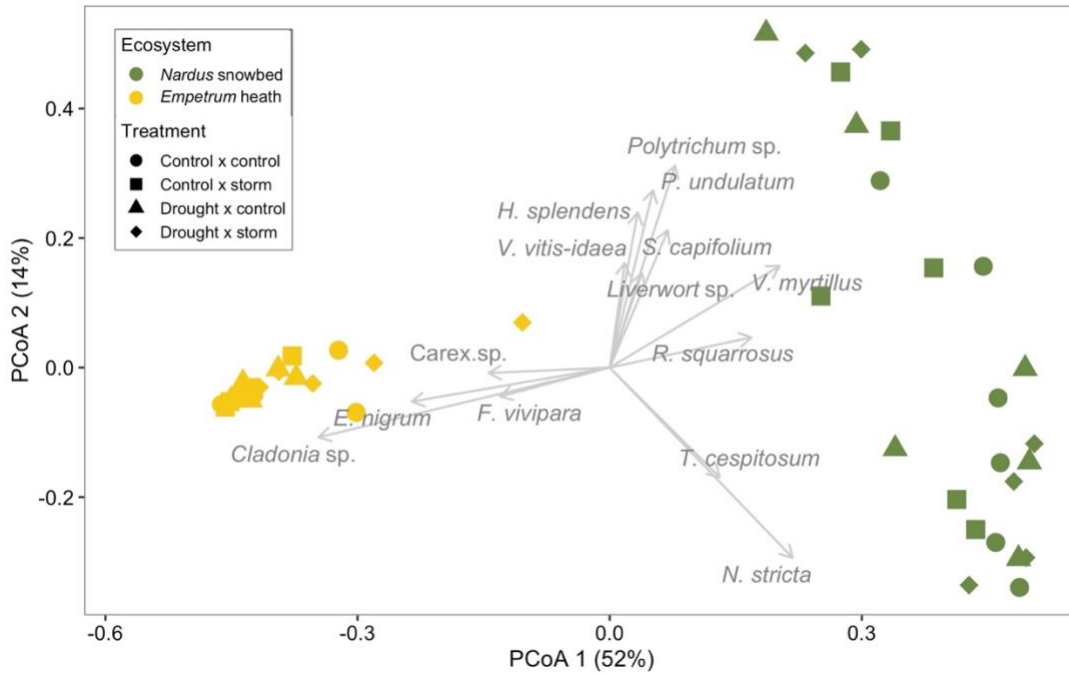
Figure 4.3. Principal coordinate analysis of vegetation community composition based on species percent cover of mesocosms. Colours represent *Nardus* snowbed and *Empetrum* heath ecosystems and shapes represent drought and control treatments. Arrows represent species significantly influencing the ordination ($p < 0.05$).
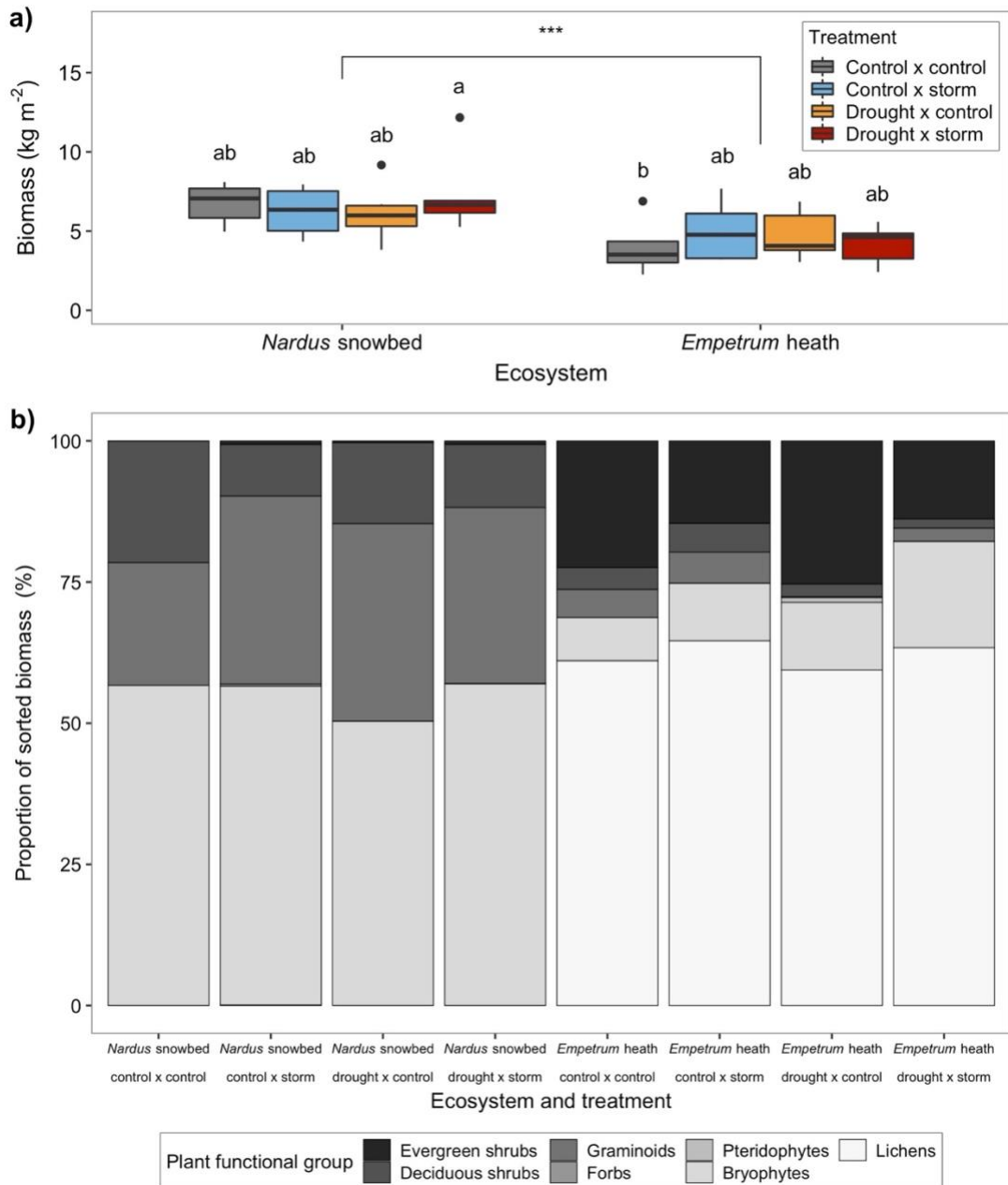
Figure 4.4. (a) Aboveground vegetation biomass (kg m^{-2}) at the end of the experiment for control x control (grey), control x storm (blue), drought x control (orange) and drought x storm (red) *Nardus* snowbed and *Empetrum* heath mesocosms. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q$_1$) and 75th (Q$_3$) quartiles, respectively. Difference between Q$_1$ and Q$_3$ is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than Q$_1$ − 1.5(IQR) or greater than Q$_3$ + 1.5(IQR). Letters on top of boxplots indicate statistical difference. Asterisks indicate significant difference between ecosystems at $p < 0.05$ when ecosystem:treatment interaction term is not considered; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. (b) Proportion of biomass sorted to plant functional groups. Data are plotted as mean values.

Table 4.1. Biomass sorted to plant functional group (PFG) from *Nardus* snowbed and *Empetrum* heath mesocosms. Data shown are mean ± s.e. (n = 6), PFGs within ecosystems which do not share a letter are significantly different at p < 0.05, * indicate significant difference between treatments.

Ecosystem	Plant functional group	Proportion of sorted biomass (%)				X^2	p
		Control x control	Control x storm	Drought x control	Drought x storm		
	Evergreen shrubs	0.04 ± 0.04 bc	0.62 ± 0.62 b	0.30 ± 0.30 b	0.61 ± 0.39 bc	0.77	0.857
	Deciduous shrubs	21.52 ± 15.74 ab	9.18 ± 2.50 ab	14.37 ± 4.28 ab	11.18 ± 2.58 abc	1.36	0.714
	Graminoids	21.73 ± 7.57 abc	33.23 ± 12.35 a	34.97 ± 11.64 a	31.14 ± 9.20 ac	1.03	0.795
Nardus	Forbs	0.00 ± 0.00 bc	0.39 ± 0.39 b	0.00 ± 0.00 b	0.08 ± 0.08 b	2.09	0.553
snowbed	Bryophytes	56.71 ± 13.14 a	56.49 ± 12.91 a	50.36 ± 12.85 a	57.00 ± 8.99 a	0.24	0.971
	Lichens	0.00 ± 0.00 bc	0.09 ± 0.09 b	0.00 ± 0.00 b	0.00 ± 0.00 b	3.00	0.392
	X^2	30.50	34.36	37.21	36.15		
	p	< 0.001	< 0.001	< 0.001	< 0.001		
	Evergreen shrubs	22.42 ± 4.88 a	14.59 ± 4.27 ab	25.34 ± 6.19 ab	13.80 ± 4.51 ab	3.41	0.333
	Deciduous shrubs	3.88 ± 1.81 ab	5.11 ± 2.87 ab	2.25 ± 0.96 abc	1.66 ± 1.10 a	1.75	0.627
	Graminoids	4.99 ± 2.73 ab	5.50 ± 2.86 ab	0.16 ± 0.10 ac	2.36 ± 2.03 ab	5.88	0.118
Empetrum	Pteridophytes	0.00 ± 0.00 b	0.00 ± 0.00 a	0.85 ± 0.85 ac	0.00 ± 0.00 a	2.67	0.446
heath	Bryophytes	7.67 ± 3.20 ab	10.21 ± 3.21 ab	11.97 ± 4.25 abc	18.81 ± 7.92 ab	0.78	0.854
	Lichens	61.04 ± 5.43 a	64.60 ± 6.19 b	59.43 ± 3.60 b	63.38 ± 11.07 b	0.07	0.995
	X^2	33.88	33.17	40.35	36.34		
	p	< 0.001	< 0.001	< 0.001	< 0.001		

Soil C and N content were twice as large in *Nardus* snowbed (C content: 33.29 ± 1.90%, N content: 1.52 ± 0.07% (mean ± s.e.)) as in *Empetrum* heath (C content: 17.34 ± 1.44%; N content: 0.67 ± 0.05%; C content: $F_{1,35}$ = 43.39, *p* < 0.001; N content: $F_{1,35}$ = 76.09, *p* < 0.001; Figure 4.5a,b). Soil C and N content did not differ between treatments within ecosystems (C content: $F_{3,35}$ = 0.18, p = 0.907; N content: $F_{3,35}$ = 0.26, p = 0.855). Soil C:N ratio was greater in *Empetrum* heath than in *Nardus* snowbed (*Empetrum* heath = 25.37 ± 0.52, *Nardus* snowbed = 21.74 ± 0.52 (mean ± s.e.); $F_{1,35}$ = 25.38, p < 0.001; Figure 4.5c) and did not differ between treatments within ecosystems ($F_{3,35}$ = 1.99, p = 0.134). Soil depth was greater in *Empetrum* heath than *Nardus* snowbed mesocosms (*Empetrum* heath = 9.39 ± 0.31 cm, *Nardus* snowbed = 6.69 ± 0.59 cm (mean ± s.e.); $F_{1,35}$ = 14.63, p < 0.001; Figure 4.5d) but did not differ between treatments within ecosystems ($F_{3,35}$ = 0.14, p = 0.939). Soil C and N pools were greater in *Empetrum* heath (C pool: 7.64 ± 0.44 kg C m^{-2}, N pool: 0.30 ± 0.02 kg N m^{-2} (mean ± s.e.)) than in *Nardus* snowbed (C pool: 4.02 ± 0.51 kg C m^{-2}, N pool: 0.19 ± 0.03 kg N m^{-2} (mean ± s.e.); C pool: $F_{1,35}$ = 25.79, p < 0.001; N pool: $F_{1,35}$ = 12.67, p = 0.001; Figure 4.5e,f). Soil C and N pools did not differ between treatments within ecosystems (C pool: $F_{3,35}$ = 0.33, p = 0.802; N pool: $F_{3,35}$ = 0.54, p = 0.659).

Microbial biomass C and N were greater in *Nardus* snowbed than in *Empetrum* heath (*Nardus* snowbed MBC: 1079.65 ± 94.61 µg C g^{-1} dry soil (mean ± se); *Empetrum* heath MBC: 491.13 ± 43.47 µg C g^{-1} dry soil; MBC: $F_{1,36}$ = 33.48, p < 0.001; *Nardus* snowbed MBN: 169.95 ± 16.17 µg N g^{-1} dry soil; *Empetrum* heath MBN: 87.67 ± 7.29 µg N g^{-1} dry soil; MBN: $F_{1,36}$ = 24.67, p < 0.001; Figure 4.6a,b). Microbial biomass C:N ratio did not differ between ecosystems ($F_{1,34}$ = 0.02, p = 0.903) or treatments within ecosystems ($F_{3,34}$ = 0.39, p = 0.760; Figure 4.6c).
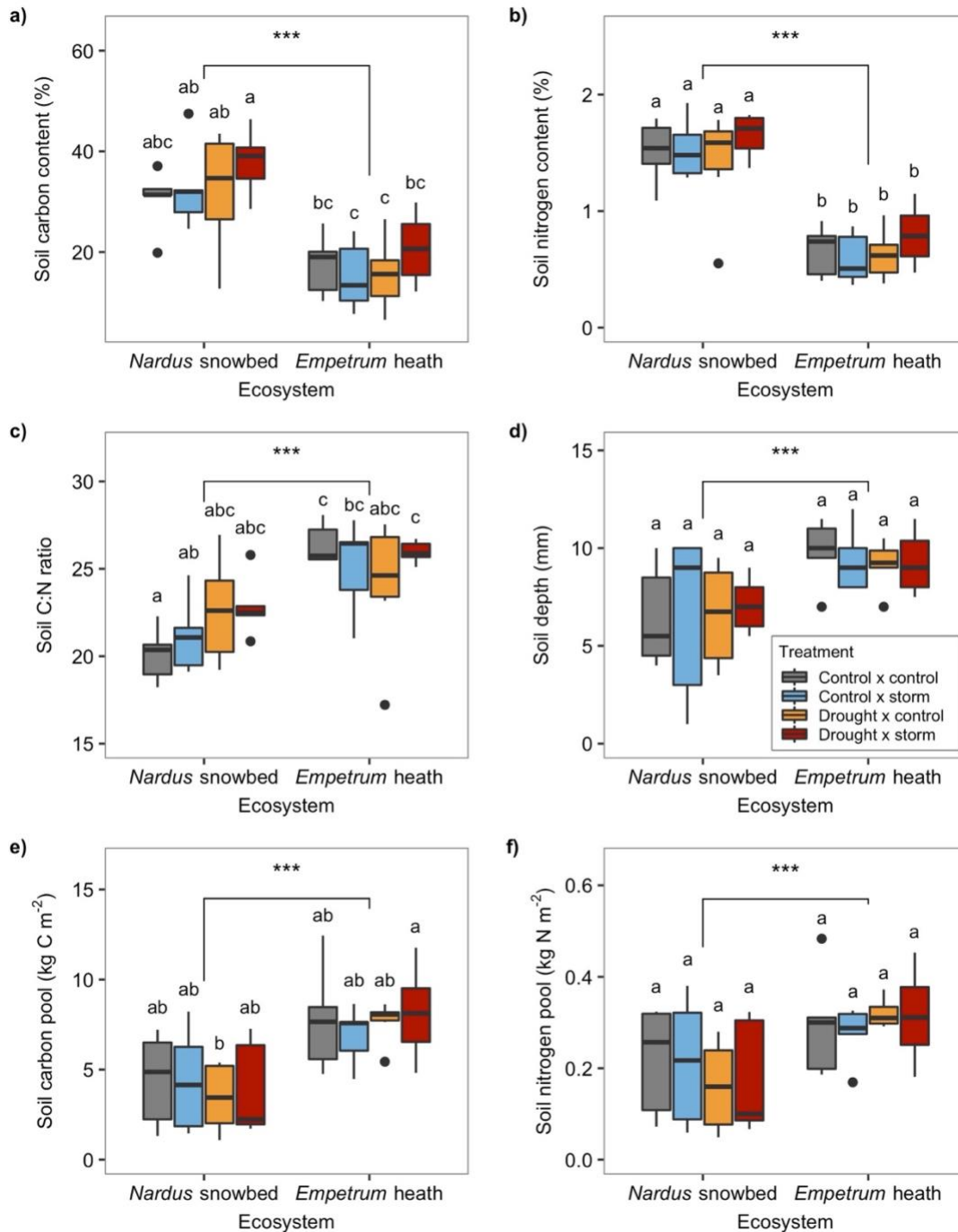
Figure 4.5. (a) Soil carbon and (b) nitrogen content, (c) soil C:N ratio, (d) soil depth, and (e) soil carbon and (f) nitrogen pools for *Nardus* snowbed and *Empetrum* heath mesocosm. Colours represent treatment combinations. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5(IQR)$ or greater than $Q_3 + 1.5(IQR)$. Letters on top of boxplots indicate statistical difference. Asterisks indicate significant difference between ecosystems at $p < 0.05$ when ecosystem:treatment interaction term is not considered; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

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Figure 4.6. Soil microbial biomass a) carbon, b) nitrogen, and c) C:N ratio in *Nardus* snowbed and *Empetrum* heath at experimental harvest. Colours represent treatment combinations. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5$(IQR) or greater than $Q_3 + 1.5$(IQR). Letters on top of boxplots indicate statistical difference. Asterisks indicate significant difference between ecosystems at $p < 0.05$ when ecosystem:treatment interaction term is not considered; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Ecosystem respiration rates did not differ in *Nardus* snowbed compared with *Empetrum* heath (Table 4.2; Figure 4.7a,b). Time of day influenced rates of ecosystem respiration, with a peak in early afternoon (Table 4.2). Day also explained ecosystem respiration rates, with lower rates during the recovery phase (Table 4.2). Drought supressed ecosystem respiration, particularly in *Empetrum* heath (Figure 4.7a,b). Although, when environmental covariates were included, increased mesocosm moisture content suppressed ecosystem respiration and greater total aboveground biomass increased rates of ecosystem respiration (Table 4.2). For four days following rewetting (10 – 13 June 2019), previously

droughted *Nardus* snowbed mesocosms had greater respiration rates than control *Nardus* snowbeds but the nature of rewetting did not affect rates of ecosystem respiration (Table 4.3; Figure 4.8). Neither drought nor storm treatments altered ecosystem respiration rates after rewetting in *Empetrum* heath (Table 4.3).

Net ecosystem exchange rates were more positive in *Empetrum* heath than *Nardus* snowbed (Table 4.2; Figure 4.7c,d). Rates of net ecosystem exchange increased with time of day, and were affected by day with decreased rates over the course of the experiment and a dip in NEE during the recovery phase (Table 4.2). Net ecosystem exchange was unaffected by drought and storm treatments (Figure 4.7c, d), however when change in moisture content is considered, a decline in moisture content reduced rates of NEE (Table 4.2).

Gross photosynthesis was greater in *Nardus* snowbed than in *Empetrum* heath (Table 4.2; Figure 4.7e, f). Rates of gross photosynthesis varied with day number and time, were greater in the morning and decreased late afternoon, and increased over the course of the experiment (Table 4.2). Vegetation community composition rather than drought and storm treatments influenced rates of gross photosynthesis; increased PCoA axis 2 values (representing increased abundance of bryophytes) limited photosynthesis and lower PCoA axis 2 values (indicating a greater abundance of graminoids) resulted in greater rates of gross photosynthesis.

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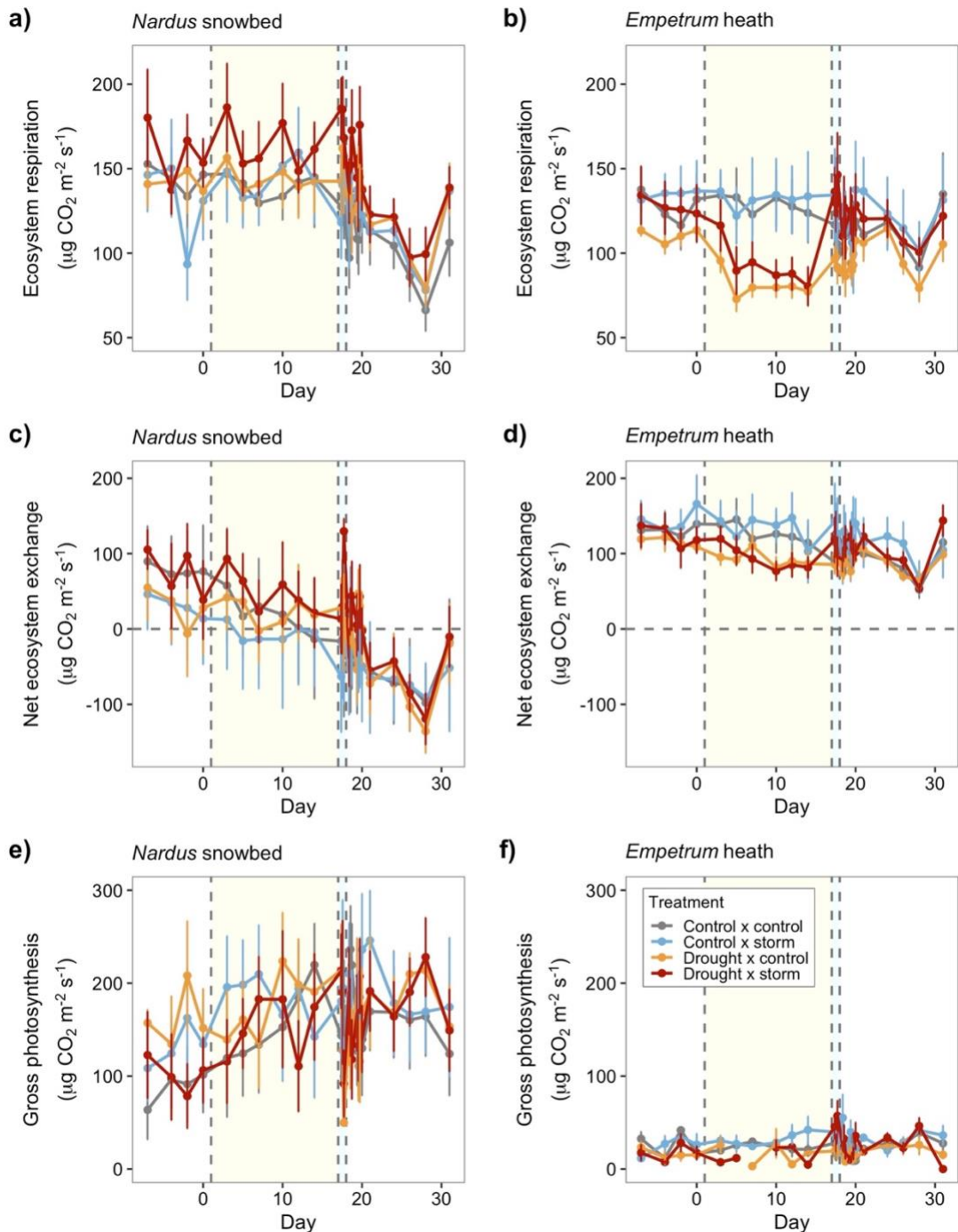
Figure 4.7. Gas fluxes from (a, c, e) *Nardus* snowbed, and (b, d, f) *Empetrum* heath mesocosm; (a, b) ecosystem respiration, (c, d) net ecosystem exchange, and (e, f) gross photosynthesis. Data show control x control (grey), control x storm (blue), drought x control (orange) and drought x storm (red) mesocosms, during baseline (white background), drought (yellow background), rewetting (blue background) and recovery (white background) phases of the experiment. Vertical dashed lines represent changes in experiential phase, horizonal dashed line (panels c and d only) represent 0 line where mesocosms swap from being a net source of CO_2 to a net sink. Data points show mean ± s.e.
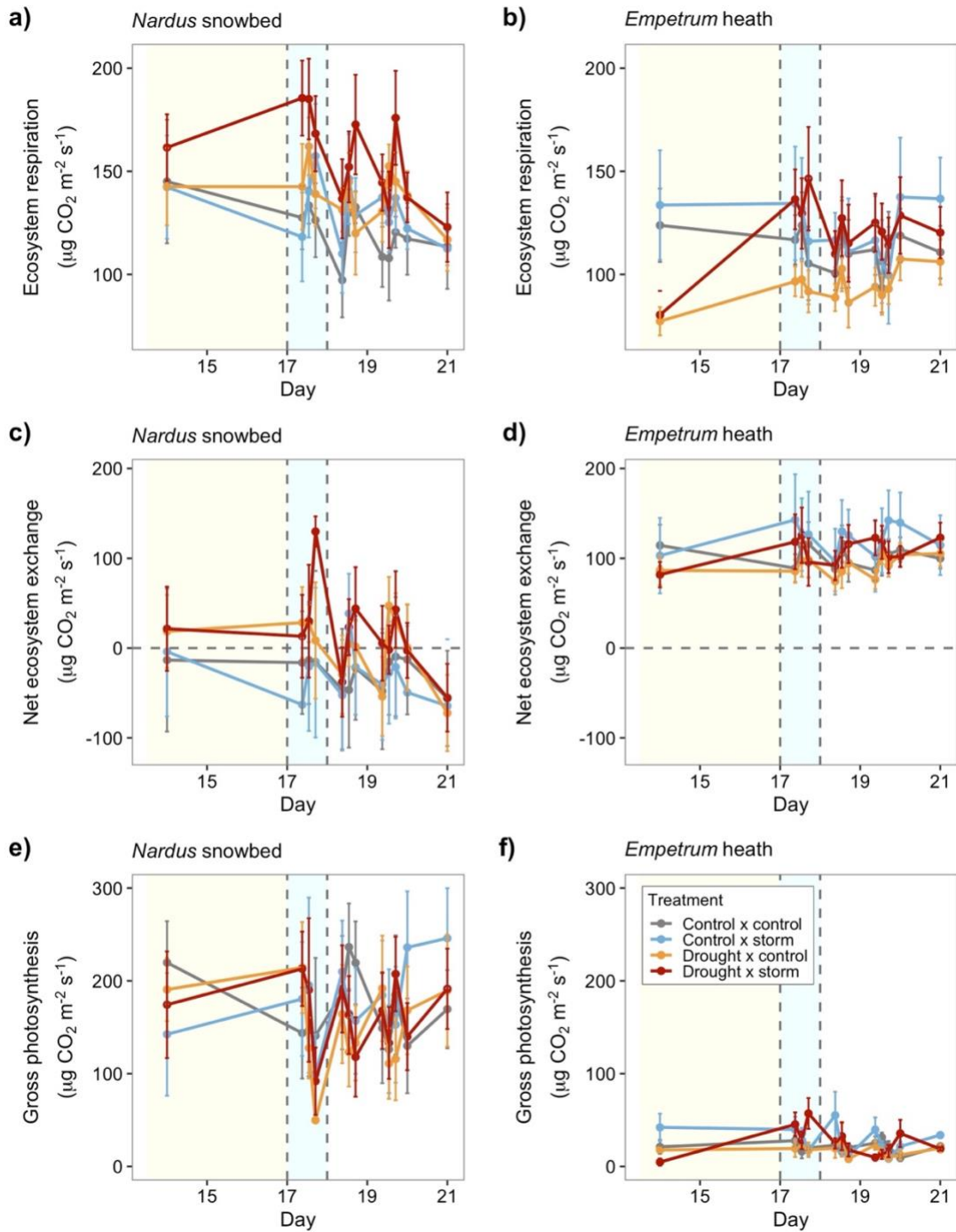
Figure 4.8. Gas fluxes from (a, c, e) *Nardus* snowbed, and (b, d, f) *Empetrum* heath mesocosm during and following the rewetting event; (a, b) ecosystem respiration, (c, d) net ecosystem exchange, and (e, f) gross photosynthesis. Data show control x control (grey), control x storm (blue), drought x control (orange) and drought x storm (red) mesocosms, during end of drought (yellow background), rewetting (blue background) and start of recovery (white background) phases of the experiment. Data points show mean ± s.e.

Table 4.2. Summary of models including ecosystem, treatment, and measures of plant community composition and soil characteristics to explain rates of gas fluxes over the duration of the experiment: ecosystem respiration (ER), net ecosystem exchange (NEE), gross photosynthesis (GP) in factorial drought x storm experiment in *Nardus* snowbed and *Empetrum* heath mesocosms. For each parameter included, direction of change (d), effect size statistic (t, F), and p value are shown. Ecosystems are abbreviated to NS (*Nardus* snowbed) and EH (*Empetrum* heath), treatments are abbreviated to C (control), D (drought), and S (storm), ↑ shows an increase in model parameter increased rates of gas fluxes, while ↓ shows an increase in model parameter decreased rates of gas fluxes, and dashes indicate no change. Variables marked with * are represented with non-linear terms (spline) and direction of response is not reported. Bold values represent significant parameters at p < 0.05.

Flux	Model parameters	Direction	Statistic		p
ER	Ecosystem	---	t =	-1.75	0.081
	Drought	**D < C**	t =	-2.35	**0.019**
	Change in moisture content	↓	t =	-3.31	**< 0.001**
	Total aboveground biomass	↑	t =	3.05	**0.002**
	Ecosystem:Drought	**NS:D ≈ NS:C**	t =	2.89	**0.004**
		EH:D < EH:C			
		NS:D ≈ EH:C			
	Day *		F =	12.22	**< 0.001**
	Time *		F =	4.92	**0.001**
NEE	Ecosystem	**NS < EH**	t =	-5.11	**< 0.001**
	Change in moisture content	↓	t =	-3.91	**< 0.001**
	Day *		F =	42.59	**< 0.001**
	Time *		F =	14.01	**< 0.001**
GP	Ecosystem	**NS > EH**	t =	8.85	**< 0.001**
	PCoA axis 2	↓	t =	-3.09	**0.002**
	Day *		F =	118.49	**< 0.001**
	Time *		F =	13.02	**< 0.001**

Table 4.3. Summary of models including ecosystem, treatment, and measures of plant community composition and soil characteristics to explain rates of gas fluxes for four days following rewetting (10 – 13 June 2019): ecosystem respiration (ER) in factorial drought x storm experiment in *Nardus* snowbed and *Empetrum* heath mesocosms. For each parameter included, direction of change (d), effect size statistic (t, F), and p value are shown. Ecosystems are abbreviated to NS (*Nardus* snowbed) and EH (*Empetrum* heath), treatments are abbreviated to C (control), D (drought), and S (storm), ↑ shows an increase in model parameter increased rates of gas fluxes, while ↓ shows an increase in model parameter decreased rates of gas fluxes, and dashes indicate no change. Variables marked with * are represented with non-linear terms (spline) and direction of response is not reported. Bold values represent significant parameters at p < 0.05.

Flux	Model parameters	Direction	Statistic		p
ER	Ecosystem	---	t =	-0.59	0.559
	Drought	---	t =	-0.68	0.495
	Total aboveground biomass	↑	t =	2.39	**0.017**
	Ecosystem:Drought	**NS:D > NS:C**	t =	2.39	**0.017**
		EH:D ≈ EH:C			
		NS:D > EH:C			
	Day *		F =	7.19	**< 0.001**
	Time *		F =	1.97	0.085

Losses of DOC in leachate were greater in *Empetrum* heath than in *Nardus* snowbed (Figure 4.9a,b; Table 4.4). Dissolved organic carbon flux varied with day, with lower rates during the drought phase and a peak at rewetting. Larger soil C pools were associated with lower DOC losses. DOC export increased with positive change in moisture content. Drought supressed DOC losses while storm led to increased DOC flux.

Total dissolved nitrogen, DON, and NH_4-N losses were greater in *Nardus* snowbed than in *Empetrum* heath (Figure 4.9; Table 4.4). Leachate fluxes of TDN, DON, NH_4-N, and NO_3-N, varied with day, with lower rates during the drought phase and a peak at rewetting. Total dissolved nitrogen, DON, and NH_4-N increased with positive changes in relative mesocosm moisture content. Drought supressed TDN and DON losses, and storm treatment increased TDN and NH_4-N. Combined drought and storm interaction lead to greatest NO_3-N export.

Leachate DOC:TDN ratios were greater in *Empetrum* heath than *Nardus* snowbed (Figure 4.9k,l; Table 4.4). Leachate DOC:TDN ratio also varied with day; ratio was greatest during baseline, lower during drought phase, and did not peak at rewetting. There was greater DOC:TDN ratio in mesocosms with smaller soil C pools, and increased DOC:TDN ratio with increasing relative mesocosm moisture content.

Total leachate losses over the experimental period varied with ecosystems and leachate flux in question. Total DOC losses were greater in *Empetrum* heath than *Nardus* snowbed ($F_{1,40}$ = 8.57, p = 0.006, Figure 4.10). There was no effect of ecosystem on total TDN, DON or NO_3-N fluxes (all p ≥ 0.05). While NH_4-N loss was greater in *Nardus* snowbed than *Empetrum* heath ($F_{1, 40}$ = 13.32, p <0.001). DOC:TDN ratio was greater in *Empetrum* heath than *Nardus* snowbed (DOC:TDN: $F_{1,40}$ = 16.54, p < 0.001).

Drought suppressed total DOC, TDN, and DON fluxes (DOC: $F_{1,40}$ = 12.26, p = 0.001; TDN: $F_{1,40}$ = 6.81, p = 0.013; DON: $F_{1,40}$ = 12.20, p = 0.001). Total NH_4-N was unaffected by drought ($F_{1,40}$ = 1.97, p = 0.168), while total NO_3-N flux increased under

drought ($F_{1,40}$ = 13.04, p < 0.001). Drought reduced DOC:TDN ratio in total leachate ($F_{1,40}$ = 5.95, p = 0.019).

Storm increased total leachate C and N fluxes (DOC: $F_{1,40}$ = 15.94, p < 0.001; TDN: $F_{1,40}$ = 60.20, p <0.001; DON: $F_{1,40}$ = 30.99, p < 0.001; NH$_4$-N: $F_{1,40}$ = 9.60, p = 0.004; NO$_3$-N: $F_{1,40}$ = 29.92, p < 0.001). The interactive effect of storm following drought led to the greatest NO$_3$-N flux ($F_{1,40}$ = 12.36, p = 0.001). Leachate DOC:TDN ratio was unaffected by storm treatment ($F_{1,40}$ = 1.13, p = 0.295).
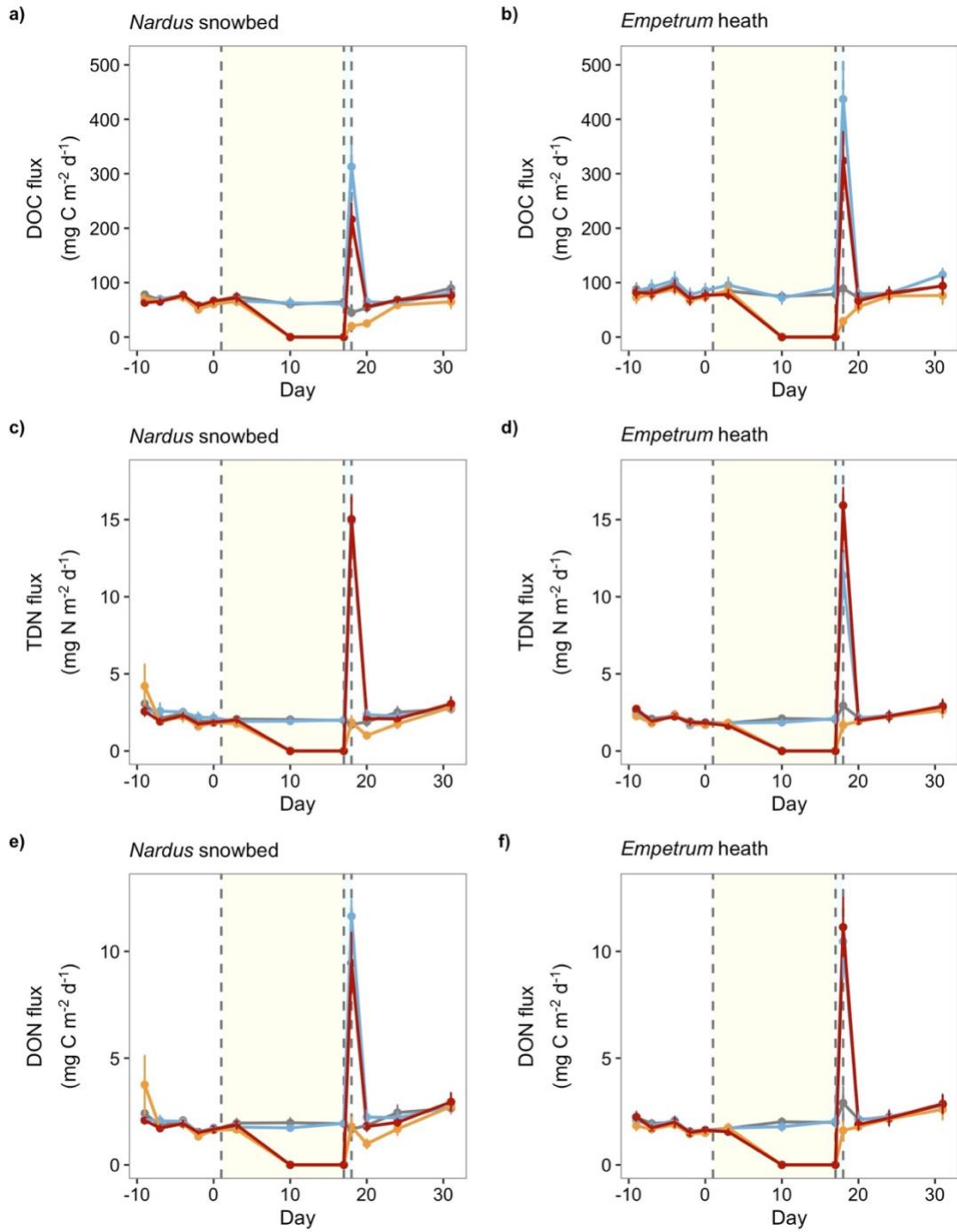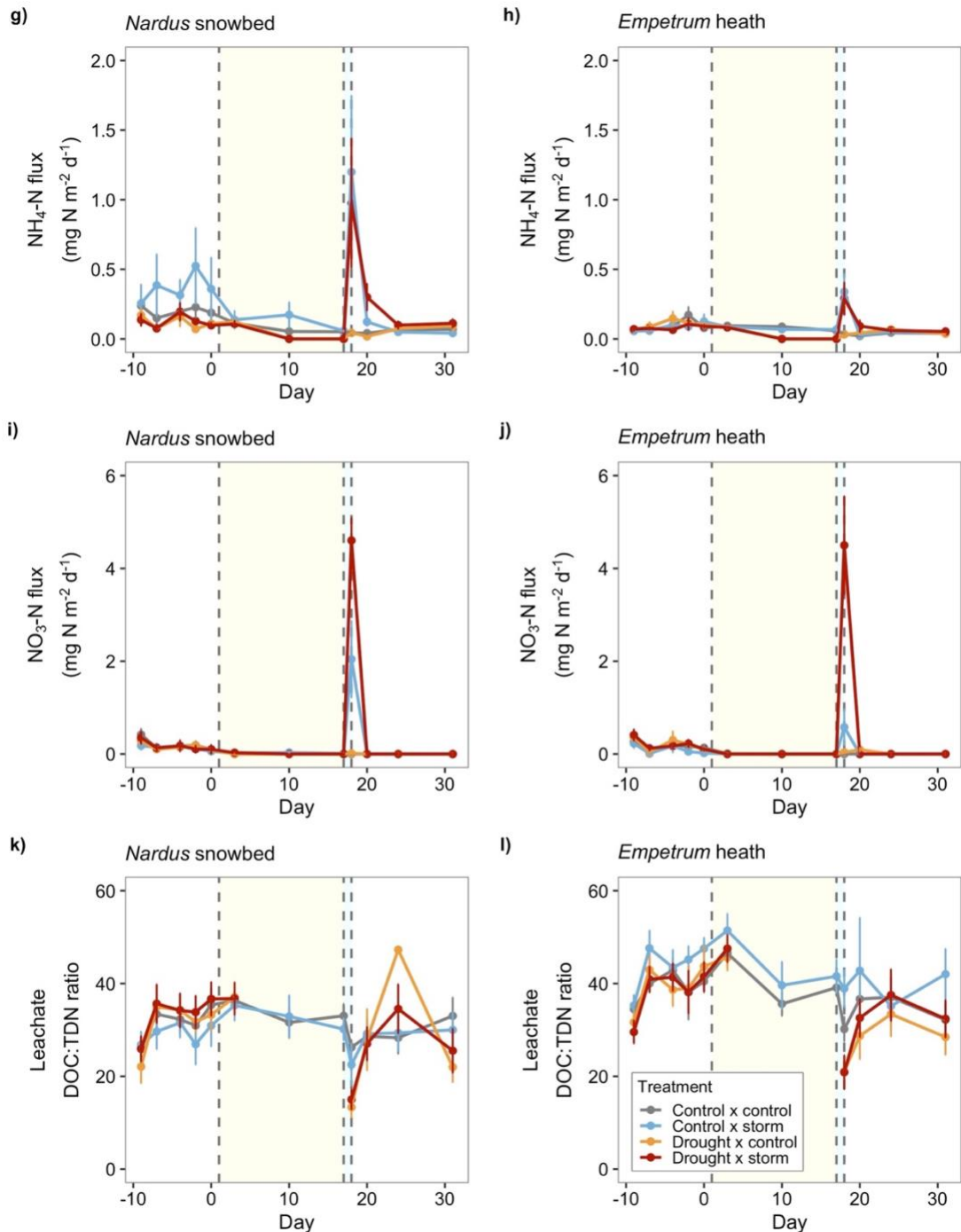
Figure 4.9. Leachate fluxes from (a, c, e, g, i, k) *Nardus* snowbed and (b, d, f, h, j, l) *Empetrum* heath; (a, b) dissolved organic carbon (DOC), (c, d) total dissolved nitrogen (TDN), (e, f) dissolved organic nitrogen (DON), (g, h) ammonium – N (NH4-N), (i, j) nitrate – N (NO3-N), and (k, l) DOC:TDN ratio. Data show control x control (grey), control x storm (blue), drought x control (orange) and drought x storm (red) mesocosms, during baseline (white background), drought (yellow background), rewetting (blue background) and recovery (white background) phases of the experiment. Data points show mean ± s.e.

Table 4.4. Summary of models including ecosystem, treatment, and measures of soil characteristics to explain rates of leachate fluxes: dissolved organic carbon (DOC), total dissolved nitrogen (TDN), nitrate-N (NO_3-N), ammonium-N (NH_4-N), and dissolved organic nitrogen (DON), and leachate DOC:TDN ratio in factorial drought x storm experiment in *Nardus* snowbed and *Empetrum* heath mesocosms. For each parameter included, direction of change (d), effect size statistic (t, F), and p value are shown. Ecosystems are abbreviated to NS (*Nardus* snowbed) and EH (*Empetrum* heath), treatments are abbreviated to C (control), D (drought), and S (storm), ↑ shows an increase in model parameter increased rates of gas fluxes, while ↓ shows an increase in model parameter decreased rates of leachate fluxes, and dashes indicate no change. Variables marked with * are represented with non-linear terms (spline) and direction of response is not reported. Bold values represent significant parameters at p < 0.05.

Flux	Model parameters	Direction	Statistic		p
DOC	Ecosystem	**NS < EH**	t =	-2.01	**0.041**
	Drought	**D < C**	t =	-2.16	**0.032**
	Storm	**S > C**	t =	2.77	**0.006**
	Change in moisture content	↑	t =	9.23	**< 0.001**
	Soil C pool	↓	t =	-2.05	**0.040**
	Day *		F =	9.37	**< 0.001**
TDN	Ecosystem	**NS > EH**	t =	-2.98	**0.003**
	Drought	**D < C**	t =	3.93	**< 0.001**
	Storm	**S > C**	t =	-2.01	**0.045**
	Change in moisture content	↑	t =	-8.88	**< 0.001**
	Day *		F =	21.09	**< 0.001**
DON	Ecosystem	**NS > EH**	t =	-2.67	**0.008**
	Drought	**D < C**	t =	3.84	**< 0.001**
	Change in moisture content	↑	t =	-9.25	**< 0.001**
	Day *		F =	19.78	**< 0.001**
NH_4-N	Ecosystem	**NS > EH**	t =	3.43	**< 0.001**
	Storm	**S > C**	t =	2.46	**0.014**
	Change in moisture content	↑	t =	3.00	**0.003**
	Day *		F =	4.98	**< 0.001**
NO_3-N	Drought	---	t =	0.03	0.977
	Storm	---	t =	0.61	0.546
	Drought:Storm	**D:S > C:C**	t =	2.11	**0.035**
		D:S > C:S			
		D:S > D:C			
	Day *		F =	16.76	**< 0.001**
DOC:TDN	Ecosystem	**NS < EH**	t =	-4.63	**< 0.001**
	Change in moisture content	↑	t =	5.40	**< 0.001**
	Soil C pool	↓	t =	-2.41	**0.016**
	Day *		F =	20.50	**< 0.001**
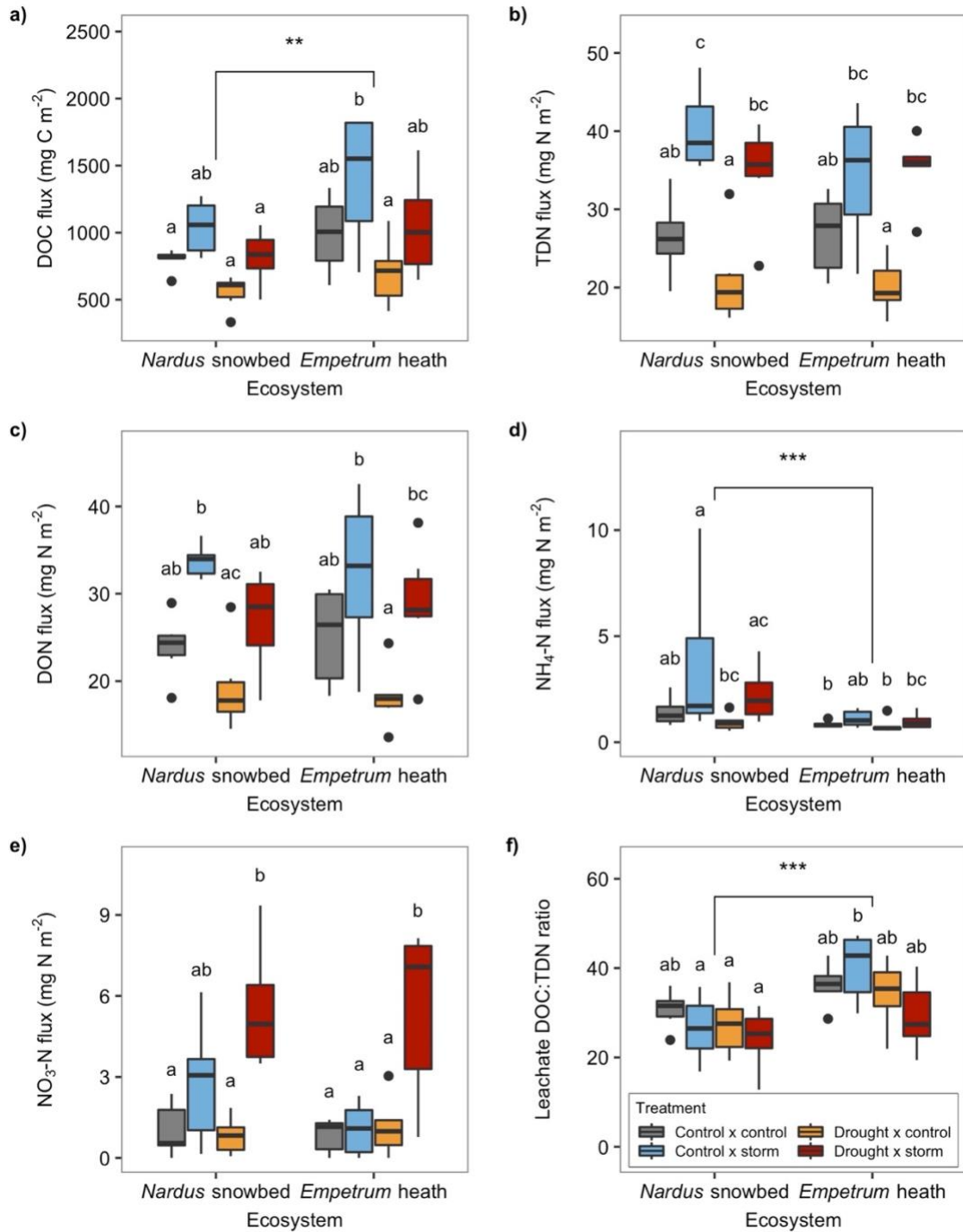
Figure 4.10. Total leachate fluxes from *Nardus* snowbed and *Empetrum* heath; (a) dissolved organic carbon (DOC), (b) total dissolved nitrogen (TDN), (c) ammonium-N (NH_4-N), (d) nitrate-N (NO_3-N), (e) dissolved organic nitrogen (DON), and (f) DOC:TDN ratio. Colours represent treatment combinations. Solid horizontal lines in the boxes represent median values, and upper and lower box edges show the 25th (Q_1) and 75th (Q_3) quartiles, respectively. Difference between Q_1 and Q_3 is the interquartile range (IQR). Black circles represent potential outliers where the data point value is less than $Q_1 - 1.5$(IQR) or greater than $Q_3 + 1.5$(IQR). Letters on top of boxplots indicate statistical difference. Asterisks indicate significant difference between ecosystems at $p < 0.05$ when ecosystem:treatment interaction term is not considered; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

4.5 Discussion

In this experiment, ecosystem type had strong influences on both gas and leachate fluxes, which were attributed to the differences in vegetation communities and soil characteristics. As hypothesised initially, *Nardus* snowbed and *Empetrum* heath responded differently to drought and storm events; this was probably also due to the differences in vegetation and soil properties.

In general, ecosystem respiration was supressed by drought. Lower soil moisture likely reduced soil microbial respiration (Orchard and Cook 1983), due to limited substrate availability and solute diffusion (Manzoni et al. 2012, 2014). Reduction of ecosystem respiration under drought was stronger in *Empetrum* heath than in *Nardus* snowbeds. The highly organic podzol soils found in *Nardus* snowbeds, had a higher starting moisture content than the shallow podzol soils in *Empetrum* heath, so despite the decline in moisture content, the *Nardus* snowbed soils likely retained sufficient moisture for microbial and plant function.

Ecosystem respiration increased in both ecosystems following rewetting, returning to control levels in *Empetrum* heath and increasing from control levels in *Nardus* snowbed. Contrary to our initial predictions however, the nature of the rewetting event following drought did not have an impact on the size of the respiration pulse. Microbial activity is reduced by drought, leading to increased availability of SOM, while rapid rewetting also leads to microbial cell lysis and the release of microbial cytoplasmic solutes, increasing availability of microbial intracellular compounds, both of which are rapidly mineralised upon rewetting (Birch 1958, Fierer and Schimel 2002, 2003). This rapid increase in respiration rates is known as the 'Birch effect' (Birch 1958). In our study this ecosystem respiration pulse was observed in *Nardus* snowbeds but was absent in *Empetrum* heath, possibly due to the higher abundance of vascular plants in the former and the dominance

of lichens in the latter. Vascular plants, under drought, preferentially allocate recently plant-assimilated C to root stores in osmolyte pools (Hasibeder et al. 2015) and may be prone to a change in the quality of root exudates (de Vries et al. 2019). The rewetting of *Nardus* snowbeds, and the resulting change in root exudates may stimulate microbial activity and enhance rates of respiration in previously droughted compared to control mesocosms. The response of changed quality of root exudates and an increase of ecosystem respiration rate to drought and rewetting has been observed previously in graminoid and forb temperate grassland species (de Vries et al. 2019). Ecosystem respiration rates were also observed to dip during the recovery phase; if microbial cytoplasmic solutes released during rewetting had been consumed (Fierer and Schimel 2003) resources may have become limited.

Greater aboveground biomass was associated with higher rates of ecosystem respiration. Changes in respiration rates have previously been linked with plant aboveground biomass, and plant aboveground biomass has been suggested as a proxy for ecosystem respiration rates (Flanagan and Johnson 2005). Greater ecosystem respiration rates have previously been recorded in graminoid dominated compared with shrub dominated systems due to the greater metabolic activity of graminoids (De Deyn et al. 2008, Ward et al. 2009, Quin et al. 2015). Graminoids also promote microbial mineralisation at a greater rate than shrubs or bryophytes due the quantity and quality of litter inputs to soil (Hobbie 1996). Vascular plants in general may also prime microbial decomposition of soil organic matter (SOM) through rhizodeposition, while bryophytes and lichens lack roots and do not pass substrates to the soil via this route (Johnson et al. 2002, Leake et al. 2006, Walker et al. 2016). Based on this, we expected greater rates of ecosystem respiration in *Nardus* snowbed than in *Empetrum* heath. Surprisingly however, despite a trend (p = 0.081) to higher ecosystem respiration in the *Nardus* snowbed which is consistent with these other studies, rates of ecosystem respiration did not differ

significantly between *Nardus* snowbed and *Empetrum* heath, despite the greater total biomass in *Nardus* snowbeds than *Empetrum* heath.

Microbial biomass was not used to explain rates of gas or leachate fluxes, as MBC was only sampled at experimental harvest and not over the course of the experiment. However, the larger microbial biomass in *Nardus* snowbed compared with *Empetrum* heath soils may have contributed to the difference in ecosystem respiration rates between these two systems. Microbial community biomass appeared unaffected by treatment. However, changes in microbial community composition and activity in mountain grasslands have previously been observed under drought alone and following a drought-rewetting event (Fuchslueger et al. 2014, 2016, 2019). Drought induced shifts in grassland plant community composition have also been shown to lead to changes in bacterial and fungal community composition (de Vries et al. 2018). Microbial community composition is a strong predictor of soil respiration rates across a land-use gradient during a dry-rewet event (Orwin et al. 2016).

Ecosystem and vegetation community composition were key factors in determining gross photosynthesis rates, rather than treatment. Photosynthesis rates were greater in bryophyte and graminoid dominated *Nardus* snowbed than in lichen and evergreen shrub dominated *Empetrum* heath. Greater variation in gross photosynthesis rates within *Nardus* snowbed than within *Empetrum* heath mesocosms was likely due to the heterogeneity in *Nardus* snowbed vegetation and increased rates of gross photosynthesis with increased abundance of *Nardus stricta* and *Trichophorum cespitosum*, as explained by PCoA axis 2. Gross photosynthesis rates increased with day over the experiment in *Nardus* snowbeds with the green up of graminoids into summer, while there was much less seasonal change in evergreen biomass in *Empetrum* heath, as has been observed with seasonal differences between gross primary productivity in graminoid and shrub dominated heath communities (Quin et al. 2015).

The greater rates of gross photosynthesis in *Nardus* snowbed were reflected in rates of NEE, with negative NEE rates indicating that *Nardus* snowbed became a C sink. *Empetrum* heath, with lower rates of gross photosynthesis, but similar respiration rates remained a C source with positive NEE. This contrasts with measurements from a field study where negative NEE and greater C sequestration was found both during the summer months and annually in upland *Calluna* heath compared with grass heath (Quin et al. 2015). This difference may reflect the fact that in higher altitude alpine situations, *Nardus* snowbeds occur on moister, more productive soils, while dwarf-shrub heaths occupy dry shallow soils in exposed locations and have lower productivity. In *Nardus* snowbed NEE became more negative as gross photosynthesis rates increased; plants were fixing more C and there were greater rates of C sequestration. Carbon sequestration rates were greatest during the recovery period, when ecosystem respiration rates were decreased. Following drought and rewetting, there is an increase in nutrient availability in the soil, including an increase in the concentration of soil amino acids (Lipson and Monson 1998). During the growing season tundra plants compete well against microbes for N in the form of amino acids but not as NH_4^+ (Schimel and Chapin 1996). Like the ecosystem respiration pulse following drought and rewetting, plant uptake of nutrients and activity (including carbon fixation) may increase as substrates become available and then decline as substrate levels reduce.

The change in nutrient availability over the course of the experiment was reflected in leachate C and N fluxes. The majority of N losses were in the form of DON. Drought reduced daily leachate DOC, TDN, and DON as we hypothesised. Leachate NH_4-N and NO_3-N were unaffected by drought but as these fluxes were small and often below the detection limits of 0.0015 mg/l and 0.007 mg/l for NH_4-N and NO_3-N, respectively, a treatment effect could have been missed. Storm treatment led to a spike in daily fluxes of

DOC, TDN, NH_4-N, and NO_3-N. Drought and storm treatments were reflected in changes in moisture content which in turn explained some daily leachate fluxes.

Storm had a greater impact on total leachate losses across the whole duration of the study than did drought. Storm treatment resulted in an increase in all five total leachate fluxes. Drought reduced total leachate losses of DOC, TDN, and DON, as we expected, but it increased total losses of NO_3-N. The nature of rewetting was important for N losses; the NO_3-N spike following rewetting and total NO_3-N losses were increased further when a storm event followed drought. Increased NO_3 concentrations in peatland pore water and forest and upland streams have previously been observed following rainfall after drought (Reynolds and Edwards 1995, Watmough et al. 2004, Juckers and Watmough 2014), with increased NO_3 leaching continuing the following year as a legacy of drought (Leitner et al. 2020). Dissolved inorganic N export is driven by precipitation (Kane et al. 2008). If plant NO_3 uptake is reduced under drought (Dijkstra et al. 2015), a pool could accumulate which is washed out during rewetting. Increases in NO_3 losses via leachate or run off could lead to acidification of soils and water, and eutrophication of downslope surface waters (Helliwell et al. 2007).

Total DOC losses were also impacted by the nature of rewetting, with greater losses from storm than from control treated mesocosms. Dissolved organic carbon available following rewetting is thought to be derived from SOM-C (Fierer and Schimel 2003). Oceanic-alpine ecosystems are large stores of old soil C (Jones et al. 2005, Britton et al. 2011, Mills n.d.), but heavy rain events could potentially lead to losses of soil C, as the intensity of rewetting events could be key in determining whether soil C is mobilised (Schimel 2018).

4.6 Conclusion

Nardus snowbeds and *Empetrum* heath are intrinsically different ecosystems in terms of their vegetation community and soil characteristics, and the microclimates these ecosystems experience. The dominant PFGs in these contrasting ecosystems have different traits in the C cycle in terms of productivity, respiration, and the quantity and quality of plant inputs to soil. Differences in vegetation community composition resulted in greater photosynthesis rates in *Nardus* snowbed than *Empetrum* heath, which contributed to negative NEE rates in *Nardus* snowbeds indicating a C sink, while positive rates of NEE in the *Empetrum* heath indicated a C source. To some extent this may have been an artefact of experimental scale, since soil respiration rates and magnitude of treatment effects in plant-soil systems have previously been found to be greater under highly controlled conditions compared to field studies (Kulmatiski et al. 2008, Crawford 2017), but our study clearly shows that C fluxes differed between these two ecosystem types. Response of ecosystem respiration rates to drought treatment was also ecosystem specific, with no treatment effect observed in *Nardus* snowbeds but supressed respiration rates under drought in *Empetrum* heath. Daily flux and total DOC losses in leachate were greater from *Empetrum* heath than *Nardus* snowbeds. Daily fluxes of TDN, DON, and NH_4-N were greater from *Nardus* snowbeds than from *Empetrum* heath, although when total fluxes are considered only NH_4-N losses differed between ecosystems.

Gaseous C fluxes were fairly resilient to drought and storm treatments and were more impacted by differences between ecosystems, particularly vegetation community composition and biomass, than by the drought or storm treatments. However, a longer drought than the 16 day duration used here, or multiple drought events may have had a greater impact on gas fluxes (Fierer and Schimel 2002, Miller et al. 2005, von Buttlar et al. 2018). Leachate losses were much more responsive to drought and storm events,

particularly NO_3-N fluxes which were very sensitive to the combination of storm and drought. As summer months are predicted to become drier but with heavy rain events (Barnett et al. 2006, Met Office 2019), C sink strength of these alpine habitats appears to be resilient to moderate duration droughts, but the sensitivity of N fluxes to drought and storm events could have implications for acidification of soils and eutrophication of surface waters, impacting both terrestrial and aquatic ecosystem functioning.

4.7 Acknowledgements

4.8 Funding

4.9 References

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5 General discussion

Cold, wet, northern biomes are important soil carbon (C) stores, estimated to contain almost a third of global soil C stocks (Post et al. 1982, Gorham 1991). Mountains are also important sources of water (Viviroli et al. 2007, Immerzeel et al. 2020) and biodiversity (Spehn et al. 2010). Less than 3% of total land area outside Antarctica is classified as mountains (Körner et al. 2011, Testolin et al. 2020), yet mountains support around 10,000 plant species.

5.1 Global change

Mountain regions are among the most rapidly changing landscapes on the planet, experiencing greater than average increases in temperature due to elevation dependent warming (Pepin et al. 2015, Hock et al. 2019, IPCC 2019). Globally, warming temperatures have resulted in decreased snow cover depth, duration, and extent in mountain regions, as well as an increase in precipitation falling as rain and a decrease in that falling as snow in low-elevation mountain systems (Stewart 2009, Hock et al. 2019, IPCC 2019). In Scotland, annual temperature has increased by 1.0 °C and winter temperature by 1.2 °C since the 1960s (Barnett et al. 2006). Duration of snow cover has declined by more than 52 days over the same period, equivalent to a more than 30% decrease (Barnett et al. 2006, Rivington et al. 2019). The intensity and number of days of heavy rain ($\geq$ 10 mm) has increased both annually and particularly in winter since 1960s, and summer precipitation has decreased by more than 18% in some parts of Scotland between 1914 and 2004 (Barnett et al. 2006).

Climate change, in combination with nitrogen (N) deposition and grazing, is driving biodiversity change in alpine regions. Survey studies have reported increased shrub and graminoid cover and reduced moss and lichen cover, while species richness has

increased due to upslope migration of species into new areas (Britton et al. 2009, Armitage et al. 2012, Pauli et al. 2012, Steinbauer et al. 2018, Scharnagl et al. 2019). Belowground, earlier snowmelt has been observed to advance seasonal transitions of soil microbial community composition and function (Broadbent et al. 2021). Global change greatly threatens the capacity of alpine ecosystems to provide vital ecosystem functions, as changes in vegetation and microbial communities could impact biogeochemical cycling and C storage (Wookey et al. 2009, Classen et al. 2015). As continental alpine systems are often the focus of research (Verrall and Pickering 2020), there is limited knowledge about the basic attributes and functioning of oceanic-alpine ecosystems, particularly responses to global change. The aim of this thesis was to address knowledge gaps regarding C cycling in oceanic-alpine ecosystems and the impacts of climate change on these C dynamics (Figure 5.1).

Thesis aim

Examine relationships between snow cover, vegetation community, and soil C pools; evaluate the impacts of changing precipitation regimes on biogeochemical cycling in oceanic-alpine ecosystems

Q1

Research questions

How does snow cover duration drive vegetation community composition and topsoil C pools?

Q2

Are oceanic-alpine ecosystems resistant and resilient to drought?

Q3

How do precipitation extremes affect C and N cycling in contrasting oceanic-alpine ecosystems?

Key findings

- Elevation and topography determined snow cover duration
- Elevation, topography, and snow cover regime drove vegetation community composition and above-ground biomass
- Differences in vegetation communities were not reflected in the topsoil C pool, microbial biomass, or microbial activity
- Sampling to > 15 cm depth is required to properly characterise difference in C pools between habitats

- ER rates were greater in *Nardus* snowbed than *Racomitrium* heath
- Vegetation community composition was a key driver of ER rates
- Drought supressed ER
- Pulse in ER in *Nardus* snowbed following rewetting
- ER fluxes in *Nardus* snowbed and *Racomitrium* heath are resilient to drought

- Drought decreased ER rates, particularly in *Empetrum* heath
- Pulse in ER rates in *Nardus* snowbed following rewetting; nature of rewetting did not determine the size of the flux
- Vegetation community composition drove NEE and GP
- Negative NEE indicates *Nardus* snowbed became a C sink; positive NEE indicates *Empetrum* heath remained a C source
- Storm increased total leachate losses of C and all forms of N
- Drought reduced total leachate losses of DOC, TDN, and DON
- Drought increased NO_3-N losses; drought followed by storm event led to greatest NO_3-N losses

Main conclusions and recommendations

- Vegetation community composition is important in determining rates of gas and leachate C and N fluxes
- Currently stable old soil C may be negatively affected by global change via:
  - Expansion of vascular plants, particularly shrubs, into snowbed communities, impacting biogeochemical cycling
  - Losses of C as DOC in leachate and via pulses of ER following rewetting dry soil
- Drought-rewetting events may lead to losses of nitrate resulting in soil acidifcation and eutrophication of surface waters downslope

Recommendations

Examine relationships between snow cover regimes, vegetation communities, and ecosystem C pool while considering soil to a greater depth

Evaluation of soil microbial communities and function in response to drought and storm events is needed for predicting impacts of climate change

Figure 5.1. Schematic of thesis structure summarising the main research aim, questions, key findings, conclusions, and recommendations. Fluxes are abbreviated to ER (ecosystem

respiration), NEE (net ecosystem exchange), GP (gross photosynthesis), DOC (dissolved organic carbon), TDN (total dissolved nitrogen), DON (dissolved organic nitrogen), and NO_3-N (nitrogen in the form of nitrate).

5.2 Soil carbon

In Chapter 2, I examined the relationships between snow cover duration, vegetation community composition, and soil C pools. Elevation and topography regulated snow cover duration. In turn, snow cover duration, elevation, and topography were key drivers of vegetation community composition and biomass (Figure 5.2a). Gradients of snow cover duration have previously been associated with variation in plant community composition via regulation of soil moisture and temperature, light availability and the length of the growing season (Rodwell 1991, 1992, Nagy and Grabherr 2009, Carlson et al. 2015). Differences between snowbed and non-snowbed vegetation communities were greater at higher elevation sites, indicating the effects of topography and snow cover could be more important with increasing elevation. Snowbed communities were dominated by graminoids, while non-snowbed communities were dominated by evergreen shrubs, as seen previously with shrub dominance in alpine heath, and *Nardus stricta* and moss dominance in snowbeds (Britton et al. 2011). These differences in functional composition of the vegetation communities would be expected to lead to differences in C dynamics via contrasting photosynthesis rates, quality and quantity of inputs into soil, presence or absence of roots or rhizoids, and associations with soil microbial communities, and thus to impact on the development of soil C pools (Chapin et al. 1996, De Deyn et al. 2008).

Rosanne C. Broyd – February 2022
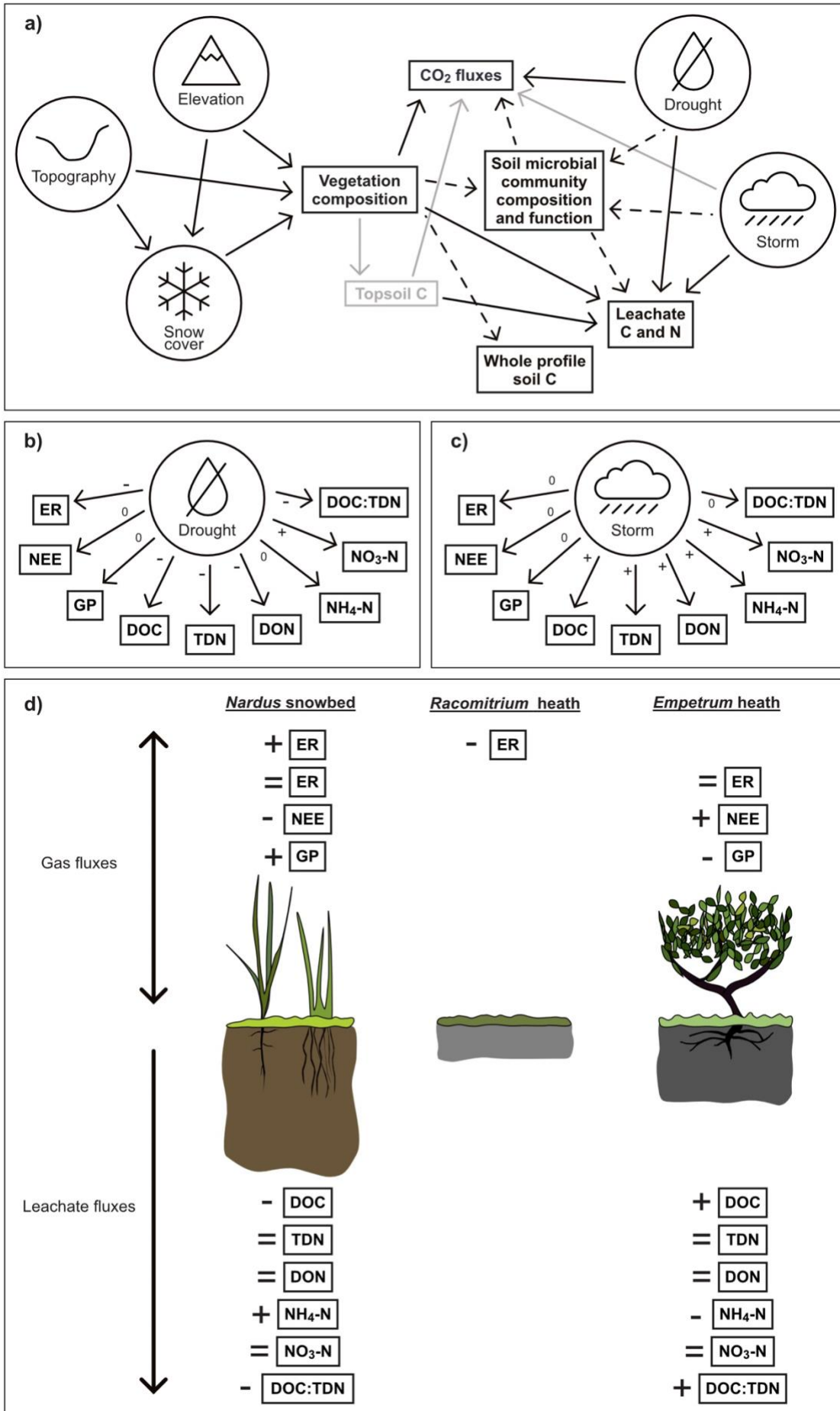
Figure 5.2. (a) Conceptual diagram of relationships between environmental drivers, vegetation community composition, and biogeochemical cycling, including gas fluxes and total leachate losses in oceanic-alpine habitats. Solid lines represent relationships examined in this thesis; black lines indicate an effect was observed, grey lines indicate an effect was not observed. Dashed lines represent relationships that could be explored in the future. (b) The effects of drought and (c) the effects of storm on C and N fluxes from oceanic-alpine habitats. Responses are shown as + (increased flux rates), - (decreased flux rates), and 0 (no effect observed). (d) Overall differences in C and N flux rates between ecosystems without considering treatment effects. Relative rates of fluxes are contrasted within each row and shown as + (greater than other ecosystem), - (lower than other ecosystem), and = (no difference observed). Gas and leachate fluxes are abbreviated to ER (ecosystem respiration), NEE (net ecosystem exchange), GP (gross photosynthesis), DOC (dissolved organic carbon), TDN (total dissolved nitrogen), DON (dissolved organic nitrogen), NH_4-N (nitrogen in the form of ammonium), NO_3-N (nitrogen in the form of nitrate), and DOC:TDN (leachate DOC:TDN ratio).

Variability in alpine vegetation communities across snow cover duration, topography and elevation was not reflected in the upper organic soil C pool however. Soil C pools measured in the top 15 cm of the organic horizon in this study were similar to those measured in topsoil (0-10 cm) in other alpine habitats (Saenger et al. 2015), but were lower than those reported when sampling the full soil profile including organic and mineral soil horizons (Garcia-Pausas et al. 2007, Djukic et al. 2010, Britton et al. 2011). In this study, organic horizon depth varied from 4 cm to ≥ 110 cm with greatest organic horizon depth recorded at the lower altitude sites. It seems likely that sampling to only 15 cm depth is insufficient to properly characterise soil C pools in these alpine habitats, particularly at low-intermediate altitudes. Our limited sampling effort of organic horizon soil C pools to 15 cm depth thus likely contributed to not observing the expected differences in soil C pools between vegetation types. Future studies should consider full profile sampling of C stocks.

5.3 Carbon fluxes

In Chapter 3, I evaluated whether ecosystem respiration rates in oceanic-alpine ecosystems are resistant and resilient to a drought event. Ecosystem respiration rates were greater in *Nardus* snowbed than *Racomitrium* heath and vegetation community composition

was a key factor in determining ecosystem respiration rates (Figure 5.2a,d). The greater abundance of vascular plants, particularly graminoids and forbs, in *Nardus* snowbed than the moss dominated *Racomitrium* heath likely contributed to greater respiration rates, as vascular plants have greater respiration rates than mosses (Ward et al. 2013, Gavazov et al. 2018), and the presence of roots in vascular plants may enhance soil microbial respiration via rhizodeposition of recent photo-assimilate (Johnson et al. 2002, Leake et al. 2006, Walker et al. 2016).

Despite *Nardus* snowbeds and *Racomitrium* heath being intrinsically different and contrasting ecosystems in terms of their vegetation community, soil characteristics, and the microclimates these ecosystems experience, there was no difference in the resistance or resilience of these habitats to drought. Drought suppressed respiration (Figure 5.2a,b) in both *Nardus* snowbed and *Racomitrium* heath. Reduced soil moisture likely limited substrate availability and solute diffusion, resulting in lower rates of microbial respiration (Orchard and Cook 1983, Manzoni et al. 2012, 2014). Following rewetting, there was an increase in ecosystem respiration rates which exceeded control levels in *Nardus* snowbeds, however, as this was observed three days after rewetting, it was likely not the rapid pulse in respiration seen after rewetting dry soils known as the 'Birch effect' (Birch 1958). As the rate and intensity of rewetting could be important factors in determining whether C is mobilised and respired by microbes upon rewetting (Schimel 2018), I developed the drought-rewetting manipulation further, exploring the impact of the nature of rewetting on biogeochemical cycling in *Nardus* snowbed and *Empetrum* heath in Chapter 4.

In Chapter 4 ecosystem respiration rates did not differ between *Nardus* snowbed and *Empetrum* heath (Figure 5.2d) and were not explained by vegetation community composition, but increased with greater aboveground biomass. Ecosystem and vegetation community composition were however, key factors driving rates of gross photosynthesis. Photosynthesis rates were greater in the bryophyte and graminoid dominated *Nardus*

snowbed than in the lichen and evergreen shrub dominated *Empetrum* heath. The greater rates of gross photosynthesis in *Nardus* snowbed were reflected in rates of NEE; negative NEE rates indicating that *Nardus* snowbed became a C sink. *Empetrum* heath, with lower rates of gross photosynthesis, but similar respiration rates remained a C source with positive NEE.

The differences in gas fluxes between plant communities observed in both Chapters 3 and 4 point to the importance of vegetation community composition in regulating C cycling (Figure 5.2a). Global change is impacting the distribution of plant species in alpine areas, and expansion of vascular plants into bryophyte dominated alpine snowbeds has been observed in mountain regions globally (Britton et al. 2009, Sandvik and Odland 2014, Matteodo et al. 2016, Scharnagl et al. 2019, Liberati et al. 2019, Palaj and Kollár 2019). Shrub expansion into snowbeds has also been observed and attributed to warming temperatures and reduced snow cover (Weijers et al. 2018, Scharnagl et al. 2019). This study suggests that such changes in the distribution of key plant functional groups and vegetation types will likely have implications for C sink strength in alpine areas as *Nardus* snowbed appears to have a more negative NEE than *Empetrum* heath, for example. Soil respiration rates and the magnitude of treatment effects in plant-soil systems have previously been found to be greater under highly controlled conditions compared to field studies (Kulmatiski et al. 2008, Crawford 2017) therefore our study may not be an exact analogue of the real world, but clearly shows the relative difference in C cycling between ecosystems. It will be important to understand the gas fluxes and C sink strengths of all the different elements of alpine mosaics in order to understand how global change-driven shifts in vegetation composition will impact on overall C emissions and sequestration in alpine ecosystems.

Contrasting habitat responses to drought were more evident in the Chapter 4 study than in Chapter 3. Ecosystem respiration was generally suppressed by drought in this

experiment (Figure 5.2a,b), but the response was greater in *Empetrum* heath than *Nardus* snowbed, despite *Empetrum* heath typically experiencing more variable microclimate than *Nardus* snowbed. Following rewetting, as in the Chapter 3 study, ecosystem respiration rates rapidly increased in *Nardus* snowbed, however, contrary to expectations, the nature of the rewetting event did not dictate the magnitude of the respiration pulse. Leachate fluxes were more sensitive than gas fluxes to precipitation extremes. Daily and total fluxes of leachate dissolved organic carbon (DOC) were greater in *Empetrum* heath than *Nardus* snowbed, and were suppressed under drought and increased by storm rewetting (Figure 5.2a,b,c). Our studies suggest that projected drier conditions may reduce C losses in terms of ecosystem respiration and DOC during dry spells, but there could be pulses of C released during rewetting, and intense rainfall events may exacerbate this. Frequency of drought-rewet events will probably be important in determining the overall effect on biogeochemical cycling and microbial function, as has previously been observed in microbial C and N dynamics in soil incubations (Fierer and Schimel 2002).

5.4 Nitrogen fluxes

In Chapter 4 effects of drought and storm events on both C and N fluxes were considered. Nitrogen fluxes in leachate were very responsive to both drought and storm events (Figure 5.2a,b,c). Drought stopped daily leachate export during the treatment phase, and total leachate losses over the experimental period. Drought suppressed export of total dissolved nitrogen (TDN) and dissolved organic nitrogen (DON), but increased losses of nitrate (NO_3-N). Storm increased total losses of all forms of N in leachate and export of NO_3-N was greatest when drought was followed by storm. If summer months become drier with heavy rainfall events, as predicted (Barnett et al. 2006, Met Office 2019), this may lead to increased export of NO_3 in leachate. Increases in NO_3 losses via leachate or

run off could lead to acidification of soils and water, and eutrophication of surface waters (Helliwell et al. 2007), which may impact ecosystem functioning of terrestrial and aquatic habitats downslope.

5.5 Limitations, opportunities, and future work

Conducting research in alpine regions often involves remote sites with limited access. In Chapter 1, partly for logistical reasons, sampling of soil C stocks was limited to the top 15 cm of the organic horizon. Contrary to perceptions of alpine soils as having only shallow organic horizons, this 15 cm sampling depth was insufficient to fully determine the relationships between snow cover, vegetation community and ecosystem carbon pool. Sampling C stocks to a greater depth or, preferably, over the full soil profile, for a wider range of habitat types and over a wide altitudinal range, is recommended in order to fully understand C stock differences between alpine habitats and potential impacts of snow cover change on soil C store and C dynamics.

Collection of mesocosms for ex-situ experiments enabled high frequency measurements of gas and leachate fluxes to be made in Chapters 3 and 4. Outdoor mesocosm incubation for the first drought experiment (Chapter 3) experienced challenges including disturbance by birds, wind driven rain under the shelter, and changeable weather and led me to conduct the second drought experiment (Chapter 4) in a controlled environment room thus limiting daily variation in temperature and sunlight, and allowing a greater focus on treatment effects. However, ex-situ experiments isolate mesocosms from the hydrological regime that they would normally experience, and soil respiration rates and magnitude of treatment effects in plant-soil systems have previously been found to be greater under highly controlled conditions compared to field studies (Kulmatiski et al. 2008,

Crawford 2017). It would be valuable to have field studies and measurements of gas fluxes and leachate chemistry in-situ which could corroborate the results of laboratory studies.

Summer months are predicted to become drier interspersed with heavy rain events (Barnett et al. 2006, Met Office 2019) drought-rewetting will not occur as an isolated event; previously the frequency of drying-rewetting cycles has been observed to determine C and N dynamics, but to varying degrees in grassland compared to oak forest soils (Fierer and Schimel 2002). Repeated drought-rewet cycles with bigger magnitudes of drought may drive responses to varying levels in contrasting oceanic-alpine ecosystems. Studies exploring the impact of different frequencies and magnitudes of dry-rewet cycles, across a range of alpine habitat types are needed to fully understand what the impacts on C and N stocks and fluxes might be across alpine landscapes. It will also be important to consider soil microbial community structure and function to understand the mechanisms involved, particularly what is being mobilised at rewetting, as this could have ramifications for soil C storage. Labelled isotope studies could be used to quantify the proportion of microbial respiration originating from recent plant-input, microbial necromass, or old soil organic matter.

Seasonal dynamics are also important in regulating plant and microbial activity and thus ecosystem functioning in alpine habitats (Bardgett et al. 2005). Climate change may cause advancement of seasonal transitions in microbial community structure and function (Broadbent et al. 2021) and could result in changes in C and N dynamics . In the current study I only examined C and N fluxes under growing season (summer) conditions but it is also important to consider ecosystem functioning and consequences of global change outside the growing-season if we are to have a comprehensive overview of ecosystem function and responses to global change.

5.6 Conclusions

Attributes and functioning of mountain ecosystems are often studied in continental alpine regions, while oceanic-alpine mountains are over-looked. This thesis presents novel contributions to biogeochemical cycling in oceanic-alpine ecosystems under climate change manipulations. Snow cover, topography, and elevation determined vegetation community composition and measurement of gas and leachate fluxes indicated that C and N cycling differed between alpine habitats. While leachate fluxes were responsive to precipitation extremes (both drought and storm), gas fluxes were fairly resilient to drought and storm events. These results suggest that both direct effects of altered precipitation regimes (increased frequency of summer droughts and intense rainfall events) and indirect effects via altered winter snow cover distribution and summer moisture availability impacts on plant species distributions will impact on C and N cycling and C stocks in alpine landscapes. These findings demonstrate the sensitivity of alpine ecosystems to global change and emphasise the need for more studies to explore soil communities and functions in contrasting alpine habitats, both seasonally and under environmental manipulations in order to better predict future impacts of global change in these rapidly altering landscapes.

5.7 References

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6 Appendix

6.1 Appendix A – Other work

Michel, Jennifer., Iain P. Hartley, Carmen van Meegen, Rosanne C. Broyd, Laura Reinelt, Adan Julian Ccahuana Quispe, and Jeanette Whitaker. Preferential substrate use decreases priming effects in contrasting treeline soils. Biogeochemistry. *In submission*.

My contribution to this study using the CRediT taxonomy comprised of Investigation, and Writing – review and editing.

Yeah it's a bit shit, but it's only soil at the end of the day.

-Daf, 2017