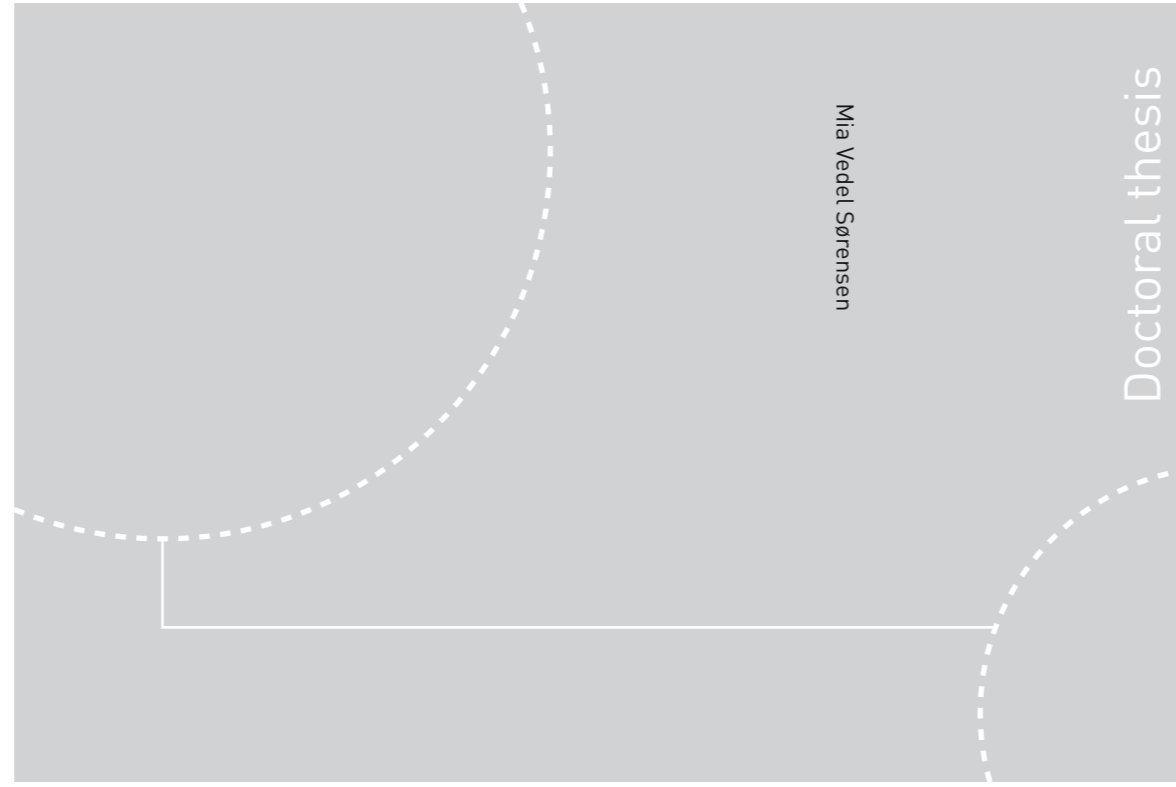


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Mia Vedel Sørensen

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Trondheim, September 2018

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Paper II. Mia Vedel Sørensen, Bente Jessen Graae, Dagmar Hagen, Brian J. Enquist, Kristin Odden Nystuen, Richard Strimbeck. Experimental herbivore exclusion, shrub introduction, and carbon sequestration in alpine plant communities. In revision BMC Ecology 11.06.2018.

Paper III. Richard Strimbeck, Bente Jessen Graae, Simone Lang, **Mia Vedel Sørensen**. Functional group contributions to net ecosystem exchange in alpine-arctic ecosystems. Submitted to Arctic, Antarctic, and Alpine Research 15.06.2018

Paper IV. Mia Vedel Sørensen, Bente Jessen Graae, Aimee Classen, Brian J. Enquist, Richard Strimbeck. Biotic and abiotic drivers of C cycling in three alpine-arctic tundra plant communities: potential mechanisms. Submitted to Arctic, Antarctic, and Alpine Research 12.06.2018.

Author contributions

Paper I:

MVS, RS, KON and BJG conceived and designed study.

MVS, REK and KON performed research. MVS analyzed data. BJE contributed to new methods. MVS wrote the paper with input from all coauthors.

Paper II:

MVS, RS, BJG, KON, DH, BJE participated in the design of the study. MVS performed fieldwork, statistical analysis, drafted, and wrote the manuscript.

MVS, RS, BJG, KON, DH, BJE contributed to the writing process and approved the final manuscript.

Paper III:

MVS, RS, BJG designed the study. MVS collected the data and processed it. RS analyzed the data. RS wrote the manuscript with input from MVS, BJG, and SL.

Paper IV:

Author Contributions: MVS, ATC, BJG, RS conceived and designed study. MVS performed fieldwork, lab work, and statistical analysis. ATC analyzed enzyme and hyphal data. BJE and ATC contributed to new methods. MVS wrote the paper with input from all coauthors.

List of abbreviations

a-bluc	α -glucosidase, a C degrading enzyme
AICc	Akaike information criterion corrected for small sample size
AM	Arbuscular Mycorrhiza
b-gluc	β -glucosidase, a C degrading enzyme
Biomass _{above}	Above-ground biomass
Biomass _{roots}	Root biomass
BP	Before Present
C	Carbon
cbh	cellobiohydrolase, a C degrading enzyme
CI	Confidence interval
CO ₂	Carbon dioxide
CWM	Community Weighted Mean
ECM	Ectomycorrhiza
ER	Ecosystem Respiration
ERM	Ericoid Mycorrhiza
GEP	Gross Ecosystem Photosynthesis
GEP ₆₀₀	GEP standardized to 600 PAR
GPP	Gross Primary Productivity
LA	Leaf Area
LAI	Leaf Area Index
LDMC	Leaf Dry Matter Content
LN	Leaf Nitrogen
LOI	Loss on ignition
Microbes sum	summed enzyme activity across all soil horizons
N	Nitrogen
NAG	N-acetylglucosaminidase, a N degrading enzyme
NEE	Net Ecosystem Exchange
NTNU	Norwegian University of Science and Technology
P	Phosphorous
PAR	Photosynthetic Active Radiation
Q10	The ratio of rates given a 10 C change in temperature
R	Respiration
R _{above}	Above-ground Respiration, plant respiration
R _{below}	Below-ground Respiration, soil respiration
SD	Standard deviation
SE	Standard error
SLA	Specific Leaf Area (area leaf per mass leaf)
SLA _{CWM}	Community Weighted Mean of Specific Leaf Area
SOC	Soil organic carbon
xylo	β -xylosidase, a C degrading enzyme

Abstract

Arctic and alpine tundra ecosystems are important for global carbon sequestration, as they store more than half of the global soil carbon (C), and these systems are predicted to have the greatest soil C loss following climate warming. Deciduous shrub cover has increased in tundra ecosystems during recent decades, but herbivory can counteract this. An open question is how shrub expansion will affect the carbon balance of these ecosystems? Where some studies predict increased ecosystem C storage with shrub expansion because of more vegetation biomass, a growing body of literature indicates that shrubs release soil C through below-ground processes. The overall aim of this thesis was to investigate how deciduous shrub expansion affects the growing season ecosystem CO₂ fluxes and C pools in an *Empetrum*-dominated heath, an herb- and cryptogam-dominated meadow, and a *Salix* shrub-dominated community in Dovrefjell, Central Norway. Additionally, experimental treatment effects of exclusion of small and large herbivory together with introduction of *Salix* transplants was measured, and abiotic and biotic drivers of C dynamics identified.

We found that the meadow and shrub communities had greatest C sequestration (GEP) and turnover (ER), but the total ecosystem C pool in the meadow stored twice that of the shrub community, because of more C in the organic soil. The heath stored one and a half times more C than the shrub community, despite of fixing least C (GEP).

Two years of herbivory exclusion resulted in significant effects in the heath community only, where we found increased standing biomass of dwarf shrubs and reduced ER. Effects of *Salix* introduction were weak, but the results from this thesis provide important baseline data for future studies. With a sequential harvest experiment, we identified that the dominant functional group in each community contributed most to GEP and aboveground respiration. ER was dominated by soil respiration in the meadow community (88 %), and contributed 63 % and 40 %, respectively in the heath and shrub communities. Based on these measurements we suggested a mechanistic framework for important abiotic and biotic drivers of GEP and above- and below-ground respiration. Soil moisture, specific leaf area, and above-ground biomass turned out to be the most important drivers. Additionally we found that potential soil microbial activity was linked to specific leaf area and both was highest in the meadow.

The results from this thesis indicate how shrub expansion into alpine tundra communities may influence the summer C cycling differently depending on plant community. Also, soil C pools might decrease due to below-ground differences and processes happening outside of the growing season. In this way, shrub expansion into alpine ecosystems might contribute to increased atmospheric CO₂ through a net CO₂ release from below-ground pools.

Sammendrag - norsk bokmål

Tundra på fjellet og i Arktis lagrer mer enn halvparten av det globale karbon i jorden, og samtidig forventer man at det er disse økosystemene som vil frigjøre mest karbon som følge av klimaendringenes høyere temperaturer. De siste tiårene har det blitt mer kratt og busker i tundraøkosystemene, men beiting kan bremse denne gjengroingen. Når det gjelder hvordan busker og kratt påvirker karbonbalansen i disse økosystemene er resultatene hittil motstridende. Noen studier mener at gjengroing bidrar til økt karbonlagring som følge av mer biomasse, mens andre tyder på at buskene via underjordiske prosesser heller frigir karbon bundet i jorda. Formålet med denne avhandlingen var å undersøke hvordan gjengroingen av løvbusker på fjellet påvirker karbondioksidflukser og -lagre i ei kreklinghei, ei eng og et vierkratt på Dovrefjell. Videre ble det undersøkt hvordan eksklusjon av beite og planting av vierplanter påvirker disse prosessene, og hvilke abiotiske og biotiske faktorer som har størst påvirkning på karbonfluksene.

Vi fant ut at eng og vierkratt både fikserte (GEP) og slapp ut (ER) mest karbondioksid om sommeren. Likevel var det enga som totalt lagret mest karbon, dobbelt så mye som vierkrattet, på grunn av store mengder karbon lagret i det organiske jordlaget. Kreklingheia lagret en og en halv gang mer karbon enn vierkrattet, til tross for lavest GEP. Det var bare i kreklingheia vi fant endringer i vegetasjon og karbonflukser som følge av to års fravær/eksklusjon av beite. Her hadde biomassen av dvergbusker økt og utslippet av karbondioksid (ER) var lavere. Effekten av vierplantingen var ubetydelig etter så kort tid, men resultatene fra dette studiet utgjør et viktig grunnlag for framtidige studier. Et høstingseksperiment hvor de funksjonelle plantegruppene ble fjernet sekvensielt viste at det hovedsakelig var de dominerende gruppene av vegetasjon som bidro mest til både karbonfiksering og overjordisk respirasjon. ER var i enga dominert av respirasjon fra jorden (88 %), hvor jordrespirasjonen utgjorde 63 og 40 % i kreklingheia og vierkratt. Basert på disse resultatene utarbeidet vi et mekanistisk rammeverk for hvordan viktige abiotiske og biotiske faktorer påvirker karbonfiksering og over- og underjordisk respirasjon (utslipp). Markfuktighet, spesifikt bladareal og overjordisk biomasse var de viktigste faktorer. I tillegg fant vi ut at potensiell mikrobisk jordaktivitet var koplet med spesifikt bladareal, og at begge var høyest i enga.

Resultatene fra denne avhandlingen tyder på at gjengroing av busker på fjellet kan påvirke karbonomløpet midt i vekstsesongen ulikt avhengig av hvilket plantesamfunn som er under gjengroing, og at lagring av karbon i jorda kan avta på grunn av jordprosesser utenfor vekstsesongen. Dermed kan flere og større busker på fjellet føre til at mer karbon blir frigitt enn fiksert, og bidra til økte karbondioksidnivå i atmosfæren.

Resumé - dansk

Alpin og arktisk tundravegetation rummer mere end halvdelen af jordens kulstoflagre, og modeller forudsiger at det er i disse økosystemer at frigivelsen af kulstof vil være allerstørst i et varmere klima. De sidste ti år har kratvegetationen øget markant i tundra økosystemer, men herbivorer kan potentielt mindske denne trend. Ifølge litteraturen er der ikke enighed om hvordan disse vegetationsændringer påvirker kulstofbalancen, da nogle studier viser en total stigning i kulstoflager på grund af den større plantebiomasse ved øget udbredelse af krat, mens andre studier viser at kratvegetation frigiver kulstof fra jorden. Det overordnede formål med denne afhandling var at undersøge hvordan den øgede udbredelse af løvfældende kratvegetation påvirker sommer økosystem kulstoffluxer og -lagre i en revling-domineret hede, en eng og et pilekrat i Dovrefjell, midt Norge. Desuden undersøgte vi effekter af herbivoriudelukkelse og pileplantning, samt hvilke abiotiske og biotiske faktorer som er vigtige for kuldioxid(CO₂)-fluxer.

Vi fandt ud af at eng og pilekrat fikserede (GEP) og frigav (ER) mest CO₂, men at den totale økosystem kulstoflagring var størst i engen, som lagrede dobbelt så meget som pilekrattet, på grund af den større mængde kulstof i det organiske jordlag. Heden lagrede halvanden gang så meget som pilekrattet, selvom GEP her var lavest. Efter to år med herbivoriudelukkelse, fandt vi kun i heden signifikante effekter pga. øget biomasse af dværgbuske og reduceret ER. Effekten af pileplantningen var ubetydelig efter så kort tid, men resultaterne fra dette studie er vigtige baggrundsdata for fremtidige studier. Et eksperiment hvor vi høstede en funktionel grupper af gangen, viste at de dominerende funktionelle grupper i hvert af de tre plantesamfund, bidrog mest til både GEP og respiration over jorden. ER var i engen domineret af respiration fra jorden (88 %), hvor jordrespirationen udgjorde 63 og 40 % i heden og pilekrattet. På basis af disse resultater foreslog vi en mekanisk ramme for hvordan vigtige abiotiske og biotiske faktorer påvirker GEP og over- og underjordisk respiration. Vi fandt frem til at jordfugtighed, specifikt bladareal, samt overjordisk biomasse var de vigtigste variabler. Desuden var potentiel ekstracellulær mikrobisk aktivitet i jorden koblet til specifikt bladareal og var højest i engen.

Resultaterne fra denne afhandling antyder at den øgede udbredelse af krat i alpin tundra kan påvirke sommerkulstofcyklus i forskellig retning, alt efter hvilket plantesamfund krattet udbreder sig i, og de antyder at processer under jorden uden for vækstsæsonen kan forårsage tab af kulstoflagring i jorden. Hvis dette er tilfældet, kan vegetationsforandringer øge kulstofkredsløbet og forårsage positiv tilbagekobling til atmosfæren.

Introduction

High-latitude alpine and arctic tundra ecosystems store more than half of global soil carbon (C) (Tarnocai et al. 2009), yet these sensitive systems are predicted to have the greatest soil C losses following climate warming (Crowther et al. 2016), with potential positive feedback to atmospheric CO₂ levels. During the last 30 years, deciduous shrub cover has increased in the arctic and alpine tundra. This is evidenced by a “greening” from satellite images, which has been linked to increases in above-ground biomass and observations of deciduous shrubs (Tape et al. 2006; Cannone et al. 2007; Tømmervik et al. 2009; Myers-Smith et al. 2011; Epstein et al. 2012; Epstein et al. 2015). These vegetation changes are closely linked to warmer temperatures, altered soil moisture levels, and longer growing seasons, and is predicted to increase further with future climate change (Settele et al. 2014; Myers-Smith et al. 2015; Martin et al. 2017; Myers-Smith & Hik 2018). Other important drivers of shrub expansion are changes in herbivory and human land use together with increased atmospheric CO₂ concentrations and N-deposition (Post & Pedersen 2008; Ravolainen et al. 2011; Speed et al. 2013; Zhu et al. 2016; Martin et al. 2017; Normand et al. 2017).

Several climate-carbon cycle models have predicted the increased shrub cover to enlarge the tundra biome sink capacity by increasing both above-and below-ground C storage (Euskirchen et al. 2009; Qian et al. 2010; Todd-Brown et al. 2014). However, some field studies have found less soil C and higher C cycling beneath deciduous shrubs, indicating that expansion and increased growth of shrubs in tundra vegetation will release soil C (Mack et al. 2004; Wilmking et al. 2006; Sjögersten & Wookey 2009; Hartley et al. 2012; Cahoon et al. 2012a; Parker et al. 2015). Still other studies found no changes in soil C with increased shrub cover (Sistla et al. 2013). Changes in plant community structure affect both abiotic and biotic drivers of C dynamics as plants influence ecosystem processes above and below the ground. One big uncertainty in global carbon models as well as in chamber-derived CO₂ flux studies is how C dynamics are affected by the ongoing shrub expansion and resulting vegetation shifts (Abbott et al. 2016; Chadburn et al. 2017; Virkkala et al. 2017).

In the following, I will outline how shrub expansion can alter abiotic and biotic drivers of tundra carbon dynamics and how herbivores influence C dynamics.

Abiotic and biotic effects of vegetation composition on tundra carbon dynamics

On a global scale, tundra vegetation is generally nutrient poor with low productivity (Christensen et al. 2000; Beer et al. 2010), and on a regional and local scale, it is a mosaic of different plant communities, dominated by different plant species with characteristic life strategies and growth rates. Deciduous shrubs occur in vast tundra areas and have done so through thousands of years but with fluctuating dominance (Hultén & Fries 1986; Naito & Cairns 2011; Paus et al. 2015). Heath and meadow are common plant communities in

alpine-arctic tundra, and they are subject to the recent “greening” and shrub expansion (Molau & Alatalo 1998; Björk & Molau 2007; Cannone et al. 2007). The vegetation in both plant communities is low-statured. Heath vegetation is dominated by evergreen dwarf shrubs and is much more nutrient poor, less productive, and covered in less snow than meadow vegetation that is dominated by herbaceous forbs and graminoids (Makarov et al. 2003; Wardle et al. 2004; Sundqvist et al. 2011).

Shrub expansion into heath and meadow will increase plant height and shade the soil surface, lowering the summer soil temperature with potential influence on microbial activity and nutrient cycling (Sturm et al. 2005; Myers-Smith & Hik 2013), thereby reducing soil respiration (Cahoon et al. 2012a; Semenchuk et al. 2016). Snow cover may be deep in shrub communities as the branches trap and accumulate snow (Sturm et al. 2005), and this can increase winter soil respiration if snow depth is increased by shrub expansion (Grogan & Jonasson 2006). The shrub canopy can also affect evapotranspiration (Christiansen et al. 2018) and the timing of spring snow-melt (Sturm et al. 2005). As temperature and soil moisture are primary controls of carbon fluxes and soil carbon (Körner 2003; Sjögersten et al. 2006; Berdanier & Klein 2011; Cahoon et al. 2012a; Dahl et al. 2017), shrub expansion is expected to affect C budgets through alterations in microclimate.

Shrub expansion alters species composition and thereby the plant functional traits dominating the plant community. Functional groups have been widely used to characterize plant species influence on ecosystem function in northern high latitudes, and they are often related to functional traits (Chapin et al. 1996; Dorrepaal 2007; Ward et al. 2009; Freschet et al. 2013; Díaz et al. 2015). Functional traits can reflect the plant’s effects (effect traits) on the environment and energy balance (Lavorel & Garnier 2002). Functional traits can be regarded on a scale of resource investment (c.f., the leaf economic spectrum, Reich et al. 1997; Wright et al. 2004). The relative growth rate is high when leaf photosynthesis is high, and that is controlled by both leaf area and leaf nitrogen, since nitrogen (N) is invested in proteins in the photosynthetic apparatus (Reich et al. 1997; Wright et al. 2004). However, plant investment in recalcitrant compounds and structure for defense against herbivory and rough climatic stresses weighs against a high relative growth rate, and is reflected in the area per mass of leaf or specific leaf area (SLA) as well as in the leaf dry matter content (LDMC) (Wright et al. 2004; Díaz et al. 2015; Pierce et al. 2016). Evergreen shrubs are on one side of the spectrum with high amounts of defense compounds (Tybirk et al. 2000), and low SLA, high LDMC, and low LN, presumably photosynthesizing less on an area or mass basis. On the other side of the spectrum, deciduous shrubs, graminoids, and forbs with high SLA and low LDMC, have higher productivity and photosynthesize more (Wardle et al. 2004; Wookey et al. 2009; Freschet et al. 2010; Veen et al. 2015). The leaf properties affect the decomposability of the leaves and litter quality, and thereby control the release and availability of nutrients to the soil (De Deyn et al. 2008; Hodgson et al. 2011; Bardgett

2017), that in turn affects the heterotrophic respiration and soil C pools (Cornelissen et al. 2007b; De Deyn et al. 2008; Veen et al. 2015).

Recently, root traits received increased focus in many studies (Freschet et al. 2013; Roumet et al. 2016). Both root exudates and root litter influence the soil C pool (Rasse et al. 2005; De Deyn et al. 2008), and root respiration contributes to the below-ground autotrophic respiration. Root distribution and production differs between graminoid and shrub dominated tundra, as shrubs grow less productive and more shallow roots than graminoids (Mack et al. 2004; Iversen et al. 2015). The microbial community, including root-associated fungi, can stimulate plant productivity, and act as a vector for plant C build-up in the soil (Van Der Heijden et al. 2007; Phillips et al. 2013; Averill & Hawkes 2016). Evergreen dwarf shrubs are associated with ericoid mycorrhiza (ERM), and graminoids and forbs often with arbuscular mycorrhiza (AM) (Michelsen et al. 1998; Cornelissen et al. 2001; Becklin & Galen 2009; Becklin et al. 2012), whereas deciduous shrubs are often associated with ectomycorrhiza (ECM) (Väre et al. 1992; Iversen et al. 2015). The ECM associated with deciduous shrubs in arctic-alpine ecosystems have been linked to soil C loss in shrub tundra but not in heath tundra communities (Hartley et al. 2012; Clemmensen et al. 2015; Parker et al. 2015). This is because they might act as decomposers and can mediate rhizosphere priming and together with other root exudates release C from the soil (Kuzyakov 2002; Talbot et al. 2008; Kuzyakov 2010; Lindahl & Tunlid 2015). The rate of decomposition can be measured by the potential soil microbial activity. The content of primary C constituents in plant litter (cellulose, hemicellulose, pectin and lignin) varies with litter quality and vegetation C:N ratios, and therefore influences the potential activity of microbial C-degrading enzymes (Linkins et al. 1990; Sinsabaugh et al. 1994; Sinsabaugh et al. 2002; De Deyn et al. 2008; Hernández & Hobbie 2010; Bardgett 2017). Breakdown of organic material requires the activity of many different organisms, and extracellular enzymes are produced by bacteria, archaea and fungi, but basidiomycete fungi play the major role in lignin and cellulose degradation (Burns et al. 2013). We therefore expect the C-degrading microbes to vary with shrub expansion and vegetation woodiness.

The effect of herbivores on shrub expansion and C dynamics

Herbivores affect vegetation composition and ecosystem structure (Estes et al. 2011; Olofsson et al. 2012), by consumption, trampling, and by adding N via feces (Van Der Wal & Brooker 2004). Via consumption and trampling, herbivores can reduce tall deciduous shrub growth, and maintain low-growing tundra vegetation (Den Herder et al. 2004; Olofsson et al. 2009). Herbivores may therefore counteract the C cycle effects of shrub expansion by reducing the vegetation biomass and decreasing rates of C cycling (Cahoon et al. 2012b; Speed et al. 2014; Metcalfe & Olofsson 2015).

Still, when diving into the literature (Table 1), there is not much consensus on either C fluxes or soil C storage consequences of herbivory (Susiluoto et al. 2008; Martinsen et al. 2011; Tanentzap & Coomes 2012; Cahoon et al. 2012b; Köster et al. 2015; Metcalfe & Olofsson 2015; Austrheim et al. 2016; Andriuzzi & Wall 2017; Lara et al. 2017). Regarding gross ecosystem photosynthesis (GEP), most previous studies found herbivory decreased C fixed by the vegetation (Sjögersten et al. 2008; Cahoon et al. 2012b; Vaisanen et al. 2014; Metcalfe & Olofsson 2015). Potential mechanisms for decreased GEP can be altered functional group composition, loss of leaf area, reduced vegetation height, reduced above-ground biomass, and reduced biomass of plant roots (Austrheim et al. 2007; Diaz et al. 2007; Klumpp et al. 2009; Pajunen et al. 2012; Cahoon et al. 2012b; Speed et al. 2014; Köster et al. 2015; Metcalfe & Olofsson 2015). Yet, other studies found no difference in GEP with herbivory (Susiluoto et al. 2008) or an increase over a 50 year experiment due to changes in plant community composition from graminoid to moss, due to absence of lemmings (Lara et al. 2017). Herbivores can also add feces, which in turn can enhance GEP due to increased plant nutrient availability (Van Der Wal & Brooker 2004; Piñeiro et al. 2010). Ecosystem respiration (ER), have in previous studies been reported not to differ with grazing and browsing (Susiluoto et al. 2008; Cahoon et al. 2012b; Köster et al. 2015; Metcalfe & Olofsson 2015; Lara et al. 2017). In other studies, ER decreased (Sjögersten et al. 2008; Sjögersten et al. 2011; Andriuzzi & Wall 2017) due to reduction in biomass, removal of plant litter, or soil compaction due to trampling (De Deyn et al. 2008; Piñeiro et al. 2010; Andriuzzi & Wall 2017). However, Vaisanen et al. (2014) found increased ER with heavy grazing of reindeer, as compared to lightly grazed plots. Increased ER with herbivory can occur with more productive vegetation such as graminoids, or due to trampling if soil temperature increase due to lower vegetation cover and insulation (Van Der Wal & Brooker 2004). Grazing can also promote root exudation, that can stimulate microbial activity which thereby increase heterotrophic respiration (Bardgett & Wardle 2003; Tanentzap & Coomes 2012) and GEP (Van Der Heijden et al. 2007). While a meta-analysis found that herbivores decrease soil respiration in the subarctic, sheep presence in temperate grasslands can increase soil respiration (Andriuzzi & Wall 2017). The opposing results of C sequestration from alpine and arctic ecosystems are because ecosystem effects of herbivory vary with plant community, herbivore species, herbivore pressure, and temporal and spatial scale of the experiment (Tanentzap & Coomes 2012; Austrheim et al. 2016; Barrio et al. 2016; Lara et al. 2017). Additionally, many different processes such as plant defense mechanisms are involved, and they might interact with climate and historical context (Diaz et al. 2007). Over the past decades, small and large herbivore densities (both domestic and wild) have changed in arctic-arctic ecosystems (Ims et al. 2008; Austrheim et al. 2011), including Norway (Henden et al. 2011; Rekdal & Angeloff 2015; Framstad 2016). It is consequently very timely and important to better understand the herbivory impact on shrub expansion and C cycling (Ims et al. 2008; Post & Pedersen 2008; Olofsson et al. 2012; Ravolainen et al. 2014).

Table 1: Examples of suggested mechanisms of herbivory ecosystem effects on the carbon balance, here either above-ground biomass, Gross ecosystem photosynthesis (GEP), Ecosystem respiration (ER) or soil carbon (C). Up-ward arrows indicate hypothesized increase; downward arrows a hypothesized decrease. nd = no difference. References with * indicate that the study measured the carbon response.

Herbivory ecosystem effects	Mechanism	Carbon balance response					Reference
		above-ground biomass	GEP	ER	Soil C		
Plant defoliation Selective grazing -> Influencing species or functional group composition	Loss of leaf area, lower vegetation height	↓	↓	↓	nd		Diaz et al. 2007, Metcalfe & Olofsson 2015*, Sjögersten et al. 2008*, Sjögersten et al. 2011*
	And/or Deciduous shrubs ↓ And/or Bryophytes ↑ And/or Lichens ↓	↓	↓	nd	nd		Cahoon et al. 2012b*, Metcalfe & Olofsson 2015*, Austrheim et al. 2007, Pajunen et al. 2012, Takala et al. 2014, Körster et al 2015*, Speed et al. 2014*
	Graminoids -> moss		↑	nd			Lara et al 2017*
Consumption	Reduce root biomass		↓		↓		Klumpp et al 2009*
	Stimulate microbial activity		↑	↑	↓		Bardgett & Wardle 2003; Tanentzap & Coomes 2012*
Enhance roots exudates	Above-ground biomass ↓ if affecting soil temp ↑	↓					van der Waal & Brooker 2004 van der Waal & Brooker 2004
	Soil compaction (reducing water availability and root growth) Reduce N mineralization		↓	↓	↓		Pinero et al. 2010, Andruizzi & Wall 2017
Trampling	Plant litter removal (litter quantity)			↓	↓		De deyn et al. 2008
	Add available N via feces -> stimulate microbial activity	↑	↑	↑			Pinero et al. 2010*, van der Waal & Brooker 2004, Stark & Väisanen 2014*
Influen- cing N cycling							

Aim and questions

The overall aim of this thesis was to study the carbon budget associated with deciduous shrub expansion in an *Empetrum*-dominated heath, a herb-and cryptogam dominated meadow, and a *Salix* shrub dominated community.

In this thesis, I define the carbon budget, as the ecosystem CO₂ fluxes and C pools. Mid-growing season carbon fluxes were used as an approximation for growing season fluxes and C pools was the carbon contained in the above-ground vegetation, litter, roots, and organic and mineral soil.

Specific questions asked:

- 1) Are shrub communities carbon sources or sinks, and more or less so compared to heaths and meadows? (Paper I)
- 2) What is the effect of herbivore exclusion on carbon cycling in the three communities? (Paper II)
- 3) What biotic and abiotic variables drive the carbon dynamics in alpine communities? (Paper III, IV)
- 4) What happens to carbon balance during shrub expansion in heath and meadow? (Paper I, II, IV)

We will answer the above questions by:

- a) Comparing the three common alpine plant communities
- b) Experimentally manipulating herbivory with exclosures and simulating shrub expansion with introduction of *Salix* transplants

Study sites and methods

Study sites

The study area is located in the Fennoscandian tundra (Sonesson et al. 1975) in the Southern Scandes, around 1100 m a.s.l. in the low-alpine zone above the forest-line in Dovrefjell, Central Norway (62°N, 9°E), 5-10 km from Hjerkin. The Fennoscandian tundra is part of the oro-arctic (c.f., Virtanen et al. 2016), and a mosaic of different plant communities, and we chose to work in plant communities with large homogenous vegetation, to be able to set up a full experimental design. The communities in focus were an *Empetrum*-dominated heath, an herb-and cryptogam-dominated meadow, and a *Salix*-dominated shrub community (Figure 1). The three communities were situated on two neighboring mountains (Mt. Hjerkinshøe 1288 m and Mt. Armodshøkollen 1274 m) with similar elevation, but the shrub and heath communities were south facing, whereas the meadow was south-west facing (Figure 2). The soil profiles in the three communities were podzolic, with a partial albic horizon in the shrub community and a well-developed albic horizon in the heath (Sjögersten & Wookey 2009) (Figure 3). Soils in all three communities were developed from glacial moraines, and the bedrock was metavolcanic in the heath and shrub communities, and shale in the meadow (NGU 2015). The climate in the area is continental and one of the driest in Norway with means (1961-1990) of 700 mm for annual precipitation and 298 mm for the growing season. The annual mean temperature in the area is -1 °C and 7.1 °C during the growing season (New et al. 2000).

The Dovrefjell have according to Paus et al. (2015) been ice-free as early as 16-18,000 years ago (whereas others claim 12,000), and the ice melted first from the mountain tops, so there might have been local ice caps in certain places (Paus et al. 2015). About 9000 years before present (BP) the forest-line was ca 170 m higher than present, and started to retract again around 8500 years BP (Paus & Haugland 2017). There may have been human impact in the area from 4-5000 y BP (Paus & Haugland 2017), but animal husbandry in the area began about 400 years BP, and probably intensified around year 700 with permanent settlement (Risbøl et al. 2011). A preliminary study indicated that the age of a *Salix* individual from the shrub community was 61-73 years (Emilia Guitierrez Merino, unpublished). Aerial photos show that the shrub community was covered with shrubs 30 years ago (Figure 4).

The most important herbivores at present in the area are domestic Norwegian white sheep (*Ovis aries*) present at low-intensity with up to 25 sheep per km² (NIBIO 2017). Smaller but also important herbivores are the rodents, voles (*Microtus agrestis*, *M. oeconomus*, and *Myodes rufocanu*) and lemmings (*Lemmus lemmus*). The area experienced rodent peak years in 2007, 2011, and 2014, but not in 2015 (Framstad 2016). Ptarmigan (*Lagopus lagopus* and *L. muta*), hare (*Lepus timidus*), moose (*Alces alces*), and occasionally wild reindeer (*Rangifer tarandus*) are present or pass through the area.

For detailed community characteristics see Table 1 in **Paper I** and Table 1 in **Paper IV**.

Experimental and sampling design

In 2013, eight replicate blocks of four treatments in a 2×2 factorial design were randomly selected and established in each community. The treatments consisted of plots (50 × 50 cm) with and without herbivore exclosures, and plots with and without *Salix* introduction (*Salix* transplants) (Figure 2b). Herbivore exclosures (80 × 80 × 50 cm) with a lid, excluded both small and large herbivores and was dug about 5 to 10 cm into the ground. The *Salix* introductions consisted four willow transplants, planted in June 2014 (Figure 5). The willow saplings were from cuttings of *Salix* bushes in the vicinity of the experimental sites, cultivated during the winter in a plant nursery (Norske Naturplanter AS, Færvik, Norge) (Hagen & Evju 2014). See also detailed description in **Paper II**.

We attempted to plant willows in 2013, by sampling *Salix* cuttings from Kongsvoll botanical garden cultivating them in the NTNU greenhouse at Dragvoll in May 2013. However, a very warm spring in Trondheim caused the cuttings to die and the attempt failed. We also tried using live plants taken from roadsides at Hjerkinn in 2013, but they did not survive the transfer.

Outside of the experimental plots but within each block in each community, we sampled leaf traits and hyphal ingrowth.

Six blocks from each community were randomly selected for above-ground biomass harvest in neighboring harvest plots (0.25 × 0.25 m in heath and meadow and 0.5 × 0.5 m in shrub community to catch the heterogeneity of woody biomass) both in 2013 and 2015. An adjacent soil pit was additionally dug in 2015 to measure the below-ground properties.

Measurement overview

To estimate C fluxes in the three communities we measured Net Ecosystem Exchange (NEE) and Ecosystem Respiration (ER) in the growing seasons of 2014 and 2015 (**Paper I, II, IV**). The method followed Sloat et al. (2015), Arnone and Obrist (2003), Street et al. (2007), Jasoni et al. (2005), and Williams et al. (2006), but measurement equipment and chamber design were adjusted for pack-frame transport in the Norwegian mountains (Figure 6). In 2014, we attempted to measure early, mid, and late growing season, however, we decided to not include the early and late measurements, due to minor phenological differences (Figure S1, Appendix V). In 2014 we also measured diurnal C fluxes in the early growing season in the heath (26.-27. June) and shrub community (2.-3. July), and in the heath mid and late growing season. These data were not reported in the papers but can be seen in Appendix V. The contribution of each functional group to NEE was additionally measured with a sequential harvest experiment conducted during biomass harvest in 2015 (**Paper III**).

Microclimate was surveyed during C flux measurements. Surface temperature was measured with temperature loggers from autumn 2013 to autumn 2015, soil moisture was

measured in early, mid and late season in 2015, and snow depth was measured one time in 2015 and 2016 in each community (**paper I, IV**).

To determine the above-ground standing C pools, biomass was harvested in both 2013 and 2015. The biomass harvested in 2013 was used to identify the C and N concentrations of the functional groups, whereas the biomass harvested in 2015 was used to determine biomass characteristics of the vegetation (**Paper I, III, IV**), but also to model the estimated biomass in each of the experimental plots (**Paper II**).

The below-ground C pools of roots and soil were determined from the soil pits that were sampled in 2015 (**Paper I and IV**). In the same soil pits, microbial activity of the soil community was assessed by assaying the potential extracellular enzyme activity of α -glucosidase (a-gluc), β -glucosidase (b-gluc), cellobiohydrolase, β -xylosidase (xylo), cellobiohydrolase (cbh), and N-acetylglucosaminidase (NAG) for each soil horizon (**Paper IV**). Enzymes that are important in C degradation and break down carbohydrates and polysaccharides were a-gluc, b-gluc, cbh, and xylo, and cbh. NAGase mineralizes nitrogen from chitin, and thus is produced by fungi to acquire N (Read & Perez-Moreno 2003; Bell et al. 2013). Mycorrhizal hyphal mass was measured from ingrowth bags, buried below the soil surface between the organic and mineral soil horizon from mid June to September 2015 in each block in the three communities. These data were not fit for analysis as there were poor ingrowth in some plots, but the data is reported as background data (**Paper IV**).

Vegetation analysis was performed during mid-growing season in 2013, 2014, and 2015. The analysis in 2013 was based on plant cover in percent, and the abundances were used to estimate which plants to sample for leaf traits (**Paper IV**). In 2014 and 2015, the analysis was performed by the pinpoint method additionally measuring vegetation height. In 2014, cryptogam species were identified (**Paper I**). In 2015, *Salix* transplant performance were measured as well. Harvest plots were analyzed to the level of functional groups (**paper I, II, III, IV**).

Leaf traits (leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC)) were sampled in 2013, 2014, 2015, and 2016 according to Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013). Community weighted means (CWM) were calculated (**Paper IV**) following Violle et al. (2007) and Garnier et al. (2004) based on abundances from the vegetation analysis in 2015.

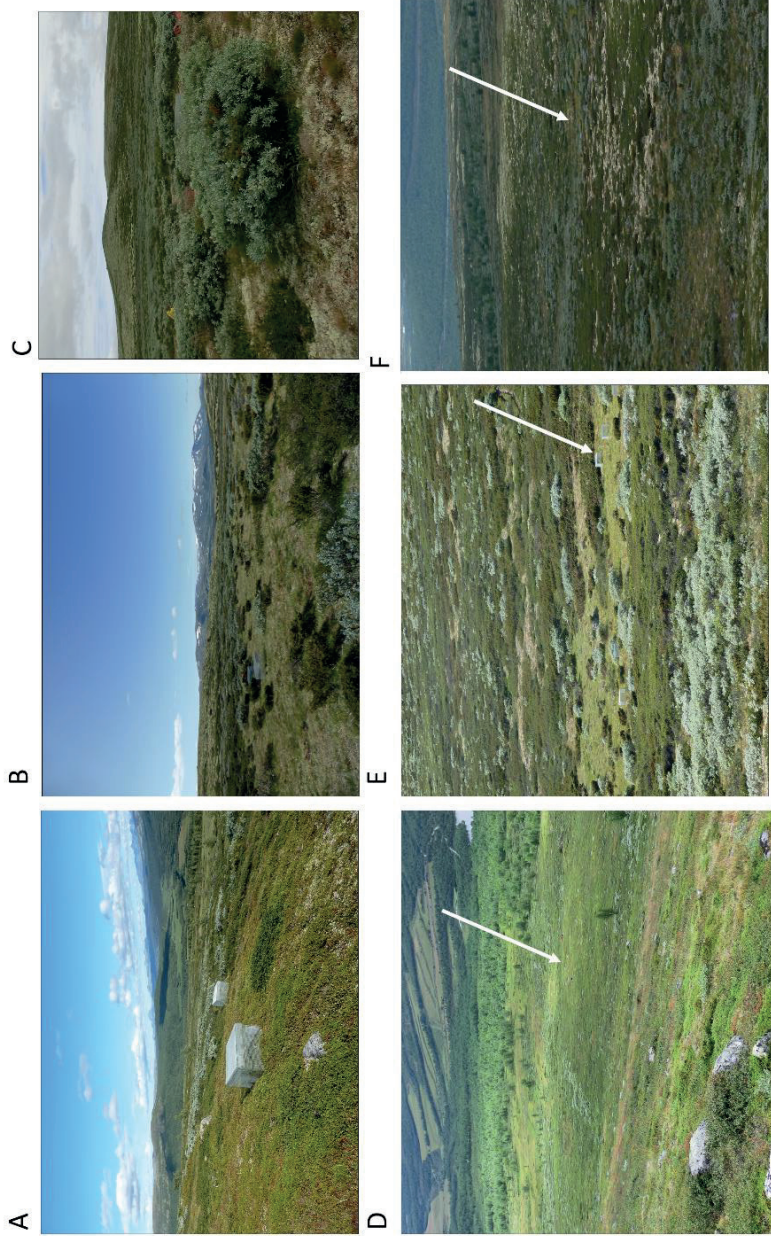


Figure 1: The three plant communities on the same elevation (A, B, C), and from the nearest mountain top (D, E, F). A, D) the heath, B, E) the meadow, and C, F) shrub communities respectively. The white arrows point toward the area where the plots are located.

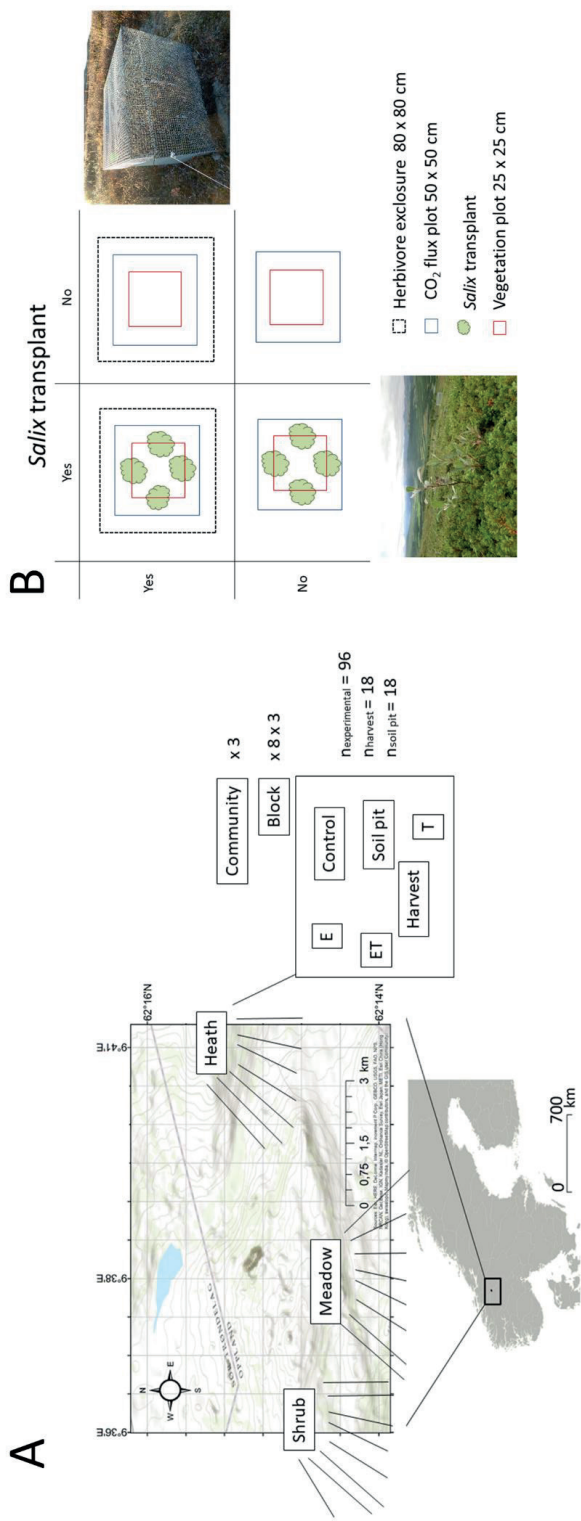


Figure 2: A) Study area and sampling design, and B) experimental design with herbivore enclosures and *Salix* introduction with *Salix* transplants.

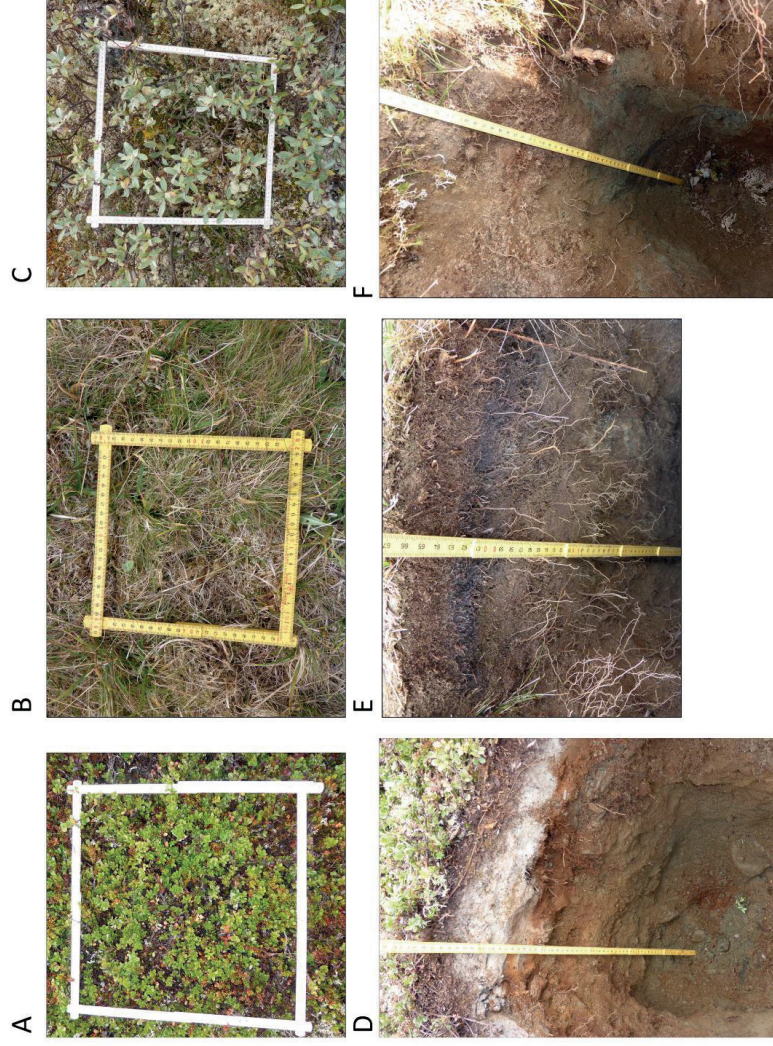


Figure 3: Soil profiles. The above-ground vegetation (A, B, C) growing over the soil profiles in representative plots from A,D) heath, B,E) meadow, and C, F) Salix shrub communities.

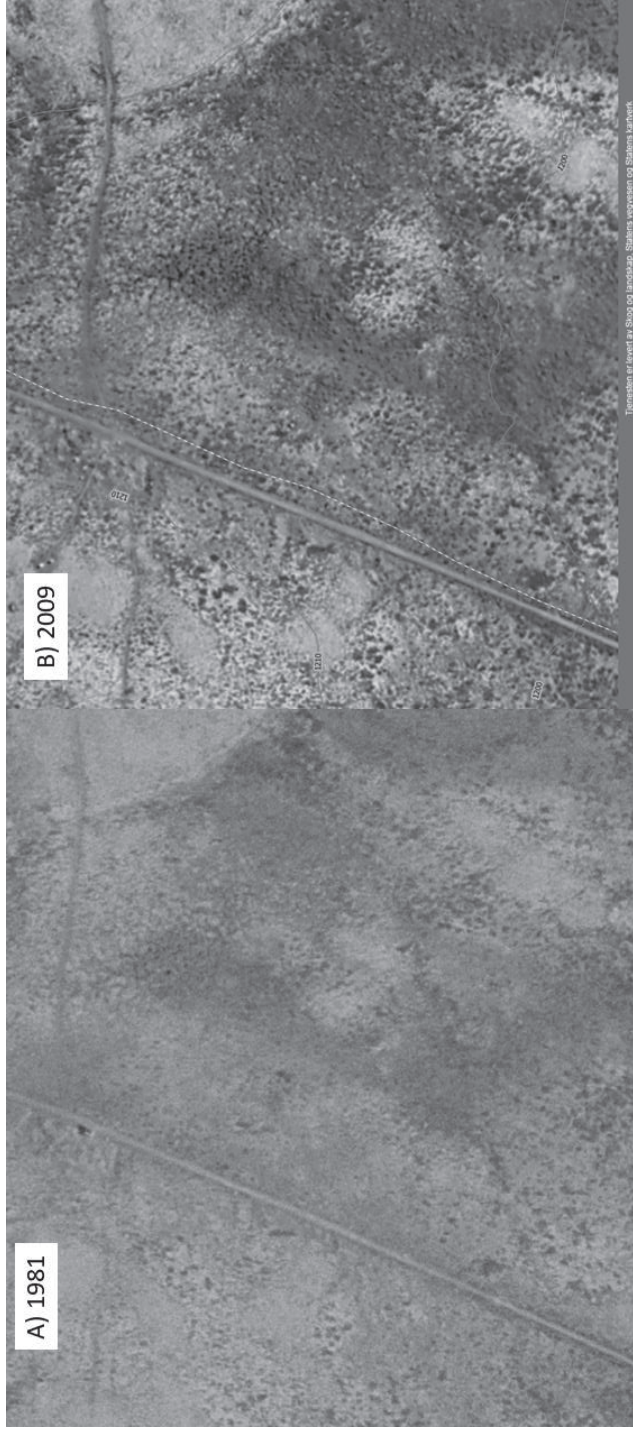


Figure 4: Air photos of the Salix shrub community in A) 1981 and B) 2009. Our plots are on the right side of the main trail (Den Gamle Kongevegen). The vegetation seem to be covering the same area, but might have become taller. Photos were taken A) 5700-5800 m over the sea from Statens Kartverk, B) from «Norge i bilder», Skog og landskap, Statens vegvesen and Statens kartverk.

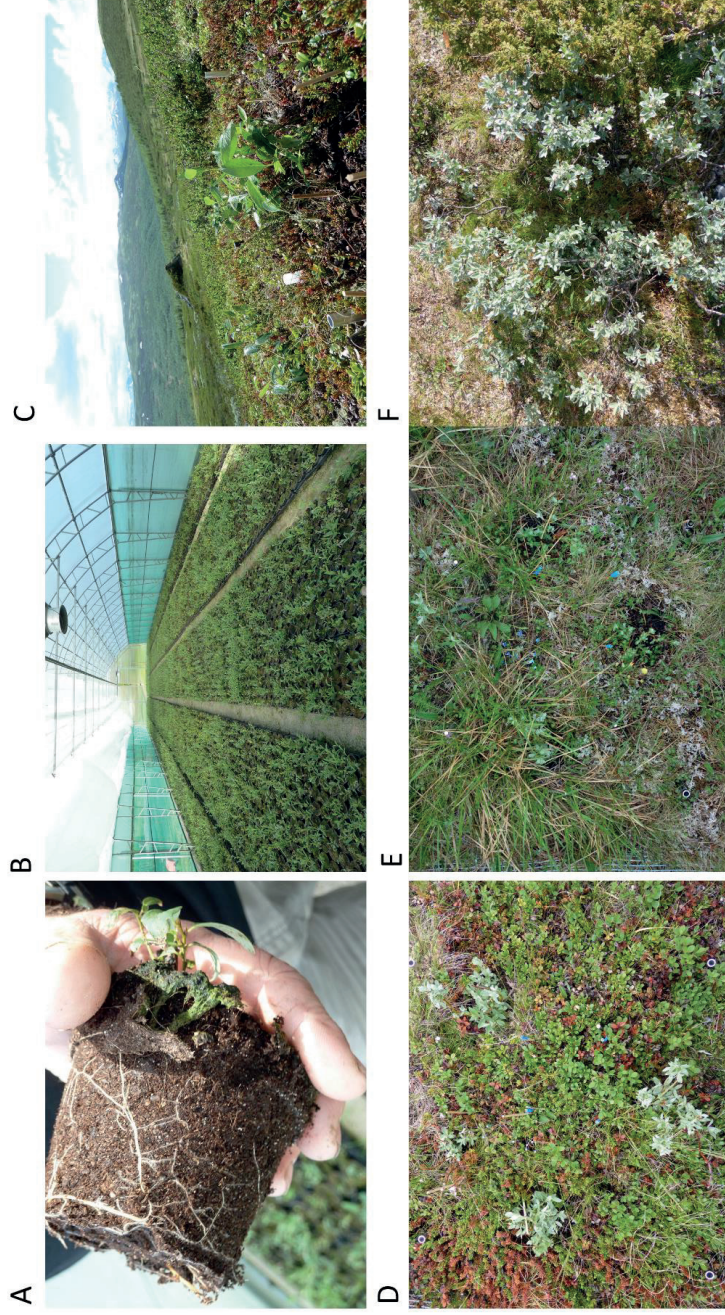


Figure 5: A, B, C) Transplants from greenhouse and planting in June 2014. D, E, F) *Salix* introduction with transplants in heath, meadow and shrub community as a control in August 2015.

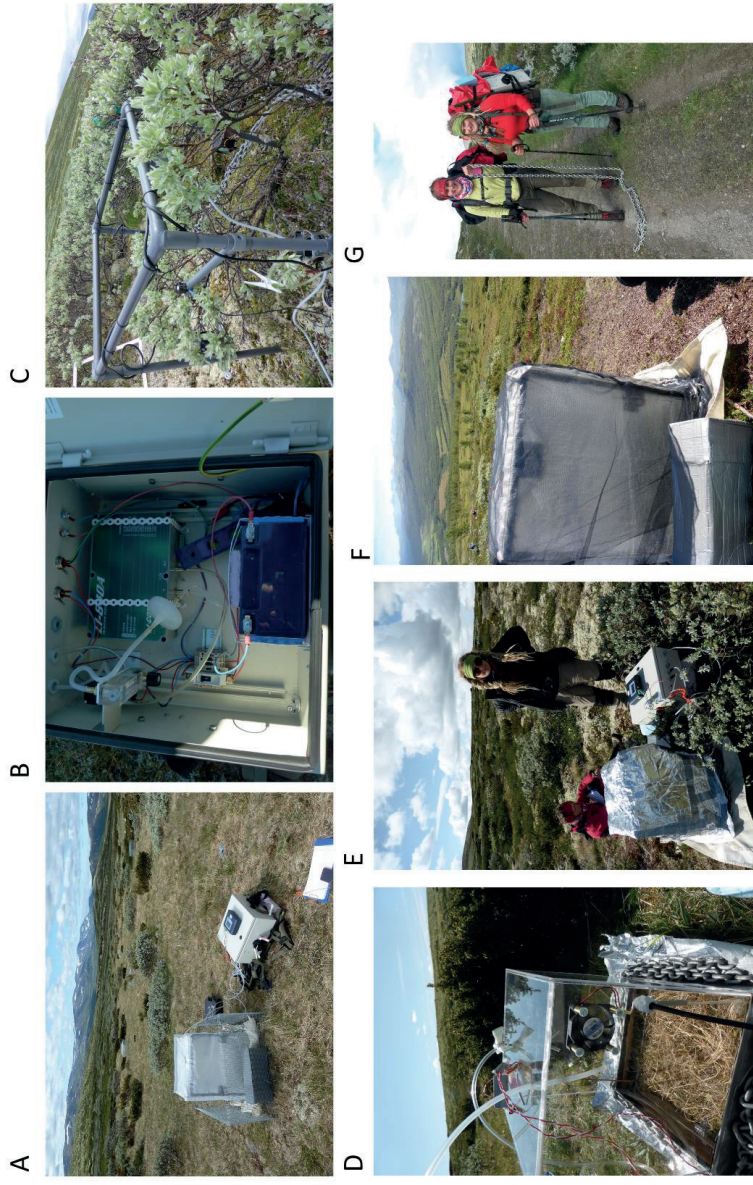


Figure 6: A) CO₂ equipment setup during light measurement inside an enclosure in the meadow community. B) Inside the CO₂ box. C) The CO₂ chamber skeleton for the 50 x 50 cm chamber. D) The small 25 x 25 cm chamber used in sequential harvest experiment. E) CO₂ equipment setup during dark measurement in the shrub community. F) Tull cover of CO₂ chamber during light curve measurement. G) Transport of equipment by foot to the sites.

Main results and discussions

The shrub community was the greatest summer sink, but shrubs might still be draining the pool

Comparing C pools and fluxes in **Paper I** revealed that the shrub community, despite being the greatest sink (in relation to net ecosystem exchange (NEE)) during mid-day growing season measurements and having the largest above-ground C pool, stored least total ecosystem carbon (Figure 2, **Paper I**). This was because the organic soil C pool was much smaller in the shrub community than in the heath and meadow communities. This finding was opposite to predictions from global climate-carbon models (Euskirchen et al. 2009; Qian et al. 2010; Todd-Brown et al. 2014), but confirmed field study findings on *Betula nana* shrubs in heath and tussock tundra (Mack et al. 2004; Wilmking et al. 2006; Sjögersten & Wookey 2009; Hartley et al. 2012; Cahoon et al. 2012a; Parker et al. 2015).

Additionally, early growing season diurnal measurement in the heath and shrub community indicated that the shrub community overall acted as a CO₂ sink while the heath was a source during early growing season (Appendix V). Regardless of the shrub community being the greatest sink, ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP) were equal in the meadow and shrub community, and surprisingly, total ecosystem carbon in the meadow was twice that of the shrub community. The differences were primarily in the soil organic carbon pool, and we therefore concluded that summer growing season flux measurements could not explain the soil carbon differences between the communities. More likely, differences in fluxes in other seasons could be responsible for this pattern, as the tundra switches from sink to source outside of the growing season (Bardgett et al. 2005; Euskirchen et al. 2012; Vaisanen et al. 2014; Westergaard-Nielsen et al. 2017). For example, root growth in shrubs is asynchronous to above-ground growth and happens outside the “growing season” but not in graminoids (Blume-Werry et al. 2016; Sloan et al. 2016). Thus, different plant functional groups distribute the photosynthesized carbon differently, both temporarily and spatially, and deciduous shrubs have more shallow roots than graminoids (Mack et al. 2004; Iversen et al. 2015) and this in turn affects soil C pools (Rasse et al. 2005; Dietzel et al. 2017).

Shrubs and root-associated microbes might also induce soil C priming (Kuzyakov 2002, 2010; Hartley et al. 2012; Clemmensen et al. 2015; Parker et al. 2015). A study on deciduous *Betula pubescens* did show that a great amount of old C was degraded during winter, presumably due to depletion of the labile C fixed the previous growing season (Hartley et al. 2013). In addition to seasonal variance, we acknowledge that long-term history and vegetation changes might be at play as well (Bardgett et al. 2005), and to study the drivers of the soil carbon stocks further requires soil carbon age and high resolution historical vegetation data. Presumably, elevations around 1100 m a.s.l. were covered in coniferous and deciduous forest 9000 years BP (Paus et al. 2015), but how this affected local differences between the three communities is not known.

Herbivore exclusion increased above-ground biomass and reduced ecosystem respiration in the heath community only

To investigate the importance of herbivory for C cycling, we estimated standing biomass and measured C sequestration in a full factorial design where small and large mammals were excluded from the three communities (**Paper II**). We hypothesized that cessation of grazing and browsing would increase GEP and ER. Moreover, we expected the treatment effects to be greatest in the meadow, as the vegetation is most palatable in this community.

The experiment (**Paper II**) revealed significant treatment effects in the heath community, but not in the meadow and shrub communities. Two years of herbivore exclusion in heath increased the standing biomass due to increased biomass of dwarf shrubs. Moreover, the biomass of bryophytes and ER were reduced (Figure 2 and 3, Paper II). Our finding of increased dwarf shrub biomass corresponds to previous enclosure studies in tundra heath vegetation (Olofsson et al. 2009; Köster et al. 2015; Vowles et al. 2017). Decreased trampling and presence by sheep seems to be the most probable cause of the increase of above-ground biomass and reduction of ER in the heath community. Firstly, because evergreen dwarf shrubs often are avoided as food by herbivores due to their high content of secondary compounds (Danell et al. 1994; Tybirk et al. 2000; Christie et al. 2015). Secondly, sheep rest and chew their cud in heath communities (Rekdal & Angeloff 2015) and we observed sheep feces, torn out plot marking poles, and wool on the enclosures in the heath. Sheep might still be grazing on forbs and to some extent graminoids in the heath. This could explain the marginally higher graminoid biomass inside the enclosures. Moreover, sheep grazing has been shown to favor the grazing-resistant *Polytrichum* species (Austrheim et al. 2007) that are persistent in the heath, and this could explain the lower biomass of bryophytes in the enclosures. Thirdly, the reduced ER within enclosures in the heath could be caused by limited substrate availability (Stark & Väisänen 2014) due to reduced nitrogen additions via feces.

The increased biomass in the enclosures could cause an increase in shading of the understory and soil, which potentially could explain the decreased biomass of bryophytes (Klanderud & Totland 2005; Walker et al. 2006; Pajunen et al. 2012; Takala et al. 2014). This vegetation shading can also explain the decreased ER, as the lower soil temperature can decrease microbial activity and thereby soil respiration.

An alternative explanation to a trampling effect and vegetation shading could be an enclosure effect. We did find lower summer soil temperatures inside the enclosures in the heath and the meadow communities (Table S2, **Paper II**), so a trampling effect is difficult to distinguish from an enclosure effect.

Other important biotic and abiotic drivers of C dynamics in alpine plant communities are explored in the following.

Drivers of carbon dynamics in alpine communities

In **Paper III** we identified the contribution of functional groups to ecosystem photosynthesis and respiration, and in **Paper IV**, which abiotic and biotic drivers influence C cycling in the three communities. Biotic drivers in this context were leaf traits, biomass, C:N ratios, and microbial activity.

We found that the greatest contributors to above-ground respiration and photosynthesis were the dominant plant functional types in each plant community (Figure 2, **Paper III**), but dwarf shrubs and herbs contributed substantially in the shrub community. An important result from **Paper III**, in relation to disentangling drivers of C dynamics, was identifying the fraction of above- and below-ground respiration in the three communities. In **Paper III** the fraction above-below-ground respiration was based on the sums of adjusted respiration estimates of from each functional group, and here we found that about 60 % of ER in the shrub community was from the above-ground vegetation and about 40 % from below-ground processes. In the heath community below-ground respiration contributed with 63 % of ER, and in the meadow community, ER was primarily driven by below-ground respiration, which constituted 88 % of ER. This result confirmed our hypothesis from the discussion in paper I that the equal respiration in the meadow and shrub community was caused by different mechanisms. To identify whether mechanisms related to plant, soil, or microbes were responsible for the different fluxes, we tested a hypothesized framework (see Figure 1 from Paper IV). Based on the sequential harvest experiment in **Paper III** we used ER from pre-harvest and bare soil measurements adjusted for temperature, and we separated ER in above- and below- ground respiration. Due to the more sophisticated calculation method in **Paper III**, the above-and below-ground respiration estimates of the shrub community in particular, was there about 10 % smaller due to corrections for excess respiration after removal of cryptogams. We used the fractions of above-and below-ground respiration (63, 88, 51 %, for the heath, meadow and shrub community, respectively), to specifically test which processes could be responsible for the above-and below-ground ecosystem fluxes. Essential abiotic drivers of GEP and ER are light and temperature, but to reduce degrees of freedom in the statistical analysis, we chose to keep those factors constant and standardize GEP and ER in relation to those variables.

Soil moisture was the most important driver of GEP across community (Figure 5 a-c in **Paper IV**) and several other studies also highlight the importance of soil moisture for plant growth and ecosystem photosynthesis (Sjögersten et al. 2006; Dahl et al. 2017; Westergaard-Nielsen et al. 2017). We hypothesize that the mechanisms behind the importance of soil moisture is primarily nutrient availability and nutrient mineralization, because desiccation limits the flow of nutrients to plant roots, and limits microbial activity that is responsible the for nutrient mineralization (Körner 2003; Berdanier & Klein 2011).

Total above-ground biomass was most important for above-ground respiration, but the effect was not significant. The most important driver of below-ground respiration was the community weighted mean of specific leaf area (SLACWM) (**Paper IV**). We attributed the effect of SLA to the decomposition rate, as labile leaves decompose faster

and provide more food for microorganisms, thereby increasing heterotrophic respiration (Questad et al. 2007; De Deyn et al. 2008; Bardgett 2017). Carbon degrading enzyme activity was highest in the meadow community, and decreased with vegetation woodiness and increased with SLACWM. This is likely because SLA is correlated with leaf nitrogen (Wright et al. 2004), and can be a surrogate for nitrogen availability (Hodgson et al. 2011). We suggest nitrogen and substrate availability was highest in the AM-dominated meadow (Phillips et al. 2013), as total soil nitrogen was twice as high as in the heath and shrub community, and both soil organic C and pH was higher in the meadow. Nitrogen availability stimulates microbial activity (Hobbie et al. 2002) that in turn stimulates heterotrophic respiration (Hernández & Hobbie 2010), and this can then explain why SLA was a good predictor of below-ground respiration.

Carbon balance during shrub expansion in heath and meadow

The effects of shrub expansion on heath and meadow plant communities were studied experimentally by simulating shrub expansion via *Salix* introduction of transplants. Unfortunately, the experiment at the time of measurement was too premature to have any significant effects on C fluxes, and effects of community structure were weak since only biomass of deciduous shrub and graminoids increases were significant in the heath community (**Paper II**). By using a comparative approach of the three communities and identifying drivers controlling the C balance, we suggested how shrub expansion into alpine tundra heath or meadow communities potentially could change the summer C cycling in different directions (Figure 5d-e in **Paper IV**). Shrub expansion in heath and meadow can increase summer C sequestration. In the heath, increased community weighted SLA with deciduous shrub expansion could cause increased GEP and in both heath and meadow communities, GEP might increase due to increased soil moisture. Past and present-day studies have found shrub expansion to conserve soil moisture (Mann et al. 2002; Naito & Cairns 2011; Myers-Smith et al. 2015, but see Christiansen et al. 2018). Yet we only predict increased summer ER during shrub expansion in heath communities, not in nutrient-rich and productive meadows. In the meadow and heath communities both, we expect increased above-ground respiration due to estimations in **Paper III**, and more above-ground biomass. Below-ground respiration on the other hand could potentially decrease in the meadow due to lower root productivity and lower decomposability of leaf, woody stems and roots in the shrub community (Cornelissen et al. 2007b; Iversen et al. 2015; Veen et al. 2015; Christiansen et al. 2018). Although the shading effect of taller shrubs might decrease the below-ground respiration, and further studies are needed to evaluate this impact as well. Still, when taking the total ecosystem C stocks of the three communities into account (Figure 8 and **Paper I**), we speculate that shrub expansion into both meadow and heath vegetation will increase C cycling, because the soil C pool under the shrub community was markedly lower as compared to the other two communities. We conclude, that this most likely is due to processes outside of the growing season (see also discussion **Paper I**).

Synthesis, perspectives, and future studies

This thesis has contributed to knowledge on how shrub expansion will affect the carbon balance of tundra ecosystems on a local scale. Our results show, based on measurements in Dovrefjell, that alpine meadow vegetation contains large C pools, and indicates that shrub expansion may drain these pools, most likely due to below-ground processes outside of the growing season. The current global-climate carbon models will need to be revised, if our results can be replicated in other locations.

A first step to fix the knowledge-gap and contradictory predictions from field measurements and global carbon models, could be to couple local scale carbon budgets like the ones from this study, with regional scale carbon budgets and plant community distribution in the landscape (Virkkala et al. 2017). Yet in order to do so, knowledge of abiotic and biotic drivers controlling CO₂ fluxes are essential. This thesis have established which variables are important for C cycling in the three alpine communities, and it highlights the importance of below-ground processes. Specifically the results suggested that soil moisture, specific leaf area, and above-ground biomass are the most important drivers, and that specific leaf area and potential microbial activity may be linked, as both was highest in the meadow community. This thesis underlines that an important area for future studies, is more knowledge on how C cycling and pools relate to mycorrhizal abundance in arctic-alpine ecosystems (Phillips et al. 2013; Soudzilovskaia et al. 2015). This kind of data would potentially be able to explain the C pool differences in the plant communities. Knowledge of C cycling drivers in arctic-alpine plant communities subjected to shrub expansion are also important for modeling the ecosystem response to climate change. Based on the patterns of the three alpine ecosystems in this study, we suggest that shifts in functional group composition due to shrub expansion in alpine meadows and heaths influences summer C cycling differently depending on plant community, as ER might increase in the heath, and decrease in the meadow communities.

Experimental treatments excluding small and large herbivores together with introduction of *Salix* transplants will provide important knowledge on how shrub expansion dynamics influence vegetation composition and carbon fluxes in the years to come. For example, such knowledge is important for management of both domestic and wild animals. After two years of herbivory exclusion, we found increased biomass of dwarf shrubs and reduced ecosystem respiration. This thesis have provided important baseline data from the experimental treatment with *Salix* introduction, as this is a controlled way to simulate shrub expansion. Successional studies such as “space for time”-studies are needed and valuable in order to learn about ecosystem consequences of shrub expansion (Martin et al. 2017; Myers-Smith & Hik 2018). However, with the *Salix* introduction we are able to provide interesting long-term data, as we with this method know the exact succession history. In establishment of future studies, more replicate communities are favorable to avoid pseudoreplication (however see discussion of this issue in **Paper I**).

According to Chapin III et al. (2009) ecosystem flux measurements are a valid model for carbon dynamics when ecosystems are in equilibrium. Yet, in the case of biological disturbances such as insect outbreaks, fires, storms, frost damage, etc., these measurements are not representative of the full ecosystem (Chapin III et al. 2009; Hayes et al. 2011; Dahl et al. 2017). In this thesis, we have assumed equilibrium, however our plant communities are presumably under change due to climate change and human land use changes, as this was the very premise of this study: That shrubs are expanding in these tundra ecosystems, and therefore *per se* being in a disequilibrium state (Normand et al. 2017). The area including our heath community additionally experienced browning due to frost damage of evergreen shrubs in winter 2014-2015 (Phoenix & Bjerke 2016; Bjerke et al. 2017), but since it was constant across the heath and not different over the treatments we did not include this in the analysis (**Paper II**). How this 'browning' affects carbon dynamics should be investigated in future studies, although the overall trend in the arctic-alpine is still a 'greening' (Epstein et al. 2015).

The results from this thesis indicates the importance of CO₂ flux measurements outside of the growing season. Winter, spring, and autumn fluxes are important for carbon dynamics in arctic-alpine arctic ecosystems, although it is essential to measure right after snow melt in spring, and late enough in the autumn. We attempted this in 2014. However, in early season we were too late due to an early snow melt that year (late June) and the vegetation was already green and flowering, and in late season we measured fluxes too "early", as leaves were not withered yet, due to a long growing season and warm September (early September). Future studies should also implement diurnal flux measurements.

This thesis (**Paper IV** in particular) has demonstrated the importance of soil moisture for GEP. This relationship was based on simultaneous measurements of fluxes and soil moisture. To scale up the tundra carbon budgets and for use in global carbon models, we therefore need better soil moisture data, with both diurnal and seasonal variations in different vegetation types (Roux et al. 2013; Abbott et al. 2016). This will, in combination with high-resolution air and soil temperature measurements, improve our chances for scaling up tundra carbon budgets.

Besides soil moisture, the importance of community weighted leaf functional traits from the leaf economic spectrum were also demonstrated in this thesis. We only used vascular plant traits for calculating the community weighted means of leaf traits. However, including the different cryptogam traits might tell us more about the ecosystem functioning and their influence on the C dynamics (Knowles et al. 2006; Cornelissen et al. 2007a; Jonsson et al. 2015; Sancho et al. 2016). Still, community weighted means of SLA for vascular plants did not capture the amount of leaf area in a community, and the use of leaf area index (LAI) should instead be tested in future studies (Chapin 2003; Street et al. 2007).

The importance of soil moisture and community weighted mean of SLA was most likely due to the importance of nutrient availability. As both nitrogen (N) and phosphorous

(P) are essential nutrients for plants, accessibility of both should be quantified in future studies. Turner et al. (2004) suggest that there often is a large pool of bioavailable phosphorus in arctic soils, so that N-limited mesic tundra might not necessarily be P limited as well (Turner et al. 2004), and this was the case in a heath and meadow community in Abisko (Sundqvist et al. 2011). Yet, the Dovre Mountain tundra-ecotone system has high concentrations of bioavailable P (Turner et al. 2004), and our phosphatase enzyme activity analyses did not work properly because the method was not suitable for too high P-levels (**Paper IV**). This suggest that our plant communities were not P-limited, although P levels still may differ between the sites due to differences in the weathering of shale underlying the meadow and metavolcanic bedrock underlying the heath and shrub communities.

Acknowledgements

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This PhD-project started as an initiative to make collaborations between plant ecology and plant physiology, and my supervisors **Bente Graae** and **Richard Strimbeck** has been responsible for taking the initiative to start this ECOSHRUB project, and has with their complementary supervision and knowledge, guided me through difficult times. Bente is always responsive with feedback and discussions, poses valuable questions, and have after 5 years convinced me that 70 % dark chocolate can be delicious. Rick have good creative ideas, a logical approach to most things, always bring delicious cookies, and taught me how to ski down-hill on cross-country skies in the mountains.

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Paper I



Photo: The Shrub community

Draining the Pool? Carbon Storage and Fluxes in Three Alpine Plant Communities

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ABSTRACT

Shrub communities have expanded in arctic and alpine tundra during recent decades. Changes in shrub abundance may alter ecosystem carbon (C) sequestration and storage, with potential positive or negative feedback on global C cycling. To assess potential implications of shrub expansion in different alpine plant communities, we compared C fluxes and pools in one *Empetrum*-dominated heath, one herb- and cryptogam-dominated meadow, and one *Salix*-shrub community in Central Norway. Over two growing seasons, we measured Gross Ecosystem Photosynthesis, Ecosystem Respiration (ER), and C pools for above-ground vegetation, litter, roots, and soil separated into organic and mineral horizons. Both the meadow and shrub communities had higher rates of C fixation and ER, but the total ecosystem C pool in the meadow was twice that of the shrub community because of more

C in the organic soil horizon. Even though the heath community had the lowest rates of C fixation, it stored one and a half times more C than the shrub community. The results indicate that the relatively high above-ground biomass sequestering C during the growing season is not associated with high C storage in shrub-dominated communities. Instead, shrub-dominated areas may be draining the carbon-rich alpine soils because of high rates of decomposition. These processes were not shown by mid-growing season C fluxes, but were reflected by the very different distribution of C pools in the three habitats.

Key words: carbon; soil carbon; gross ecosystem photosynthesis; net ecosystem exchange; ecosystem respiration; *Salix*; heath; meadow; Tundra; *Empetrum*.

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Author Contributions MVS, RS, KON and BJK conceived and designed study. MVS, REK and KON performed research. MVS analyzed data. BJE contributed to new methods. MVS wrote the paper with input from all coauthors.

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INTRODUCTION

Shrub communities have expanded in arctic and alpine tundra during recent decades (Tape and others 2006; Cannone and others 2007; Tømmervik and others 2009; Myers-Smith and others 2011; Epstein and others 2012). According to the fifth IPCC report, these vegetation changes are linked to climate change and are expected to continue in response to the projected temperature increases

(Settele and others 2014). Tundra-dominated biomes function as large carbon (C) stores, with most C below-ground in active and permafrost soil layers (Körner 2003; Campioli and others 2009). Northern circumpolar soils store an estimated 50% of the global below-ground organic C pool (Tarnocai and others 2009). However, global soil C distribution models are still incomplete (Todd-Brown and others 2013), and quantification of the soil C pool tends to be underestimated because many studies only report pools from the top 30 cm of the soil (Ward and others 2016).

Currently there is no consensus on how shrub expansion in northern high latitudes will affect ecosystem C budgets, but there appear to be three key predictions. First, increases in above-ground biomass have been suggested to result in larger C storage because of more plant biomass, greater litter fall and thereby more soil C (Qian and others 2010). The increase in above-ground biomass leads to more net CO₂ sequestration (Michaletz and others 2014), and indeed, such a change in net C uptake has also been predicted by several C cycle models for the twenty-first century (Euskirchen and others 2009; Qian and others 2010; Todd-Brown and others 2014). Although these models cannot predict all the fine-scale changes in temperature and precipitation patterns that can affect the magnitude of C fluxes (Euskirchen and others 2009; Cahoon and others 2012), they do appear to consistently predict an increase in ecosystem C pools. Second, several studies show that shrub expansion will cause a net C release (Mack and others 2004; Sjögersten and Wookey 2009; Cahoon and others 2012; Parker and others 2015). Recent field studies have reported rapid C turnover and high respiration rates in shrub-dominated tundra (Cahoon and others 2012; Parker and others 2015) and smaller C pools beneath arctic shrub tundra than beneath heath and tussock tundra (Wilmking and others 2006; Parker and others 2015), suggesting a net C release because a loss of soil C is already happening. Third, shrub expansion may have neutral impacts on C storage. This was shown in an experiment with two decades of warming, where tussock tundra turned into shrub tundra. Despite altered decomposer activity in the mineral soil, there was no difference in total C pools between shrub and tussock tundra (Sistla and others 2013). Thus, empirical studies do not support model predictions of greater ecosystem C storage in shrub communities, and understanding how vegetation changes affects tundra ecosystem C stores remains a challenge.

Carbon flux measurements provide snapshots of the dynamics of ecosystem C sequestration and C

release. In contrast, ecosystem C pools reflect the long-term integration of the fluxes and turnover for periods spanning decades to centuries. Carbon pools reflect the potential amount of C that may be lost to the atmosphere (Wilmking and others 2006). To achieve a better understanding of ecosystem-level changes in C cycling caused by shrub expansion and vegetation changes, studies should simultaneously focus on ecosystem C fluxes and C pools.

Understanding the effects of shrub expansion on tundra ecosystem C pools is complicated by several ecosystem processes (Wookey and others 2009; Myers-Smith and others 2011). Cornelissen and others (2007) found that deciduous and evergreen shrub litter is more recalcitrant than herbaceous litter and suggested that the slower decomposition rate of shrub litter could lower respiration and C release to the atmosphere. However, decomposition rates of evergreen dwarf shrub litter dominating heath vegetation are even slower than litter from deciduous shrubs (Veen and others 2015). Therefore, changes in litter quality and leaf traits with deciduous shrub expansion may affect C turnover differently depending on the community being replaced.

Shrub expansion also alters soil temperatures (Sturm and others 2005; Myers-Smith and Hik 2013), which can further alter soil respiration (Cahoon and others 2012; Semenchuk and others 2016). Shrub expansion into tundra heath might increase snow depth because the shrub canopy traps more snow than shorter tundra vegetation. More snow insulates the soil, increases the winter soil temperature, and stimulates winter soil respiration, that is, the “shrubs–snow hypothesis” (Sturm and others 2001a; Grogan and Jonasson 2006; Myers-Smith and Hik 2013). In summer, shrubs decrease summer soil temperatures because of shading (Myers-Smith and Hik 2013). Sturm and others (2005) have suggested that these temperature alterations affect nutrient cycling and thereby soil respiration, though this was not confirmed by a short-term experimental manipulation with artificial shrub canopies (Myers-Smith and Hik 2013).

Additionally, shrub expansion might alter the fungal and microbial community (Wookey and others 2009), because deciduous shrubs are associated with ectomycorrhizal fungi, whereas tundra heath and meadow vegetation are often associated with ericoid and arbuscular mycorrhiza, respectively (Väre and others 1992; Newsham and others 2009; Becklin and others 2012). This shift in symbionts has been proposed to increase C cycling and soil respiration in shrub communities (Deslippe and

Simard 2011; Clemmensen and others 2015; Parker and others 2015).

Tundra forms a mosaic of co-occurring vegetation types associated with different productivity, snow depth, nutrient-, and moisture conditions (Sonesson and others 1975; Sundqvist and others 2011). Though the patchiness of the vegetation in heterogeneous alpine landscapes is well known, few studies have described the variation in carbon fluxes and pools in these landscapes. Heath and meadow are two very common vegetation types in the alpine tundra that are both prone to shrub encroachment under climate change (Molau and Alatalo 1998; Björk and Molau 2007). Meadows are, apart from having more snow, often more nutrient rich and productive than heaths (Wardle and others 2004; Björk and Molau 2007). However, C budget consequences of shrub encroachment in tundra ecosystems have only been estimated for Alaskan tussock (Wilkinson and others 2006) and Fennoscandian heath tundra (Parker and others 2015). Therefore, consequences of shrub expansion in Fennoscandian alpine meadows are not well understood, and there is a need to study both heath and meadows with comparable methods.

Betula and *Salix* spp. are the two principal genera of expanding shrubs in the Fennoscandian tundra (Naito and Cairns 2011). *Betula nana* has been the focus of most field studies (Myers-Smith and others 2011; Parker and others 2015), yet the impact of *Salix* expansion is likely to be just as important on ecosystem function (Sturm and others 2001b; Tape and others 2006; Myers-Smith and others 2011). First, *Salix*-shrub species dominate vast tundra areas in northern high latitudes (Hultén and Fries 1986). Second, *Salix*-shrub species growth and population structure fluctuate with herbivory (Ravolainen and others 2011; Speed and others 2013), and herbivory intensity is also changing in these systems (Austrheim and others 2011; Olofsson and others 2012).

To understand potential implications of *Salix*-shrub expansion in heterogeneous alpine landscapes, the objective of this study was to compare carbon budgets of three alpine plant communities in Central Norway. We measured daytime mid-growing season ecosystem C fluxes (GEP and ER) and sampled above-ground, litter, and below-ground C pools in one *Salix*-dominated shrub community, one *Empetrum*-dominated dwarf shrub heath, and one herb-and cryptogam-dominated meadow. We compared shrub community C fluxes to those of heath and meadow and quantified where and how much C is stored in the three sites with different communities.

MATERIALS AND METHODS

Field Site and Plant Community Descriptions

Ecosystem C fluxes and total C storage were determined for alpine communities located around 1100 m a.s.l. in the low-alpine zone near Hjerking (62°N, 9°E) in the Dovre Mountains, Central Norway (Figure S1). The area has a continental climate (Moen 1998), and from 1960 to 1990 the annual and growing season mean temperatures were -1.0 and 7.1 °C, respectively, and mean precipitation for the same periods was 700 and 298 mm (New and others 2000). We investigated three dominant alpine communities: (1) an *Empetrum*-dominated dwarf shrub heath, (2) an herb- and cryptogam-dominated meadow, and (3) a *Salix*-dominated shrub community (*Salix glauca* L. and *S. lapponum* L.). Species composition and characteristics of the three communities are given in Table 1. All three communities were situated on podzolic soil profiles, with a partial albic horizon in the shrub community and a well-developed albic horizon in the heath (Sjögersten and Wookey 2009). Underlying geology in the heath and the shrub community was metavolcanic bedrock, while the meadow community was underlain by shale, yet all three communities had a thick layer of till deposits from glacial moraines (NGU 2015). All sites experienced low-intensity Norwegian white sheep (*Ovis aries*) summer grazing and browsing up to 25 sheep per km² (NIBIO: <http://kilden.skogoglandskap.no/>). Voles (*Microtus agrestis*, *M. oeconomus*, and *Myodes rufocanus*), lemmings (*Lemmus lemmus*), moose (*Alces alces*), and occasionally wild reindeer (*Rangifer tarandus*) are present in or pass through the field sites.

Study Design

This study was part of a larger experiment with four different treatments and therefore required a larger number of plots within each site. However, although we had eight replicate blocks within each community type, the communities themselves were not replicated because logistic restrictions only allowed one site per community. These three sites were chosen carefully for having a large area with homogeneous vegetation, and the three communities were therefore situated on different but neighboring mountain slopes that varied slightly in topography. Plots from all sites had similar slopes, aspects, and elevation. The surrounding topography differed, with the heath site more exposed to wind and the meadow and willow

Table 1. Plant Community Descriptions

	Heath	Meadow	Shrub
Slope	South facing	Southwest facing	South facing
Snow depth March 2015 (cm) 0	38.34 ± 4.4	50.88 ± 23.6	20. May
Snowmelt 2014	21. April	18. May	4. June
Snowmelt 2015	2. May	15. to 19. May	19.5 ± 7.9
Vegetation height 2014 (cm)* 5.6 ± 1.6	6.2 ± 2.4	8.4 ± 1.9	20.8 ± 7.1
Vegetation height 2015 (cm)* 6.7 ± 1.5	Forbs and graminoids		Deciduous shrub canopy
Abundant species (relative abundance (%))*	Low evergreen dwarf shrubs		
	<i>Empetrum nigrum</i> L. (39.0)	<i>Deschampsia cespitosa</i> (L.) P. Beauv. (17.0)	<i>Salix glauca</i> L. (36.7)
	<i>Arctostaphylos uva-ursi</i> (L.) Spreng. (34.8)	<i>Avenella flexuosa</i> (L.) Drejer (13.9)	<i>Salix lapponum</i> L. (15.8)
	<i>Vaccinium vitis-idaea</i> L. (16.1)	<i>Anthoxanthum nipponicum</i> Honda (12.0)	<i>Avenella flexuosa</i> (L.) Drejer (16.7)
		<i>Festuca ovina</i> L. (11.6)	<i>Saussurea alpina</i> L. DC. (4.8)
		<i>Carex bigelowii</i> Torr. ex Schwein. (8.5)	<i>Carex bigelowii</i> Torr. ex Schwein. (3.9)
		<i>Thalictrum alpinum</i> L. (7.7)	<i>Vaccinium myrtillus</i> L. (3.5)
		<i>Antennaria dioica</i> (L.) Gaertn. (3.9)	<i>Galium boreale</i> L. (3.2)
		<i>Leontodon autumnalis</i> L. (3.1)	<i>Festuca ovina</i> L. (2.3)
		<i>Ranunculus acris</i> L. (3.1)	<i>Trientalis europaea</i> L. (2.3)
		<i>Saussurea alpina</i> L. DC. (3.1)	
		<i>Astragalus alpinus</i> L. (2.3)	
	Lichens		
	<i>Flavocetraria cucullata</i> (Bellardi) Kärnefelt & Thell (44.4)		
	<i>Cladonia mitis</i> ** (Sandst.) Ruoss (22.2)	<i>Achillea millefolium</i> L. (1.9)	
	<i>Alectoria ochroleuca</i> (Hoffm.) A. Massal. (8.3)	<i>Agrostis capillaris</i> L. (1.5)	
	<i>Cladonia rangiferina</i> (L.) F. H. Wigg. (5.6)	Lichens***	
	<i>Cladonia sensu lato gracilis</i> (L.) Willd. (5.6)	<i>Stereocaulon alpinum</i> Laurer ex Funck (73.1)	<i>Cladonia mitis</i> ** (Sandst.) Ruoss (37.0)
	<i>Cetraria islandica</i> (L.) Ach. (2.8)	<i>Cetraria islandica</i> (L.) Ach. (25.0)	<i>Cladonia stellaris</i> (Opiz) Pouzar & Vezda (24.1)
	Bryophytes		
	<i>Polytrichum</i> sp (42.1)	Bryophytes***	
	<i>Dicranum flexicaule</i> Brid.(26.3)	<i>Hylocomium splendens</i> (Hedw.) Schimp. (24.5)	<i>Cladonia stygia</i> (Fr.) Ruoss (14.8)
		<i>Barbilophozia hypopodioides</i> (Wallr.) Loeske (18.6)	<i>Cladonia rangiferina</i> (L.) F. H. Wigg. (7.4)
		<i>Aulacomnium palustre</i> (Hedw.) Schwägr. (16.7)	Bryophytes
	<i>Polytrichum juniperinum</i> Hedw. (15.8)	<i>Hylocomiastrum pyrenaicum</i> Spruce (12.7)	<i>Pleurozium schreberi</i> Hedw. (28.3)
	<i>Ceratodon purpureus</i> (Hedw.) Brid. (5.3)	<i>Santonia uncinata</i> (Hedw.) Loeske (9.8)	<i>Polytrichum commune</i> (20.8)
		<i>Pleurozium schreberi</i> (Willd. Ex Brid.) Mitt. (6.9)	<i>Hylocomium splendens</i> (Hedw.) Schimp. (18.9)

Mean characteristics ± SD of the *Empetrum*-dominated dwarf shrub heath (Heath), meadow (Meadow), and the *Salix*-dominated shrub communities (Shrub) in Dovre Mountains, Central Norway. Vascular and cryptogam species listed are the most abundant in each of the communities in 2014*, calculated with a 90% threshold of cumulative relative abundance. Relative abundance (%) is indicated in parenthesis for each species.

* Vegetation height and abundance are from only 25 cm × 25 cm of the 50 cm × 50 cm plot for C flux measurements. Relative abundance to total abundance was found with the pin-point method and assessed separately for vascular, lichen, and bryophyte species.

** Can also be *Cladonia arbuscula* (Wallr.) Rabenh.

*** Cryptogams in meadow only for blocks 1–7.

sites being more sheltered. These topographical differences presumably caused the differences in the dominant vegetation. The lack of several replicate sites for each community could be seen as pseudoreplication (*sensu* Hurlbert 1984; Heffner and others 1996) and limits the generality of our study. We present and compare the three sites with different community composition knowing that other site-specific conditions might be at play and acknowledge this in the interpretations (see further in the discussion). In each community, eight replicate blocks were randomly selected for measurements. In each block, there was a plot for C flux measurement (0.5×0.5 m), and a neighboring plot for harvest, measuring 25×25 cm in the heath and the meadow communities and 50×50 cm in the shrub community to capture the heterogeneous distribution of woody biomass. A soil pit (50×50 cm) was additionally dug adjacent to the plot for harvest. The size of the blocks varied in the three communities, and average distance among blocks within community was 49.3 m in the shrub community, 19.3 m in the meadow community, and 26.9 m in the heath community. Across the communities, the average distance \pm SD between nearest flux plots was 31.8 ± 15.6 m, thus reducing spatial autocorrelation of factors controlling C fluxes and storage (Marriott and others 1997).

Carbon Flux Measurements

Carbon dioxide fluxes were measured in each block ($n = 8$) in each plant community. The measurements were taken during mid-growing season (second and third weeks of both July and August) in 2014 and 2015. The growing season during 2014 was dry and warm, whereas in 2015 the site was wetter and cooler (Table S1).

A collapsible $0.5 \text{ m} \times 0.5 \text{ m} \times 0.6 \text{ m}$ polyethylene chamber (Arnone and Obrist 2003) (Shelter Systems Translucent Greenhouse covering, Shelter Systems, Menlo Park, California, USA) on a PVC tubing frame was used for closed-system measurement of CO_2 and H_2O using a LI-840A $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer (LI-COR Inc., Lincoln, Nebraska, USA) and a SQ2010 datalogger (Grant Instruments Ltd., Cambridge, UK). A sampling tube entered the center of the chamber roof and sampled 40 cm above the soil surface. A return tube, attached to one of four chamber legs, led the sampled air out of the chamber. The chamber legs were fitted on permanent aluminum plot poles, and the chamber fabric was held down and sealed during measurements by a 5-m long chain weigh-

ing 5 kg. For dark measurements, we used an opaque hood to block out the light (Street and others 2007) (photosynthetically active radiation; PAR during dark measurements ranged from -4 to $68 \mu\text{mol m}^{-2} \text{ s}^{-1}$). Four fans mixed the air inside the chamber for 30 s prior to and during each measurement.

Measurements began within 30 s after sealing, with a total measurement period of around 120 s. Flow rate, planned to be 0.8 l min^{-1} , ranged from 0.55 to 0.9 l min^{-1} . In each plot, both a light measurement and a dark measurement were performed. Linear regression was used to determine the rate of the CO_2 change in the chamber (Jasoni and others 2005). Net Ecosystem Exchange (NEE) was calculated from the light measurements and Ecosystem Respiration (ER) from the dark measurement. As NEE is the difference of ER and Gross Ecosystem Photosynthesis (GEP), GEP was calculated by subtracting ER from NEE. Heskell and others (2013) suggest that daytime dark measurements might overestimate ER. To test whether ER was different during day and night, we measured ER during night time in the heath in 2014 and found no difference (Figure S2). We therefore assume that our data are representative of mid-growing season ER. Gross Ecosystem Photosynthesis is reported as a decrease in CO_2 concentration, that is, as negative, and ER is reported as an increase in CO_2 concentration, that is, as positive. When reporting NEE, a negative denotes that the community is a CO_2 sink, whereas a positive represents a CO_2 source.

Because of logistical difficulties in getting to remote alpine plots, our C flux measurements were taken at different time points throughout the day, rather than simultaneously. Therefore to control for variable light intensities, we standardized GEP from 2015 to $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR (Appendix 1 Supplementary information), by doing light curve measurements using three levels of shading (Williams and others 2006; Street and others 2007). We found no significant differences from non-standardized results, and we therefore chose to use non-standardized GEP data in the final results (Figure S3).

During all flux measurements, light (PAR) was measured with a LI-190S quantum sensor (LI-COR Inc., Lincoln, Nebraska, USA) placed at a distance of 20 cm from the chamber leg and 15 cm below the chamber roof. Air temperature was measured with PT100 sensors inside the chamber at a height of 40 cm above the soil surface and outside the chamber at a height of 60 cm above the soil surface. Surface temperature (at 1 cm depth) was

measured daily every four hours with temperature sensors (iButtons, Maxim Integrated Products, Sunnyvale, California, USA). The exact surface temperature at C flux measurement time and date was estimated by interpolation. Soil temperatures were measured at 8 cm depth and soil moisture at 5 cm depth in 2014 with a SM150 (Delta-T Devices Ltd, Cambridge, UK) and in 2015 a TRIME-PICO32 sensor (IMKO, Germany).

Above-Ground Carbon Pools

Because of logistical constraints, above-ground vegetation biomass and litter was destructively sampled from the harvest plots in only six randomly selected blocks per community ($n = 6$) during the mid-growing season in July 2015. Prior to harvest, we determined the C flux and functional composition of the harvest plots, and these were not significantly different from adjacent C flux plots (NEE: ANOVA $F_{1, 35} = 0.462$, $p = 0.501$, ER: $F_{1, 33} = 0.173$, $p = 0.680$, see Table S2 for functional group differences). The harvested above-ground vegetation was sorted into the functional groups: deciduous shrubs (*Salix glauca*, *S. lapponum*, *Betula nana*), dwarf shrubs (both evergreen and deciduous: *Vaccinium uliginosum*, *V. myrtillus*, *Salix herbacea* and *S. reticulatum*), forbs, graminoids, seedless vascular plants, lichens, and bryophytes. Litter was collected as all dead biomass on or above the ground. All plant material was oven-dried at 70°C for 72 h before weighing to an accuracy of 0.001 g. Above-ground plant and litter C pools (g C m^{-2}) were estimated by multiplying the oven-dry weight (g) by the average C concentration (mg^{-1} g) per functional group. The C concentration per functional group was determined from harvest and measurements done in 2013 from the same sites (Appendix 2, supplementary information).

Below-Ground Carbon Pools

In September 2015, below-ground C pools were sampled from the six randomly selected blocks per community ($n = 6$) using a soil pit dug to bedrock and/or the BC horizon. Total soil depths were on average 56 ± 8 cm and ranged from 42 to 70 cm. Duplicate soil samples were extracted from each horizon, identified by its color and texture. Each sample was extracted for a defined volume ($5 \times 5 \times 5$ cm) using a knife. One of the samples was used for measuring root biomass and soil pH, and the other was used to determine total soil and root C content. The samples were stored at 4°C for a maximum of 5 days before being processed.

To determine root biomass, all visible roots (both living and dead) were manually extracted from fresh soil from each horizon and then oven-dried at 60°C for 48 h and weighed. For each horizon, soil pH was measured using a 0.01 M CaCl_2 in a 1:3 soil-to-solution mixture.

To determine soil and root C content, soil was oven-dried at 60°C until it reached a constant mass. Roots and stones (> 2 mm) were removed from soil. Roots were washed, oven-dried, and homogenized by grinding prior to chemical analyses (MF 10 basic IKA Werke). Soil organic matter was determined for each soil sample from all horizons via loss on ignition (LOI) in a furnace at 550°C for 5 h. Soil samples were then bulked per horizon to determine C concentrations for both soil and roots via elemental combustion (ECS 4100, Costech). Average LOI per horizon ($\text{Fraction}_{\text{LOI}}$ (%)) was significantly correlated with bulked soil C concentration (C concentration (%): $\text{C concentration (\%)} = 0.43575 * \text{Fraction}_{\text{LOI}} (\%) - 0.25687$, $p < 0.0001$, $r^2 = 0.918$, $n = 74$). This relationship between $\text{Fraction}_{\text{LOI}}$ (%) and C concentration (%) was used to extrapolate C concentrations for eight soil horizons that were not included in our soil C concentration determination. For all soil samples, we found no evidence of inorganic C in the form of carbonates determined by effervescence following the addition of 1 M HCl (see Hodgson 1997). Soil organic carbon (SOC) (kg C m^{-2}) was therefore calculated by multiplying the C concentration (%) per horizon by horizon thickness (m) and bulk density (kg m^{-3}). Following these calculations, horizons were then pooled into organic versus mineral based upon whether they lost more than 80% of mass during LOI or they did not, respectively (Hodgson 1997). Root C pool (g C m^{-2}) was estimated by multiplying the oven-dry weight (g) by the C concentration (mg^{-1} g).

Statistical Analysis

Linear mixed effects models following Gaussian distributions were used to estimate the differences in means of C fluxes among the three communities and the two growing seasons, 2014 and 2015 using R (R Core Team 2015; lme4 package; Bates and others 2015). To meet the model's assumptions, ER, GEP, and NEE were transformed using the natural logarithm. Within the model, fixed effects were community type and year and the interaction between these two factors. The models controlled for repeated measures, because plot was considered a random effect. Proportion of variance explained by fixed factors, R marginal, and proportion of variance explained by both fixed and random factors, R conditional (Nakagawa and Schielzeth 2013;

Johnson 2014), were estimated using restricted maximum likelihood (REML) (piecewiseSEM package; Lefcheck 2016). Differences in ER, GEP, and NEE among the three communities were analyzed using multiple comparisons for linear mixed effect models with the Tukey method (multicom package; Hothorn and others 2008).

To identify where the greatest variation in C flux measurements occurred in space and time in our alpine ecosystem, we performed a variance component analysis, where the C flux variance was partitioned into between-year, among-community, among-plot, and within-plot components. As we were interested in variation due to plant community identity, variance components were obtained from linear mixed effects models fitted with plot nested within community as random factors. This approach provided an estimate of the variance of each factor listed above, except between-year variance. The variance explained between years was estimated as the reduction in total random-effects variance when year was included in the model as a fixed factor in the model.

We used one-way ANOVA to determine differences in plant and soil C pools among communities. Data that did not meet the assumptions of the parametric analysis were natural log-transformed. Statistically significant differences were analyzed using multiple comparisons with a Tukey's honestly significant differences test. Similarly GEP standardized to 600 ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) was analyzed using one-way-ANOVA. The use of ANOVA in pseudoreplicated studies (or unreplicated studies) has been criticized by Hurlbert (1984) and Heffner and others (1996) because of the lack of independence of the replicated samples—in this case within each community. We, however, like Oksanen (2001) and Schank and Koehnle (2009) conform to the rationale that *not* testing for significant differences among sites with replicate samples would be a greater weakness in a scientific paper than testing the data for differences, acknowledging that the differences might be caused either by the "treatment" tested (in our case "community") or by other factors associated with the spatial site encompassing the "treatment" (community). We therefore use ANOVA acknowledging this limitation on the general applicability of the results.

RESULTS

Greater C Fluxes in Meadow and Shrub Communities

Daytime growing season flux measurements showed that average Gross Ecosystem Photosynthesis (GEP)

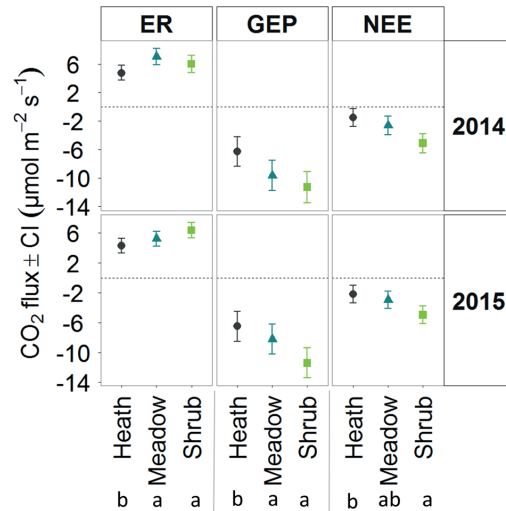


Figure 1. Means for ecosystem respiration (ER), gross ecosystem photosynthesis (GEP), and net ecosystem exchange (NEE) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) \pm 95% confidence intervals (CI) during mid-growing season for an alpine *Empetrum*-heath (gray circles), meadow (turquoise triangles), and *Salix*-shrub (green squares) plant communities in Dovre Mountains, Central Norway. Estimates are from linear mixed effect models fitted with community and year as fixed factors, and plot as random factor. The letters denote significant differences ($p < 0.01$) among the communities, tested using multiple comparisons for linear mixed effect models with the Tukey method ($n = 68$).

and Ecosystem Respiration (ER) were significantly greater ($p < 0.001$, $p < 0.05$) in both the shrub (GEP: $-11.6 \pm 2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, ER: 6.7 ± 1.0) and the meadow communities (GEP: $-9.0 \pm 2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, ER: $6.4 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in the heath community (GEP: $-6.6 \pm 2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, ER: $4.9 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Figure 1). In 2014, GEPs in the meadow and shrub communities were more similar than in 2015. Even though all three ecosystems had negative NEE, indicating net C uptake, the rate in the shrub community was significantly greater ($p < 0.0001$) ($-4.81 \pm 1.17 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in the heath ($-1.71 \pm 1.13 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the meadow ($-2.61 \pm 1.15 \mu\text{mol m}^{-2} \text{s}^{-1}$) communities.

The variance component analysis showed that 18 to 38% of the variation in C flux measurements could be attributed to among-community variance (Table 2). The remaining variance was mostly due to within-plot (36–65%) and among-plot-within-community (15–28%) variance, whereas the between-year variance was very small (0–1.4%).

Table 2. Variance Component Analysis, where C flux variance (%) was partitioned into: variance between years, among community, among plot within community, and within plot

Measurement	ER	GEP	NEE
Mean \pm SE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.65 \pm 0.10	2.10 \pm 0.15	0.94 \pm 0.29
Variance between years (%)	1.4	~0	1.3
Variance among community (%)	18.0	36.5	37.9
Variance among plot within community (%)	15.2	28.0	16.9
Variance within plot (%)	65.4	36.4	43.9

Variance components were obtained from linear mixed effects models fitted with year as a fixed factor, and plot nested within community as random factor. The variance explained by year was estimated as the reduction in total random-effects variance when year was included in the model.

Temperature, moisture, and light levels were different between and within the two measurement years (Table S3 and Table S4), and there was a significant interaction effect between year and community (Table S5). Overall, the shrub community had significantly ($p < 0.05$) lower air temperatures, surface temperatures, soil temperatures, higher moisture, and less light than the heath and the meadow (Table S3). Even though the year and community interaction had no effect on C fluxes (Table S6), the difference in environment during measurements could be reflected in the high within-plot and among-plot-within-community variance.

Low Total and Below-Ground Ecosystem C Pools in the Shrub Community

The total ecosystem C storage (above-ground + litter + below-ground) in the shrub community was only about half of what was found in the meadow and two-thirds of that in the heath ($F_{2, 16} = 7.97$, $p < 0.01$, ANOVA) (Figure 2). Despite substantial variation within the communities, there were large and significant ($p < 0.01$) differences among communities in above-ground ($F_{2, 15} = 73.30$, ANOVA), litter ($F_{2, 15} = 13.24$, ANOVA), and organic soil C pools ($F_{2, 13} = 23.46$, ANOVA) (Figure 2). There were no significant differences between communities in C pools of roots ($F_{2, 15} = 2.39$, $p = 0.125$, ANOVA) and mineral soil ($F_{2, 15} = 1.62$, $p = 0.231$, ANOVA), though when looking at root C of the organic horizon alone we found differences among the three communities ($F_{2, 13} = 6.66$, $p = 0.01$, ANOVA) (Table 3).

The variation among total ecosystem C pools was primarily due to the organic soil C pool, which made up 16, 51, and 14% of the total ecosystem C pool in the heath, meadow, and shrub communities, respectively. Differences in organic soil C pool were determined by both differences in the organic

soil depth and C concentration: The organic soil horizon was deeper in the meadow (0.09 ± 0.02 m), and shallower in the heath and shrub communities (0.04 ± 0.03 m and 0.03 ± 0.01 m, respectively). The concentration of C in the organic soil horizon was also higher in the meadow (23.4%) than in the shrub (16.1%) and the heath (14.3%) communities (Table 3). As a result of these differences, the meadow community had significantly larger ($p < 0.001$, TukeyHSD) organic soil C pools (6124 ± 2148 g C m^{-2}) than the heath (1502 ± 983 g C m^{-2}) and the shrub communities (934 ± 292 g C m^{-2}) (Figure 2). Moreover, the meadow had significantly larger root C pool in the organic horizon than the shrub ($p < 0.01$, TukeyHSD) and the heath communities ($p < 0.05$, TukeyHSD) (Table 3).

The community means of the above-ground C pool were all significantly different ($p < 0.001$, TukeyHSD) from each other: It was largest in the shrub community (771 ± 207 g C m^{-2}), intermediate in the heath (371 ± 55 g C m^{-2}) and smallest in the meadow (139 ± 29 g C m^{-2}) (Figure 2). The above-ground C pool in the heath consisted primarily of evergreen dwarf shrubs (Figure 3, Table S7). The litter C pool was significantly larger ($p < 0.01$, TukeyHSD) in the heath community as well (Figure 2). As expected, the above-ground C pool in the meadow was dominated by bryophytes, lichens, and graminoids and the shrub community by shrubs, bryophytes, lichens, and some seedless vascular plants (Figure 3, Table S7). Data available from Sørensen and others (2017)

DISCUSSION

This study demonstrates how analyzing both carbon (C) fluxes and pools helps to understand ecosystem functions in contrasting alpine tundra ecosystems. Above-ground biomass and rates of C fixation (GEP) and ecosystem respiration (ER) were

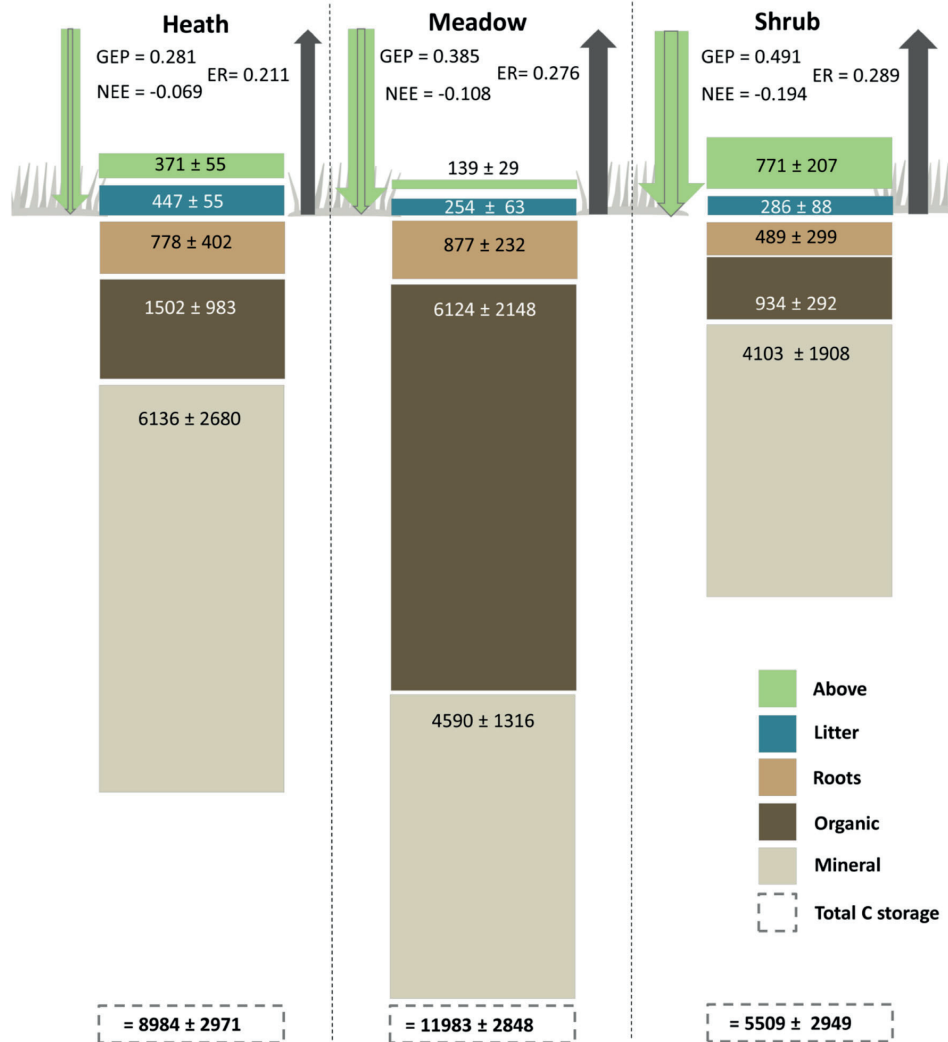


Figure 2. Carbon budgets including C pools from 2015 and estimates of C fluxes based on data from 2014 and 2015 (*GEP* gross ecosystem photosynthesis, *ER* ecosystem respiration, *NEE* net ecosystem exchange) in an alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway. The number in each box is mean C pool \pm SD (g C m^{-2}) ($n = 6$), and the area of each box is proportional to its compartment size. Arrows corresponds to *GEP* (green), *NEE* (transparent arrow within *GEP*), and *ER* (gray). Values next to arrows indicate growing season daytime fluxes ($\text{g C m}^{-2} \text{h}^{-1}$), and the width of the arrows is proportional to its flux size.

highest in the shrub community, even though total ecosystem C storage was lowest in that site. In the meadow, there were also high rates of mid-growing season C fixation. Despite high *ER*, there was a

very large below-ground C pool, so that total ecosystem C storage in the meadow was highest. In the heath, we measured low C fluxes and intermediate pools.

Table 3. Mean Characteristics \pm SD of Organic and Mineral Soil Horizons

Community	Horizon	Depth (m)	C content (%)	Root C (g m^{-2})	N pool (g m^{-2})	pH
Heath	Organic	0.04 ± 0.03	14.3 ± 7.2	269 ± 140	80 ± 73	3.5 ± 0.5
	Mineral	0.51 ± 0.08	2.1 ± 0.8	554 ± 373	314 ± 139	4.4 ± 0.2
Meadow	Organic	0.09 ± 0.02	23.4 ± 4.2	545 ± 200	438 ± 163	4.5 ± 0.3
	Mineral	0.48 ± 0.10	1.6 ± 0.6	332 ± 213	363 ± 109	4.5 ± 0.2
Shrub	Organic	0.03 ± 0.01	16.1 ± 6.9	187 ± 163	55 ± 17	3.6 ± 0.3
	Mineral	0.37 ± 0.14	2.2 ± 0.7	334 ± 235	352 ± 190	4.2 ± 0.1

Depth (m), C content (%), C in root standing stock (g C m^{-2}), N pools (g N m^{-2}), and pH in an alpine *Empetrum*-heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, Central Norway.

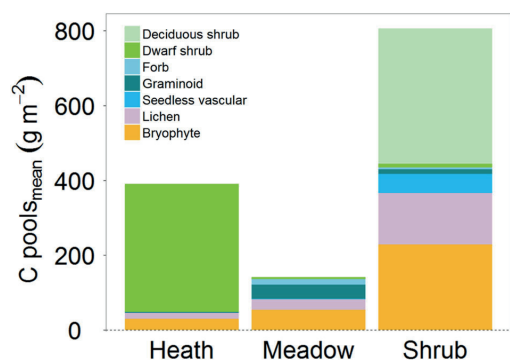


Figure 3. Above-ground C pools (g C m^{-2}). Based on sum of C pools from all functional groups and then mean over block for an alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway ($n = 6$). See standard deviations in Table S7.

Shrub and Meadow Communities Might have Faster Ecosystem C Turnover than Heath

As expected with higher biomass, the shrub community had greater gross ecosystem photosynthesis (GEP) and net CO_2 uptake than the tundra heath (Cahoon and others 2012; Parker and others 2015). Given the small above-ground biomass in the meadow, the equal GEPs in the meadow and shrub communities were unexpected. This might be because the biomass measured in the meadow is predominantly in photosynthetic tissue, whereas the majority of biomass from the shrubs is non-productive woody material.

The equally high ER in the meadow and shrub communities was also surprising, because only the meadow had large organic horizon nitrogen pools and high pH (Table 3). Higher pH has been associated with higher nitrogen availability and a higher proportion of bacteria in the soil (Eskelinen

and others 2009). High nitrogen availability can result in high ER as it stimulates microbial decomposition (Hobbie and others 2002; Mack and others 2004). In contrast, the high ER in the shrub community might be caused by high autotrophic respiration from the vegetation because of the larger standing biomass than in the meadow. Also, the high ER in the shrub community could be facilitated by higher soil moisture (Table S3), which can stimulate ER (Sjögersten and others 2012). The soil and surface temperatures were also cooler in the shrub community because of the shading effects from the *Salix* canopy (Sturm and others 2005; Myers-Smith and Hik 2013). Although ER increases with higher temperatures (Cahoon and others 2012), canopy shade helps maintain moisture. Therefore, the high mid-growing season ER in the two communities might be caused by different mechanisms related to high respiration from the standing biomass and high soil moisture in the shaded shrub community, and high microbial respiration in the nutrient-rich soils of the meadow community.

The CO_2 flux data from our three sites with different plant communities generally agree with data from similar alpine and arctic tundra systems (Figure S4) (Sjögersten and Wookey 2009; Shaver 2015). Tendencies are similar in other studies, and differences between GEP and ER for shrubs and heaths are significant (Figure S4). However, we found significantly higher ER in all three habitat types, and lower net C uptake (NEE) in the meadow compared to other studies (Table S8). Air temperatures were similar in our study and the other studies ($F_{1, 53} = 0.499$, $p = 0.499$, ANOVA), but soil temperatures might have been higher in our study because of the lack of permafrost as compared to the permafrost ground in ground near Toolik Lake (Alaska, USA). Higher soil temperatures could cause the higher ER we measured in the Dovre Mountains. A well-developed cryptogam

layer with many lichens could also contribute to the higher ER and might also have been the reason why net C uptake was smaller in our meadow, compared to other studies from a snowbed and mesic meadow in Abisko. Unfortunately, the meadow differences are less certain, because we only have a few data points on meadows from other studies for comparison. Despite the few differences, we still consider our data as representative of mid-growing season fluxes of our heath, meadow, and shrub communities in Central Norway.

Marked Differences in Soil Organic C Pools

The total ecosystem C pool in the *Salix*-shrub community was smallest; the total C pool in the meadow was twice of that in the shrub, and even though the total C pool in the heath did not differ significantly from either of the two other communities, the heath community stored on average one and a half times more C than the shrub community (Figure 2). The lack of statistical difference between the shrub and heath communities was surprising and in contrast to findings by Parker and others (2015). However, standard deviation in the data from the heath was high, probably reflecting the varied distribution of below-ground rocks of this community. The differences in total C pools were due to the large organic soil horizon C pool in the meadow. This difference could be caused by large allocation of biomass below-ground (Iversen and others 2015) and specifically as fine roots from graminoids (Sullivan and others 2007) that dominated the meadow community. Additionally, microorganisms in the meadow community could be retaining more C in the soil, for example because of the dominance of species associated with arbuscular mycorrhiza (Becklin and others 2012; Soudzilovskaia and others 2015). In contrast, the mycorrhizal fungi in the ericoid heath and the ectomycorrhizal shrub community could be degrading recalcitrant complexes (Read and Perez-Moreno 2003; Kuzyakov 2010; Lindahl and Tunlid 2015) and thereby limiting the C pool in the organic horizon in these communities (Hartley and others 2012; Clemmensen and others 2015; Parker and others 2015).

Furthermore, the shallow organic horizon and the low litter C pool in the shrub community indicate that there are relatively high rates of decomposition and litter turnover, despite the hypothesized more recalcitrant litter in the shrub community (Cornelissen and others 2007). Even

though the higher rates of decomposition were not apparent from the mid-growing season measurements of ER when comparing with the meadow, recent studies have shown that growth of roots and above-ground biomass is synchronous in graminoid-dominated vegetation, whereas root growth peaks after leaf senescence in the woody vegetation (Blume-Werry and others 2016; Sloan and others 2016). This late season growth might either use stored carbon reserves, or re-translocate carbon from senescing leaves (Sloan and others 2016). Either way, the late season growth will most likely influence the root exudates and microbial activity, which could cause priming or depletion of C in the organic horizon C pool (Kuzyakov 2002, 2010).

Our results indicate that *Salix*-shrub expansion into an alpine meadow and heath would affect the C budget in much of the same way as reported by studies on *Betula nana* expansion; increased rates of litter decomposition and efficient cycling of nutrients with the help of ectomycorrhiza might together deplete the organic soil C pools. Additionally, we speculate that in the meadow, the late root growth of the shrub community would substantially decrease the organic soil C pool.

Summer C Fluxes do not Explain Total C Pools

The differences in mid-growing season C fluxes do not explain the differences we found in C pools among the three communities (Figure 2). In all three systems, there was a negative NEE, and thus a net C uptake. However, we found that there was a higher rate of C uptake in the shrub community, where the least total ecosystem C was stored overall. We suggest that the differences are caused by processes outside the mid-growing season when we did our measurements, as previous studies have shown that tundra ecosystems are switching from sinks in the growing season and sources outside of the growing season (Euskirchen and others 2012; Vaisanen and others 2014).

The somewhat bigger C store in the heath compared to the shrub community is not surprising given that the evergreen shrubs in the heath can photosynthesize over a longer period and thereby sequester more C. This is partly because of an earlier date of snowmelt (Table 1) and thereby a longer snow free period in the heath (Grogan and Jonasson 2006). Furthermore, *Vaccinium vitis-idaea* has been demonstrated to photosynthesize even under shallow snow during winter-time (Lundell and others 2008; Saarinen and others 2011).

As predicted by the shrub-snow hypothesis (Sturm and others 2001a; Grogan and Jonasson 2006; Myers-Smith and Hik 2013), winter soil surface temperature in our shrub community was significantly higher than in the heath and the meadow (Baele and others, unpublished manuscript). Even though the snow depth in March 2015 was not significantly deeper in the shrub community than in the meadow community, the maximum snow depth was deeper in the shrub community, and snow melt took place 16–20 days later in the shrub community than in the meadow community in 2015 (Table 1). First, the meadow community might start photosynthesis much earlier and will thereby sequester more C. Second, the warmer winter soil surface temperature and the later snow melt in the shrub community could cause high winter and spring soil respiration (Semenchuk and others 2016) and thereby reduce soil C. Also, the microbial community is active in the alpine winter soils above -5°C (Schadt and others 2003; Bardgett and others 2005), and mean winter temperatures in all three plant communities were above -5°C (Baele and others, unpublished manuscript). The presence of organic polymers and phenolic compounds promotes dominance by fungal microbes (Bardgett and others 2005), and we would expect that the heath and the shrub communities would be much more dominated by fungal species during winter than the meadow that would be more bacteria-dominated during winter. These differences in litter, organic matter quality, and microbial communities could cause more degradation of the organic soil C pools during winter in both the heath and the shrub communities.

Our study shows that the C fluxes during the peak growing season explain very little of the overall C budget in the alpine communities, and it seems like the source periods outside of the growing season are important for what is happening below-ground in these ecosystems. We also learned that there is large variation in both fluxes and pools within each community. Though the three sites representing different communities could be considered pseudoreplicated, we note that the variation in fluxes within site is large compared to variation among different sites with different methods in the literature (Figure S4). This indicates the high importance of fine-scale temporal and spatial variation in nature compared to what is seen among sites and regions (Graae and others 2012; Lenoir and others 2013). This does not resolve the lack of replication of communities in this study. There is risk for confounding the community effect with the site effect. In this study, we tried to keep

the topography of the sites as similar as possible, but the mere fact that the communities differ in vegetation indicates that there are differences among sites creating the community contrasts. These various differences are often intercorrelated, and in the alpine often associated with the duration of snow cover (Graae and others 2011). Thus, it is not possible for us to keep apart the differences among sites and the differences among communities for the same reason. Undoubtedly, even more variation would appear if we had done our study with full replication in different sites and in particular if we had chosen more varied sites with respect to topography, geology, grazing pressure, etc. Results from such larger-scale studies would have increased the generality of the results and made the comparisons among sites even more robust.

CONCLUSION

Despite its limitations, the use of growing season C fluxes in combination with C pools helps to better understand ecosystem-level changes and implications of shrub expansion in tundra ecosystems. The results indicate that the relatively high above-ground biomass sequestering C during the growing season is not associated with high C storage in shrub-dominated communities compared to meadow and heath communities. Instead, shrub-dominated areas might be draining the carbon-rich alpine soils because of high rates of decomposition. These processes were not shown by mid-growing season C fluxes, but were reflected in the very different distribution of C pools in the three habitats.

Interestingly, our results raise the possibility that alpine meadow and heath communities undergoing shrub expansion will decrease total ecosystem C pools. Draining soil C pools in alpine ecosystems might in this way contribute to increased atmospheric CO_2 concentrations through a net CO_2 release from below-ground C pools.

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SUPPLEMENTARY INFORMATION

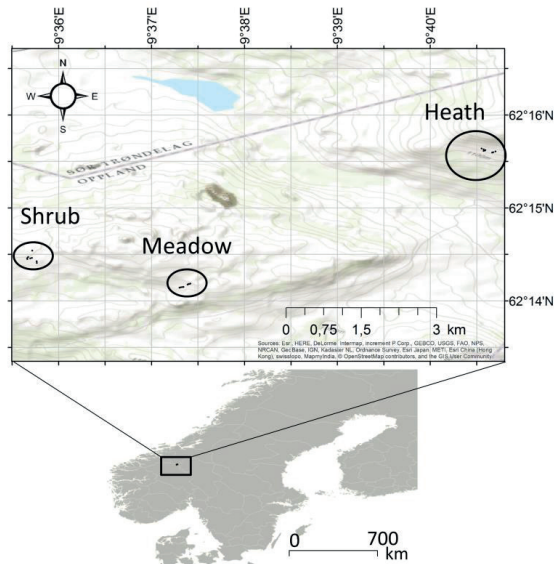


Figure S1: Location of study site and the three plant communities, in Dovre Mountains, central Norway.

Table S1: Temperature (°C), precipitation (mm), and snow cover (cm) recorded at the weather station Hjerkins II by the Norwegian Meteorological Institute (eklima.met.no) within 10 km of the study sites at 1012 m altitude. Values are calculated based on daily means. Growing season here includes the months of June, July, August, and September.

	2014	2015
Mean annual temperature (°C)	1.7	1.6
Mean growing season temperature (°C)	9.6	8.2
Annual precipitation (mm)	439.8	666.6
Growing season precipitation (mm)	191.9	264.7
Mean snow cover (cm)	15.7	16.6

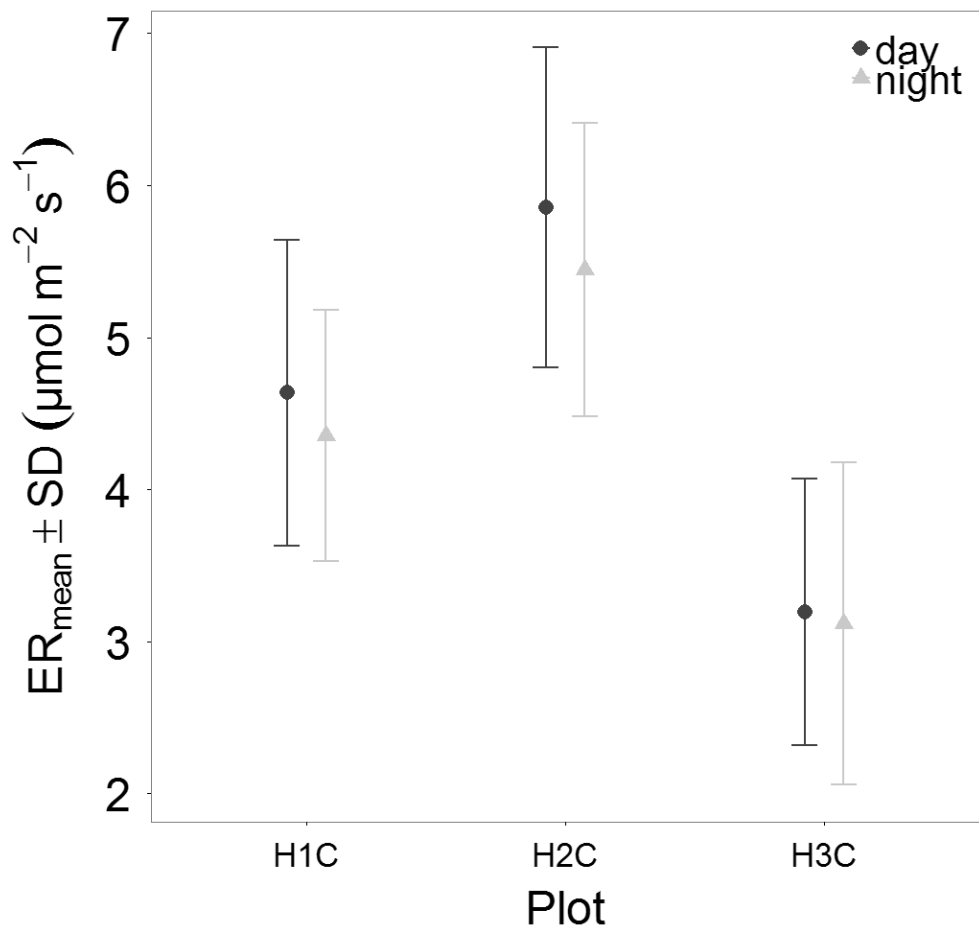


Figure S2: Mean Ecosystem Respiration (ER) \pm SD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) comparing day (dark gray) and night time (light gray) measurements on three plots during mid growing season 2014 for an alpine *Empetrum*-heath in Dovre Mountains, central Norway. There was no significant difference between day and night time measurements ($F_{1,4} = 0.063$, $p = 0.814$, ANOVA).

Appendix 1: Method GEP standardization to 600 PAR

Light curve measurements was performed one time during mid-growing season on all eight plots in each community in 2015 (n=24). One light curve measurement consisted of one measurement in full light, one measurement at three increasing levels of shading, and one measurement in full darkness (Williams and others 2006; Street and others 2007). The shading was done with three layers of black tulle.

Light response curves were derived using the nls functions in R (R Core Team 2015) with the following equation:

$$GEP = \frac{P_{max} \cdot I}{k + I}$$

Where $GEP = ER - NEE$ (ER corresponding to the dark measurements, and NEE corresponding to the four light measurements), $I =$ incident PAR ($\mu\text{mol m}^{-2}\text{s}^{-1}$), $P_{max} =$ rate of light saturated photosynthesis, and $k =$ half saturated constant of photosynthesis.

If we did not have any saturation from the light response curve, we used a fixed value of P_{max} , and tried different values, and chose the one with the best fit.

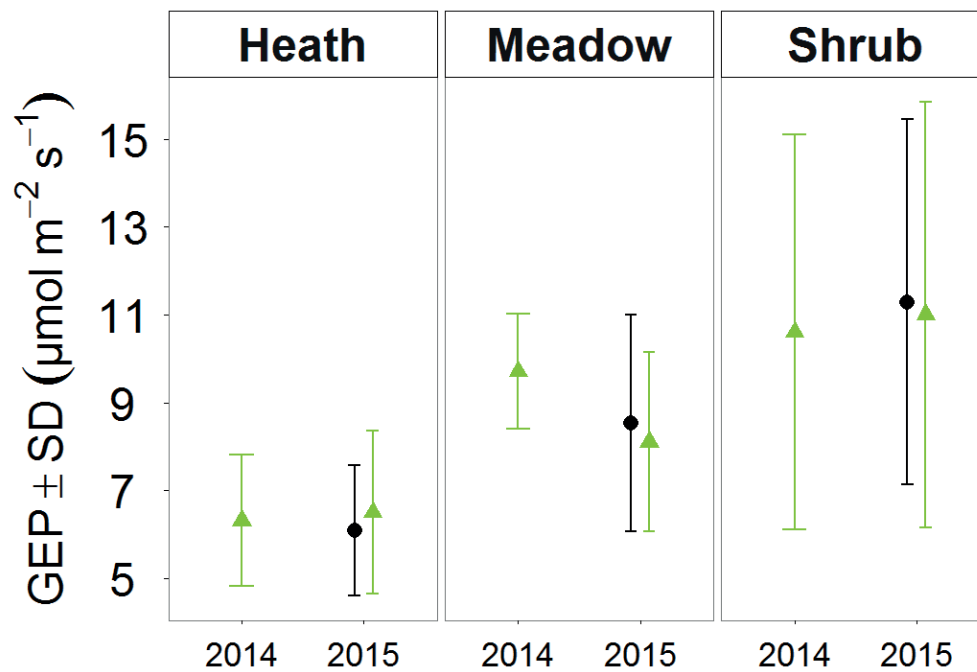


Figure S3: Mean Gross Ecosystem Photosynthesis (GEP) \pm SD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) comparing measurements standardized to 600 ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) (black) and measurements from 2014 and 2015 (green) during mid-growing season. Means are across alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, central Norway. There was no significant difference between measurements standardized to 600 ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) and non-standardized measurements in 2015 ($F_{1,4} = 0.002, p = 0.963$, ANOVA).

Table S2: Degrees of freedom, F-value, and *p*-value from one-way ANOVA tests of differences among functional group relative abundance between C flux plots and C pool harvest plots (n = 8). Each functional group within each community was tested separately. The significant differences are bold.

Community	Functional	df1	df2	F-value	<i>p</i> -value
Heath	Dwarf shrub	1	14	2.52	0.135
	Graminoid	1	12	0.11	0.743
	Forb	NA	NA	NA	NA
	Deciduous shrub	NA	NA	NA	NA
	Lichen	1	13	0.78	0.393
	Litter	1	14	1.85	0.195
	Bryophyte	1	9	0.03	0.873
Shrub	Dwarf shrub	1	9	0.88	0.373
	Graminoid	1	14	0.04	0.851
	Forb	1	13	0.28	0.603
	Deciduous shrub	1	14	0.03	0.864
	Lichen	1	11	0.25	0.630
	Litter	1	14	6.15	0.027
	Bryophyte	1	14	0.10	0.756
Meadow	Seedless vascular	1	NA	NA	NA
	Dwarf shrub	1	6	0.03	0.862
	Graminoid	1	14	0.35	0.563
	Forb	1	14	0.52	0.483
	Seedless vascular	1	3	3.30	0.167
	Lichen	1	11	7.45	0.020
	Litter	1	14	1.45	0.248
Bryophyte	1	14	7.82	0.014	

Appendix 2: Method for determination of carbon content in vegetation and litter

Vegetation was destructively sampled in 20 × 20 cm plots chosen to represent C flux plots from each block (n = 8) in each plant community, in mid-growing season 2013. Above-ground vegetation was harvested and sorted into: deciduous shrubs, evergreen shrubs, forbs, graminoids, seedless vascular plants, lichens, and bryophytes. Litter was collected as all dead biomass above the ground. All samples were stored in paper bags and oven-dried at 70 °C for 72 h. Plant biomass was cut in pieces of ≤ 1 cm mixed. Samples (mass 0.6 – 3 g) were ground (MF 10 basic IKA Werke) with a 0.25 µm mesh size and smaller samples (mass < 0.6 g) were ground in a TissueLyser II (QIAGEN GmbH, Germany). Total carbon content was measured by elemental combustion (ECS 4100, Costech).

Table S3: Environmental variables during C flux measurements (T_{air} = air temperature inside chamber (°C), T_{surface} = temperature at 1 cm depth, T_{soil} = soil temperature at 8 cm depth (°C), Moisture = soil moisture (%), Light = Photosynthetic Active Radiation inside the chamber ($\mu\text{mol m}^{-2} \text{s}^{-1}$)) in alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, central Norway. Estimates and $\pm 95\%$ confidence intervals (CI) are from linear mixed effects models fitted with community, year, and the interaction of community and year as fixed effects, and plot as random effect.

Environment	Community	2014		2015	
		Estimate	CI	Estimate	CI
Moisture (%)	Heath	25.7	± 8.1	19.4	± 9.3
	Meadow	23.4	± 8.7	27.3	± 7.4
	Shrub	35.8	± 9.2	38.0	± 7.7
T_{air} (°C)	Heath	27.8	± 2.4	21.6	± 2.2
	Meadow	29.2	± 2.6	21.9	± 2.1
	Shrub	20.9	± 2.8	21.0	± 2.2
T_{surface} (°C)	Heath	17.2	± 1.5	15.1	± 1.3
	Meadow	17.2	± 1.6	14.1	± 1.3
	Shrub	13.6	± 1.7	11.1	± 1.3
T_{soil} (°C)	Heath	14.5	± 0.7	10.7	± 0.6
	Meadow	14.5	± 0.7	10.0	± 0.6
	Shrub	12.1	± 0.8	8.4	± 0.6
Light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Heath	907	± 145	612	± 134
	Meadow	857	± 159	541	± 129
	Shrub	489	± 168	608	± 134

Table S4: Environmental variables during C flux measurements used for estimation of GEP standardized to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (T_{air} = air temperature inside chamber ($^{\circ}\text{C}$), T_{surface} = temperature at 1 cm depth, T_{soil} = soil temperature at 8 cm depth ($^{\circ}\text{C}$), Moisture = soil moisture (%)) in an alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway. Measurements were performed in 2015, n=8 in each community. Only moisture was significantly different ($F_{2, 18}=5.25$, $p = 0.016$, ANOVA) in the heath and shrub community ($p = 0.002$, TukeyHSD).

Environment	Community	Mean	SD
Moisture (%)	Heath	21.3	± 2.9
	Meadow	26.5	± 3.4
	Shrub	33.9	± 12.4
T_{air} ($^{\circ}\text{C}$)	Heath	23.3	± 3.3
	Meadow	23.7	± 2.4
	Shrub	23.1	± 2.1
T_{surface} ($^{\circ}\text{C}$)	Heath	16.2	± 4.8
	Meadow	15.0	± 2.6
	Shrub	13.2	± 2.9
T_{soil} ($^{\circ}\text{C}$)	Heath	10.6	± 1.4
	Meadow	9.7	± 2.0
	Shrub	10.2	± 1.5

Table S5: Model performance for linear mixed effect models with environmental variables during C flux measurements as response variables (T_{air} = air temperature inside chamber ($^{\circ}\text{C}$), T_{surface} = temperature at 1 cm depth, T_{soil} = soil temperature at 8 cm depth ($^{\circ}\text{C}$), Moisture = soil moisture (%), Light = PAR inside the chamber ($\mu\text{mol m}^{-2} \text{s}^{-1}$)) and plot as random effects. Number of observations (n), the proportion of variance explained by fixed factors (R_{marginal}), the proportion of variance explained by both fixed and random factors ($R_{\text{conditional}}$), Akaike information criterion (AIC), and AIC corrected for small sample size (AICc). According to AIC and AICc the models with community and year and their interaction as fixed factors were best.

Response variable	Fixed effects	N	R_{Marginal}	$R_{\text{conditional}}$	AIC	AICc
ln (Moisture)		63	0.23	0.40	51	69
T_{air}		68	0.41	0.47	389	378
T_{surface}	Community + Year + Community x Year	68	0.43	0.43	325	320
T_{soil}		68	0.81	0.83	215	220
Light		68	0.28	0.32	949	889
ln (Moisture)		63	0.18	0.35	52	66
T_{air}		68	0.81	0.83	213	218
T_{surface}	Community + Year	68	0.44	0.44	322	321
T_{soil}		68	0.81	0.83	213	218
Light		68	0.17	0.17	955	917

Table S6: Model performance for linear mixed effect models with C fluxes as response variables (ER=Ecosystem Respiration, GEP=Gross ecosystem Photosynthesis, NEE=Net Ecosystem Exchange) and plot as random effects. Number of observations (n), the proportion of variance explained by fixed factors (R_{marginal}), the proportion of variance explained by both fixed and random factors ($R_{\text{conditional}}$), Akaike information criterion (AIC), and AIC corrected for small sample size (AICc). According to AIC and AICc the models with only community and year as fixed factors were best.

Response variable	Fixed effects	n	R_{Marginal}	$R_{\text{conditional}}$	AIC	AICc
ln (ER)		68	0.22	0.35	46	66
ln(GEP)	Community + Year + Community x Year	68	0.31	0.61	40	59
ln (NEE)		68	0.33	0.52	127	139
ln (ER)		68	0.19	0.34	46	60
ln (GEP)	Community + Year	68	0.31	0.61	38	52
ln (NEE)		68	0.33	0.52	125	134

Table S7: Mean of functional group C pools \pm SD (g m^{-2}). Means are based on sum of C pools from all functional groups and then mean over block (n = 6).

	Heath		Meadow		Shrub	
	C (g m^{-2})	SD	C (g m^{-2})	SD	C (g m^{-2})	SD
Deciduous shrub	NA		NA		360.65	\pm 130.48
Dwarf shrub	343.25	\pm 69.91	4.84	\pm 9.26	10.34	\pm 16.90
Forb	NA		14.76	\pm 8.45	4.47	\pm 5.24
Graminoid	2.11	\pm 1.82	37.91	\pm 9.34	12.10	\pm 6.44
Seedless vascular	NA		1.38	\pm 1.39	51.79	\pm 72.84
Lichen	15.54	\pm 10.84	27.94	\pm 27.66	138.18	\pm 119.11
Bryophyte	29.88	\pm 36.24	53.36	\pm 31.11	227.61	\pm 188.25

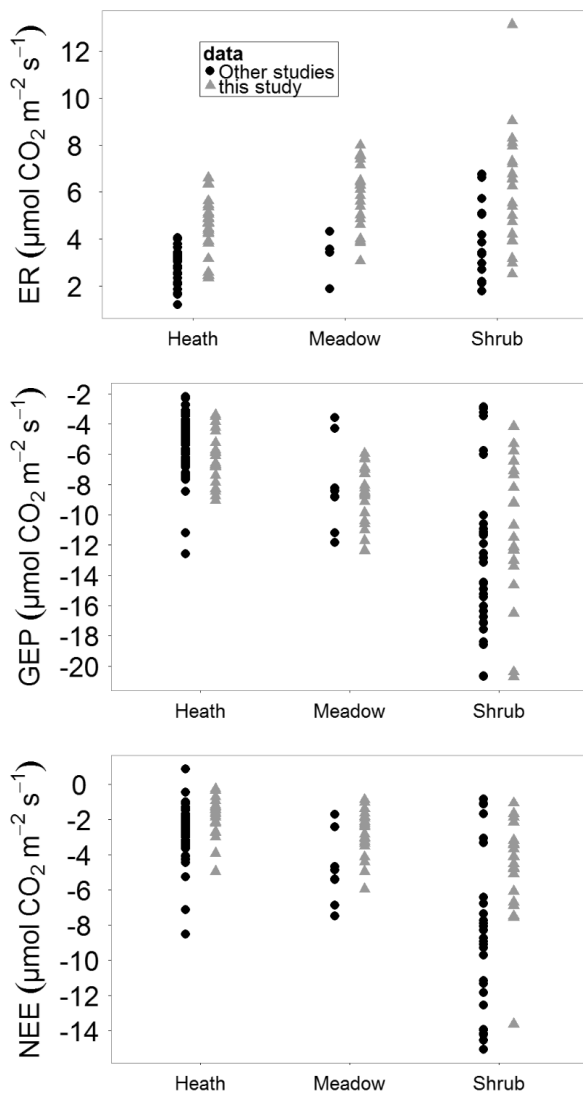


Figure S4: Comparison of mid-growing season C fluxes from present study (our study) to other studies in similar arctic and alpine plant communities. Top: Ecosystem Respiration (ER) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), middle: Mean Gross Ecosystem photosynthesis (GEP), and bottom: Mean Net Ecosystem Exchange (NEE). Other studies includes data from Toolik, Alaska and Abisko, Sweden (ITEX circumarctic CO_2 flux survey, Shaver (2015)) and from Dovre Mountains and Joatka, Norway and Abisko, Sweden (see figure 3 in Sjögersten and Wookey

(2009)). In “other studies” meadow includes both mesic meadow and snowbed, shrub includes both *Salix* and *Betula nana* dominated communities, and heath includes both heath and dry heath. Linear mixed models where community was fixed factor, and plot random factor was used to test flux differences among the three communities in “other studies”. The shrub communities had significantly greater ($p < 0.05$) GEP and NEE than the heath communities in other studies when tested with multiple comparisons for linear mixed effect models with the Tukey method. See also statistical differences between this study and other studies in table S8.

Table S8: Differences between data from this and other studies were tested for each community separately, with linear mixed models where data was fixed factor, and plot random factor, by using analysis of variance of type III with Satterthwaite approximation for degrees of freedom (* $p < 0.01$; ** $p < 0.001$; ns = non significant).

	Heath	Meadow	Shrub
ER	$F_{1, 13} = 16.84, **$	$F_{1, 10} = 16.01, *$	$F_{1, 18} = 9.71, *$
GEP	$F_{1, 17} = 1.31, ns$	$F_{1, 10} = 0.52, ns$	$F_{1, 15} = 0.061, ns$
NEE	$F_{1, 18} = 0.058, ns$	$F_{1, 10} = 6.55, *$	$F_{1, 17} = 2.73, ns$

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Paper II



Photo: Top: Sheep and herbivore exclosures, Bottom: Sheep and *Salix* near the heath community.

1 **Title:**

2 **Experimental herbivore exclusion, shrub introduction, and**
3 **carbon sequestration in alpine plant communities**

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21 **Keywords:** Gross ecosystem photosynthesis, ecosystem respiration, Salix, grazing, tundra, meadow,
22 heath, shrub expansion, herbivory, biomass

1 **Abstract**

2 **Background:** Shrub cover in arctic and alpine ecosystems has increased in recent decades, and is
3 predicted to further increase with climate change. Changes in shrub abundance may alter ecosystem
4 carbon (C) sequestration and storage, with potential positive feedback on global C cycling. Small and
5 large herbivores may reduce shrub expansion and thereby counteract the positive feedback on C
6 cycling, but herbivore pressures have also changed in the alpine-arctic tundra; the increased shrub
7 cover together with changes in herbivore pressure is leading to unpredictable changes in carbon
8 sequestration and storage. In this study we investigate the importance of herbivory and shrub
9 introduction for carbon sequestration in the short term. We measured standing biomass and
10 daytime mid-growing season carbon fluxes in plots in a full factorial plot set up where we excluded
11 small and large mammalian herbivores and introduced *Salix* by planting *Salix* transplants. We used
12 three study sites: One *Empetrum*-dominated heath, one herb- and cryptogam-dominated meadow,
13 and one *Salix*-dominated shrub community in the low-alpine zone of Dovre Mountains, Central
14 Norway.

15 **Results:** After two years, significant treatment effects were recorded in the heath community, but
16 not in the meadow and shrub communities. In the heath community cessation of herbivory
17 increased standing biomass due to increased biomass of dwarf shrubs. Cessation of herbivory also
18 reduced biomass of bryophytes and Ecosystem Respiration (ER). Except for an increase in biomass of
19 deciduous shrubs caused by the *Salix* introduction, the only effect of *Salix* introduction was an
20 increase in biomass of graminoids in the heath.

21 **Conclusions:** Our short-term study demonstrated that herbivore exclusion had small but still
22 significant effects on heath vegetation, whereas such effects were not apparent in the herb-and
23 cryptogam-dominated meadow and the *Salix*-dominated shrub community. Following the
24 treatments over more years is needed to estimate the long-term effects on community structure
25 and the consequences for C sequestration in the three plant communities. Such data are important
26 for predicting the impact of shrub expansion on C budgets from alpine regions.

1 **Background**

2 High-latitude alpine and arctic tundra ecosystems are very important for global carbon
3 sequestration, as they currently store more than half of global soil carbon (C) [1]. The large C
4 accumulation is due to short growing seasons, and low rates of decomposition caused by low
5 temperatures, waterlogging, and permafrost [2]. These high-latitude ecosystems are extremely
6 sensitive to climate changes with projections of some of the greatest C losses [3]. In recent decades,
7 shrub cover in the circumpolar arctic and alpine tundra ecosystems has increased [4-8], and climate
8 change and reduced herbivory have been proposed as the main reasons for shrub expansion [9-16].
9 The taller statured shrubs increase biomass and above-ground carbon storage, and may lead to
10 higher net summer CO₂ sequestration [17]. Therefore, modeling studies predict shrub expansion to
11 increase ecosystem carbon sequestration [18-20]. On the other hand, field studies suggest total
12 ecosystem carbon storage may decline, because shrub expansion may reduce soil carbon storage,
13 and cause increased rates of decomposition and higher ecosystem respiration [17, 21-25]. Hence,
14 more knowledge of these processes is needed, since shrub expansion can potentially alter
15 ecosystem C cycling with positive feedback to the atmosphere if plant uptake of C is lower than the
16 amount of soil C released.

17 Herbivores affect vegetation composition and ecosystem structure [26, 27] either by consumption,
18 trampling or by adding N via feces [28]. Herbivores reduce tall deciduous shrub growth, and
19 maintain low-growing tundra vegetation [15, 29, 30], and may also decrease radial growth [31].
20 Herbivores could therefore counteract the carbon cycle effects of shrub expansion by reducing
21 above-ground biomass and decreasing rates of C cycling [14, 32-35]. Still, there is not much
22 consensus on ecosystem C sequestration and storage consequences of herbivory exclusion [32, 34-
23 41]. Regarding gross ecosystem photosynthesis (GEP), most previous studies found herbivory
24 decreased carbon fixed by the vegetation [32, 34, 42, 43]. Yet, other studies found no difference in
25 GEP with herbivory [44] or an increase over a 50 year experiment due to changes in plant
26 community composition [39]. Ecosystem respiration (ER) has been reported not to differ with

1 grazing and browsing [32, 34, 37, 39, 44] or decrease [38, 42, 45]. However, one study found
2 increased ER with heavy grazing of reindeers, as compared to lightly grazed plots [43]. Grazing can
3 also promote root exudation, that stimulates microbial activity and thereby increases heterotrophic
4 respiration [35, 46]. While a meta-analysis found that herbivores decrease soil respiration in the
5 subarctic, sheep presence in temperate grasslands can increase soil respiration [38]. These opposing
6 results of carbon sequestration in alpine and arctic ecosystems are due to the fact that ecosystem
7 effects of herbivory vary with plant community, herbivore species, herbivore pressure, and temporal
8 and spatial scale of the experiment [35, 39, 41, 47].

9 Herbivore pressure in arctic and alpine ecosystems has changed over the past decades. In alpine
10 areas of Norway, land use changes involving structural changes in husbandry and abandonment of
11 summer pastures has increased the presence of browsing cervids (e.g., reindeer and moose) and
12 decreased browsing and grazing livestock (sheep) [48]. However certain areas of Norway experience
13 locally higher browsing and grazing pressure than before due to bigger herds [49]. Population cycles
14 of small herbivores such as voles and lemmings have also changed with tendencies for collapses in
15 recent decades [50, 51]. In Norway, ptarmigan populations also have declined [52]. Because of the
16 variation in herbivore densities, it is important to understand both large and small herbivore impact
17 on community structure, shrub expansion, and C cycling [10, 13, 26, 51].

18 Variation in snow-depth and nutrient and moisture conditions create mosaics of vegetation types in
19 the alpine and arctic tundra [53, 54]. Dwarf shrub-dominated heath and meadow are common
20 vegetation types in the alpine and arctic tundra that are vulnerable to shrub expansion under
21 climate change [55, 56]. Since meadow and heath communities are subject to shrub expansion, we
22 experimentally put out *Salix* transplants for shrub introduction into those two communities. *Salix*
23 transplants have previously been used in alpine nature restoration, with results such as increased
24 total biomass and lateral growth of the *Salix* after two growing seasons [57]. Still, *Salix*
25 establishment in closed vegetation may be very slow compared to establishment on bare soil [57].
26 Direct introduction provides a novel method to study the changes likely to happen with future shrub

1 expansion in in these plant communities, and here we provide important baseline data. To
2 investigate the importance of shrub expansion and herbivory for ecosystem functioning, we
3 excluded small and large mammalian herbivores and introduced *Salix* with *Salix* transplants in a full
4 factorial set-up with plots in *Empetrum*-dominated dwarf shrub heath, herb-and cryptogam-
5 dominated meadow, and a *Salix*-dominated shrub community in the low-alpine zone of Central
6 Norway. We measured day-time mid-growing season gross ecosystem photosynthesis (GEP) and
7 ecosystem respiration (ER) together with community vegetation structure represented by biomass
8 of functional groups. We addressed two main research questions: a) How does herbivore exclusion
9 affect standing biomass and carbon sequestration in heath, meadow, and *Salix* shrub communities?
10 and b) How does introduction of *Salix* transplants into heath and meadow affect standing biomass
11 and carbon sequestration, and does herbivory affect these changes?
12 We hypothesize that cessation of grazing and browsing and *Salix* introduction will increase gross
13 ecosystem photosynthesis (GEP) and ecosystem respiration (ER). Even though this has often been
14 suggested in the literature, to our knowledge no other studies have tested this, which makes this
15 study specifically timely.
16 We further hypothesize that the treatment effects will be greatest in the meadow, as this is the
17 community with the most palatable vegetation.

18 **Method**

19 **Study site**

20 The study was performed in the low-alpine vegetation zone around 1100 m a.s.l. in Dovrefjell,
21 Central Norway (62°N, 9°E) (See Supplementary Figure S1, Additional file 1). The area has a
22 continental climate [58], and from 1960 to 1990 the annual and growing season mean temperatures
23 were -1°C and 7.1 °C, respectively, and mean precipitation for the same periods was 700 mm and
24 298 mm [59]. In 2015, the annual and growing season mean temperatures were 1.58°C and 8.15°C,
25 respectively, and the mean precipitation for the same periods were 667 mm and 265 mm at the
26 closest weather station at Hjerkind 1012 m a.s.l. (Norwegian Meteorological Institute, klima.met.no).

1 The study sites were above the forest line, and we put up plots in an *Empetrum*-dominated heath, an
2 herb-and cryptogam-dominated meadow, and a *Salix*-dominated shrub community. The heath was
3 dominated by low-growing dwarf shrubs, and a few graminoids, lichens, and bryophytes. The
4 meadow was more species rich and dominated by graminoids, forbs together with lichens and
5 bryophytes. A few dwarf shrubs and seedless vascular plants were additionally present in the
6 meadow. The shrub community consisted of a deciduous shrub canopy with an understory
7 dominated by graminoids, forbs, and a thick layer of lichens and bryophytes (see detailed plant
8 species in Supplementary S1, Additional File1).

9 The three communities were situated on podzolic soil profiles, with a partial albic horizon in the
10 shrub community and a well-developed albic horizon in the heath [60]. All three communities had a
11 thick layer of till deposits from glacial moraines. Underlying bedrock in the heath and the shrub
12 communities was metavolcanic bedrock, while the meadow community was underlain by shale [61].
13 The heath and shrub community were south facing, whereas the meadow was south-west facing.

14 Snow cover during winter in the meadow and shrub community is deep (March 2015 snow depth in
15 the meadow was 38 ± 4.4 cm and in the shrub community it was 51 ± 24 cm), while it is more
16 unstable and often shallow in the heath (March 2015 snow depth was 0 cm) [17]. Animal husbandry
17 in the area began about 400 years BC, and probably intensified around year 700 with permanent
18 settlement [62]. Before 1970, animal husbandry in the study area included horses, cows, and sheep,
19 but after 1970 when most farms specialized in one animal the area was mainly used for domestic
20 Norwegian white sheep (*Ovis aries*) (Vegar Nystuen, personal communication). From the 70s to the
21 present the number of sheep in the area has been relatively stable (Vegar Nystuen, personal
22 communication) with low-intensity summer grazing and browsing with up to 25 sheep per km²[63].
23 Voles (*Microtus agrestis*, *M. oeconomus*, and *Myodes rufocanus*) and lemmings (*Lemmus lemmus*)
24 are also present, and the area experienced rodent peak years in 2007, 2011, and 2014, but not in
25 2015 [50]. Other larger herbivores present or passing through the sites are ptarmigan (*Lagopus*

1 *lagopus* and *L. muta*), hare (*Lepus timidus*), moose (*Alces alces*), and occasionally wild reindeer
2 (*Rangifer tarandus*).

3 In summer, meadows are important for sheep summer grazing, as they are more productive and
4 nutrient rich than heaths, whereas heaths are common resting sites for the sheep [49, 55, 64]. In
5 early summer, *Salix* twigs in shrub communities are browsed by sheep [65], and *Salix* shrubs may
6 provide both forage and shelter for smaller animals such as ptarmigans and rodents during both
7 summer and winter [52, 66]. During winter, deep snow cover in meadows and shrub communities is
8 important for rodents that are feeding on bryophytes [67], and *Salix* twigs above the snow are
9 browsed by ptarmigan [68]. The heaths are also easily accessible for winter grazing, because of the
10 shallow snow cover [49]. The three different types of plant communities may therefore respond
11 differently to changes in herbivore exclusion [42]

12 **Experimental design**

13 In late June 2013, eight blocks were randomly selected for treatment in each community. In each
14 block, we established four plots with different experimental treatments: Plots with and without
15 herbivores and plots with and without *Salix* transplants. The experiment hence was a 2 x 2 factorial
16 design in eight replicates (Figure 1).

17 We excluded both small and large herbivores with 80 x 80 x 50 cm exclosures with a lid in early July
18 2013. The exclosures were made of galvanized steel mesh with mesh size 1.27 x 1.27 cm [12, 69-71],
19 that were dug about 5 to 10 cm into the ground (Figure 1).

20 To introduce *Salix*, four *Salix* transplants or rooted willow cuttings, were planted into half of the
21 plots. This was due to difficulties in species determination at such a small stage a mixture of *Salix*
22 *glauca* L. and *S. lapponum* L.. Cuttings of *S. glauca* and *S. lapponum* were collected in the vicinity of
23 the experimental sites in October 2013 and brought to a plant nursery (Norske Naturplanter AS,
24 Færvik, Norge). The cuttings were stored at 0 °C until January 2014, and then planted vertically in
25 commercial plant soil and cultivated during the winter in a greenhouse. In May the willows were
26 planted in 10 cm diameter pots, put outside and topped (long twigs were cut to improve below-

1 ground growth). By June 2014 the plants were trimmed to about 10 cm height, before planting in
2 the field [72]. In 2015, the average height of the plants was 12.6 ± 3.6 SD cm. Mortality was two out
3 of 192 in 2015, both outside the exclosures, one in each the meadow and shrub community. In 2015,
4 a harvest plot was established within each block for biomass measurements (see below).

5 **Carbon fluxes**

6 Carbon dioxide fluxes were measured in each of the 50 x 50 cm experimental plots (177
7 measurements on 96 plots, and most was measured twice) during mid-growing season in 2015 on
8 sunny days only. Fluxes were measured using a closed-system composed of a collapsible 0.5 m x 0.5
9 m x 0.6 m polyethylene chamber and a LI-840A CO₂/H₂O infrared gas analyzer (LI-COR Inc., Lincoln,
10 Nebraska, USA), sealed with a 5 m long chain weighing 5 kg. For dark measurements we used an
11 opaque hood to block out the light [73]. Photosynthetically active radiation (PAR) during dark
12 measurements ranged from -2 to 128 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and flow rate averaged 0.8 L min⁻¹. To determine
13 the rate of the CO₂ change in the chamber we first corrected the CO₂ concentration for water
14 content (C') and then used linear regression to find the CO₂ flux (Jasoni and others 2005):

$$15 \quad C' = \frac{[CO_2](\mu\text{mol mol}^{-1})}{[H_2O](\text{mmol mol}^{-1})}$$
$$16 \quad CO_2 \text{ flux} = \frac{V P}{R T S} \frac{d' C}{dt}$$

17 Where V = Volume chamber (m³), P = air pressure (kPa) (estimated to be 90 kPa at our sites at 1100
18 m elevation), R = the ideal gas constant (8.314 J mol⁻¹ K⁻¹), T = average air temperature (°C) during
19 the measurement, S = surface area (m²), d'C/dt = the slope of linear regression of C' on time.

20 Each measurement started 30 s after sealing, lasted 120 s, and consisted of a light and a dark
21 measurement, and Net Ecosystem Exchange (NEE) and Ecosystem Respiration (ER) were calculated
22 from those measurements respectively. Gross Ecosystem Photosynthesis (GEP) was calculated by
23 subtracting ER from NEE. When reporting NEE and GEP, negative values denote that the plot is a CO₂
24 sink whereas positive values represent a CO₂ source. To control for variable light intensities during
25 different times of the day, we standardized GEP to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR in all control plots and half

1 of the treatment plots (See Supplementary S2, Additional File 3) but due to lack of significant
2 differences from non-standardized results, we use non-standardized GEP data in the final results
3 (See Supplementary Figure S4, Additional File 3).

4 During all flux measurements, we measured PAR with a LI-190S quantum sensor (LI-COR Inc.,
5 Lincoln, Nebraska, USA), air temperature with PT100 sensors inside (at 40 cm height) and outside
6 the chamber (at a height of 60 cm), soil temperature at 8 cm depth, and soil moisture at 5 cm depth
7 with a TRIME-PICO32 sensor (IMKO, Germany). Surface temperature (at 1 cm depth) was
8 interpolated from daily measurements every four hours with temperature sensors (iButtons, Maxim
9 Integrated Products, Sunnyvale, CA, USA).

10 For more details on the flux measurement methods see Sørensen et al. [17].

11 **Vegetation recording and biomass estimation**

12 Vegetation composition was recorded with the point intercept method [74] during the mid-growing
13 season 2015 in the vegetation plot of all the experimental plots ($n = 96$) with a 25×25 cm quadrat
14 and 25 pins (Figure 1).

15 To convert the point intercept data into standing biomass for the experimental plots, vegetation was
16 destructively sampled from the harvest plots. Due to logistics, only six out of eight blocks were
17 randomly selected per community (total $n=18$). In the harvest plots, vegetation composition with 25
18 pins and harvest, were done in 25×25 cm quadrats in the heath and the meadow communities, and
19 in 50×50 cm quadrats in the shrub community to capture the heterogeneous distribution of woody
20 biomass. The harvested vegetation was sorted into plant functional groups based on growth form, a
21 partitioning that has been shown useful for predicting vegetation effects on ecosystem processes
22 [75]. Prior to harvest, we determined C flux and functional group composition of the harvest plots,
23 and they were not significantly different from the experimental control plots [17]. The functional
24 groups were deciduous shrubs (*Salix glauca*, *S. lapponum*, *Betula nana*), dwarf shrubs (the evergreen
25 shrubs *Empetrum nigrum*, *Vaccinium vitis-idaea* and the low growing deciduous shrubs *V.*
26 *uliginosum*, *V. myrtillus*, *S. herbacea*, and *S. reticulatum*), forbs, graminoids, seedless vascular plants,

1 lichens, and bryophytes. The biomass was oven-dried at 70 °C for 72 h before weighing to an
2 accuracy of 0.001 g. To interpolate from measured biomass to estimated biomass in the
3 experimental plots, the harvested biomass was first converted to g m⁻² and regressed on the
4 absolute abundance (number of hits) of each functional group. We followed S Jonasson [74] and
5 tested four different regression models for each functional group, and chose the best model based
6 on r² (ranging from 0.564 – 0.999) and normal distribution of the model residuals (See
7 Supplementary Table S1 and S1, Additional File 2). We used parametric bootstrapping with 1000
8 replicates to get model mean estimates of biomass and 95 % confidence intervals. We use the mean
9 estimates in the results. Despite considerable variation in lower and upper limits of confidence
10 intervals, we expect the model means to represent the vegetation biomass well (See Supplementary
11 Figure S2, Additional File 2). Models were fitted across communities, except the bryophyte and
12 lichen models (see more Supplementary S1, Additional File 2). The model for deciduous shrubs was
13 only based on the shrub community because there were no deciduous shrubs present in the harvest
14 plots in the heath and meadow. This posed a problem for the estimations in the experimental plots
15 in the heath, since the vegetation was much lower statured in the heath and there was some
16 creeping *B. nana* present in three plots (See Supplementary Figure S3, Additional File 2). We
17 therefore defined *B. nana* as a dwarf shrub in the heath, but as deciduous shrub in the shrub
18 community.

19 In the heath community, there was considerable browning of some of the evergreen shrub leaves (*E.*
20 *nigrum*, *Arctostaphylos uva-ursi*, *V. vitis-idaea*), which could be due to frost drought damage during
21 the winter [76]. In the biomass models this was assumed to be live biomass, because the branches
22 still seemed alive. There was frost damage on the evergreen shrubs both inside and outside the
23 enclosures, so we assume that this did not affect differences in standing biomass and C fluxes.

24 **Statistical analysis**

25 We used one-way ANOVA to test for community differences in total biomass and tested significance
26 using multiple comparisons with a Tukey's honest significant difference test.

1 As we were interested in the treatment effects *within* each community, the data were analyzed
2 separately for each community. To determine differences in estimated biomass of the functional
3 groups we used factorial 2 x 2 ANOVA with enclosure, transplant, and their interaction as
4 explanatory variables. When data did not meet the assumptions of the parametric analysis, they
5 were ln-transformed. If transformation was not sufficient, we used non-parametric Kruskal-Wallis
6 test (PMCMR package; [77]) with one parameter representing all treatment combinations (C –
7 control, E – enclosure, ET – enclosure and transplant and T-transplant). Dunn’s test of multiple
8 comparisons of ranked sums were used to identify treatment differences (dunn.test package;[78].
9 To estimate the differences in means of C fluxes between the treatments we used linear mixed
10 effects models following Gaussian distributions (lme4 package;[79]. Gross Ecosystem Photosynthesis
11 (GEP), Net Ecosystem Exchange (NEE), and Ecosystem Respiration (ER) were ln-transformed to meet
12 model assumptions. Within the models, fixed effects were enclosure, transplant, and their
13 interaction. To control for repeated measurement during season, plot was considered a random
14 effect. Community was additionally a fixed effect, when comparing communities. Differences in GEP,
15 NEE, and ER between the communities and treatments were compared using linear mixed effects
16 models with the Tukey method (multicom package; [80]) on full models without interactions.
17 To evaluate importance of community and treatments for GEP, ER, and NEE, we used model
18 selection with AICc (dAICc < 2) as selection criteria on linear mixed effects models without
19 interactions (MuMIn package; [81]). R Core Team [82] was used for all data analysis.

20 **Results**

21 **Standing biomass and carbon sequestration in the three plant communities**

22 As expected, the meadow, heath and *Salix* shrub communities were significantly different with
23 respect to both community structure and carbon sequestration. The shrub community had highest
24 standing biomass followed by heath whereas it was smallest in the meadow community ($p < 0.0001$
25 for all differences, TukeyHSD) (Figure 2). Carbon (C) sequestration was greatest in the shrub
26 community ($p < 0.01$, Tukey) with Gross Ecosystem Photosynthesis (GEP) from -9.54 to -11.77 μmol

1 $\text{m}^{-2} \text{s}^{-1}$ and Net Ecosystem Exchange (NEE) ranging from -3.76 to $-4.79 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 3). The
2 meadow community had larger GEP (-7.35 to $-8.10 \mu\text{mol m}^{-2} \text{s}^{-1}$) and NEE (-2.71 to $-3.01 \mu\text{mol m}^{-2} \text{s}^{-1}$)
3 than the heath (GEP: -5.27 to $-6.46 \mu\text{mol m}^{-2} \text{s}^{-1}$, NEE: -1.65 to -2.25 , and $p < 0.001$, Tukey).
4 Ecosystem Respiration (ER) was higher ($p < 0.01$, Tukey) in both the shrub (5.77 to $6.78 \mu\text{mol m}^{-2} \text{s}^{-1}$)
5 and meadow communities (4.64 to $5.26 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in the heath community (3.60 to 4.50
6 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Figure 3).
7 The best models for all the three C fluxes (GEP, NEE, ER) contained only community (See
8 Supplementary Table S4, Additional File 5).

9 **Effects of herbivore exclosures**

10 In the heath community herbivore exclusion resulted in increased standing biomass ($F_{1,28} = 5.28$, $p <$
11 0.05 , ANOVA), due to increased biomass of dwarf shrubs ($F_{1,28} = 4.52$, $p < 0.05$, ANOVA) (Figure 2).
12 Within exclosures in the heath, there was a tendency for increased biomass of graminoids ($p =$
13 0.0897 , Kruskal Wallis) (Figure 2). The biomass of bryophytes was very low in the heath, and even
14 lower within the exclosures ($p < 0.05$, Dunn's test). In the heath, there was marginally less Gross
15 Ecosystem Photosynthesis (GEP) with herbivore exclosures ($p = 0.082$, Tukey) and Ecosystem
16 Respiration (ER) was significantly reduced ($p < 0.05$, Tukey) (Figure 3).
17 Within the meadow and shrub communities there were no significant effects of herbivore exclusion
18 on biomass or carbon fluxes. However, the shrub community was significantly ($p < 0.05$) drier and
19 cooler inside than outside the exclosures during C flux measurements. In the meadow community
20 surface temperature was significantly ($p < 0.05$) lower inside the exclosures than outside (Table S2,
21 Additional file 4). This corresponds to generally cooler surface temperatures inside the exclosures
22 during summer in both the heath and meadow communities. In the meadow community, surface
23 temperatures were additionally warmer during winter. There was about one cm snow within
24 exclosures in the heath, and this was significantly more than outside the exclosures where there
25 were none. Otherwise there were no significant differences in snow depth in any of the other

1 communities (Table S3, Additional File 4). Thus, the effect of reduced grazing is difficult to
2 disentangle from other enclosure effects.

3 **Effects of *Salix* transplantation**

4 In the heath, transplantation of *Salix* not only increased the biomass of deciduous shrubs ($F_{1,28} =$
5 18.84, $p < 0.001$, ANOVA) but also that of graminoids ($p < 0.05$, Dunn's test). There was also an
6 increase in biomass of deciduous shrubs due to the transplantation of *Salix* in the meadow but
7 surprisingly, it was not significant ($F_{1,28} = 3.18$, $p = 0.086$, ANOVA) (Figure 2). The transplantation of
8 *Salix* did not affect the C fluxes significantly in any of the communities.

9 **Treatment interactions**

10 Herbivore exclusion did not show significant interactions with transplantation in the heath and the
11 meadow (Figure 2 and 3). In the shrub community, there was higher standing biomass ($F_{1,28} = 5.74$, p
12 < 0.05), with enclosure and no transplant than with both enclosure and transplant (Figure 2).

13 **Discussion**

14 The aim of this study was to evaluate short-term effects of *Salix* shrub expansion and herbivory on
15 community structure and carbon (C) cycling in the arctic-alpine tundra. Contrary to expectations, the
16 effects of the treatments were strongest in the heath. After just two years, exclusion of herbivory
17 increased the standing biomass in the heath due to increased biomass of dwarf shrubs. The biomass
18 of bryophytes was reduced as was the Ecosystem Respiration (ER). *Salix* introduction effects were
19 weak, despite increased biomass of graminoids and deciduous shrubs in the heath community.
20 There were no treatment effects on the standing biomass or C fluxes in the two other community
21 types.

22 **Effects of herbivore exclusion**

23 In this study, we excluded both small and large herbivores, and previous studies have reported
24 significant results after only two growing seasons [12, 69, 71]. However, the increased standing

1 biomass in the heath and not in the meadow community were unexpected since evergreen dwarf
2 shrubs (which mainly contributed to the increased standing biomass) are often avoided by
3 herbivores due to their high content of secondary compounds [83-85]. However, the increase was
4 caused by increased growth of the evergreen shrubs, similar to previous exclosure studies in tundra
5 [14, 37, 86]. It was not an artefact of the categorization of *Betula nana* as a dwarf shrub in the heath
6 biomass models, since an analysis of dwarf shrub abundance without *B. nana* showed similar results
7 ($\chi^2 (1) = 5.27, p < 0.05, n = 31$, Likelihood ratio test).

8 The entire study area has low-intensity sheep grazing, but lack of trampling from the sheep may
9 have caused the effect of increased standing biomass with exclusion of herbivores [84, 87]. Sheep
10 often tend to rest and chew their cud in lichen heaths and similar dry, low-statured vegetation [49].
11 An installation with salt licks attracting sheep is located about 500 m from the heath, and we
12 observed sheep feces, torn out plot marking poles, and wool on the exclosures. The sheep most
13 likely graze on the forbs and to some extent the graminoids, and this could explain the marginally
14 higher graminoid biomass with cessation of grazing. Moreover, sheep grazing has been shown to
15 favor the resistant *Polytrichum* species that are present in the heath community [88] and this could
16 contribute to explaining the reduced bryophyte biomass in the exclosures. Wild reindeer
17 occasionally pass through the area, and their presence may have added to the reduced standing
18 biomass outside exclosures in the heath. However, reindeer prefer lichen and since there is low
19 abundance of lichen in the heath community, this is less likely. Still, reindeer winter grazing due to
20 the shallow snow cover in the heath community could have played a role, even though dwarf shrubs
21 are not of high preference to reindeer [85]. Despite a rodent peak in 2014, rodent densities during
22 the study years in the study area were not very high [50], so we believe that the influence of rodents
23 was minimal. Moreover, rodent grazing is most pronounced in the winter and they prefer a deep
24 snow cover over the shallow cover found in the heath [67].
25 The decrease in bryophyte abundance when vascular plant biomass increases after excluding
26 herbivores or warming with open top chambers has previously been shown in similar vegetation [89-

1 92]. This could be associated with decreased light levels due to shading by the vascular plants [91],
2 though it could also be an actual enclosure effect. In the meadow, the enclosure with lid resulted in a
3 difference in light intensity (PAR) ranging from 11 – 29 % depending on whether it was sunny or
4 cloudy [93] and we assume that there would be similar differences in the heath and shrub
5 communities. The reduced light could have affected the treatments. The microclimate was generally
6 cooler inside the enclosures during summer in the heath and the meadow. During winter surface
7 temperatures were warmer in enclosures in the meadow, despite snow depth only was significantly
8 different within the heath. Thus, the effect of reduced grazing or reduced trampling is difficult to
9 distinguish from other enclosure effects. In previous studies using these enclosures with the small
10 mesh size and lid (Ravolainen et al 2011), lack of continuous microclimatic surveys combined with
11 high herbivory levels could have disguised such a potential enclosure effect. These side effects
12 parallels problems of using open top chambers [94], and we need to find a way to eliminate this
13 problem. In the present study, the positive treatment effect of herbivore exclusion could have been
14 negated by a negative treatment impact of the enclosure itself. Alternatively can the lack of effects
15 of herbivore exclusion on the standing biomass in the meadow and shrub communities suggest low
16 herbivory levels during the experiment in these communities. We expected the effect of rodent
17 grazing to be most pronounced in the meadow and shrub communities, but the few rodents during
18 the years of the experiment could explain why we did not see any treatment effects in these
19 communities.

20 Due to the small treatment effects on the standing biomass we also saw few effects on the fluxes.
21 However, the significantly lower Ecosystem Respiration (ER) in enclosures in the heath was
22 unexpected given the greater standing biomass, but a similar trend was found with sheep grazing in
23 temperate grasslands (Andriuzzi et al 2017). A possible mechanism for reduced ER in the heath could
24 be reduced N-input within the enclosures: In the area with sheep present, feces might enhance N
25 input and increase N mineralization and microbial activity [87], which in turn could increase C cycling
26 through increased heterotrophic respiration. We found no evidence of enclosure shading effects on

1 the flux measurements. In the heath community where we found decreased ER with exclosures,
2 there were no difference in surface temperature during the flux measurements (Table S2, Additional
3 file 4). The only effects of exclosures on microclimate during the flux measurements, was lower
4 surface temperature in the meadow, and in the shrub community it were drier soil and cooler air
5 temperature. This was surprising, but the cooler temperatures may have been caused by shading
6 from the sides of the cages, whereas the drier soils in the shrub community may indicate that there
7 has been higher evapotranspiration in the plots and perhaps an undetected increase in *Salix* canopy
8 density.

9 **Effects of shrub expansion in heath and meadow communities**

10 Our use of *Salix* introduction in the present study provides a method to experimentally test effects
11 of shrub expansion, whereas previous studies have used succession or natural *Salix* recruits
12 (Ravolainen et al 2014). This experiment will bring interesting data in the years to come, as this
13 method provides knowledge of the exact succession history on plot-scale. The *Salix* transplants in
14 our experiment had in one year and almost two growing seasons, not reached a size where they
15 affected the ecosystem substantially, but these results provide important baseline data for future
16 analysis. Still, graminoid biomass was significantly greater with *Salix* introduction in the heath
17 community. However, due to the low overall graminoid biomass in this community, the increased
18 graminoid biomass was not reflected by the C flux measurements, and we believe that this result is
19 of little ecological importance.

20 The lack of shrub introduction effects in the meadow and heath community is not that surprising
21 because community processes in arctic-alpine tundra often are very slow. The results of our study
22 may indeed confirm that *Salix* establishment in closed vegetation is very slow compared to
23 establishment on bare soil [57], and potentially growing them bigger and taller before planting them
24 out and taking mycorrhizal symbionts into account could be an idea for future study designs [95].

25 **Treatment interactions - experimental manipulations?**

26 The *Salix* introduction in the shrub community was done as a control, since we did not expect to find

1 any differences in this community. The significant interaction in standing biomass with herbivore
2 exclosures and *Salix* transplants in the shrub community was therefore puzzling. This might be an
3 artefact of the heterogeneous nature of the plots in this community. Another possibility is that these
4 plots have the most disturbed shrub canopies, since we both have manipulated the vegetation by
5 digging to establish the exclosures and planting the *Salix* transplants. This may unfortunately
6 systematically have affected the standing biomass in those plots, at least in the short term.

7 **Conclusion**

8 Our short-term study demonstrated that both shrub introduction and herbivore exclusion had small
9 but still significant effects on alpine tundra heath vegetation, whereas such effects were not
10 apparent in the herb-and cryptogam-dominated meadow and the *Salix*-dominated shrub
11 community. We demonstrated that there is a potential exclosure side effect altering the
12 microclimate. We found a significant increase in above-ground biomass in the heath with herbivore
13 exclosures. This could be an effect from reduced trampling, but can also be a shading effect from the
14 exclosure. Following the treatments over more years is needed to estimate the long-term effects on
15 community structure and the consequences for carbon sequestration in the three plant
16 communities. Such data are important for predicting the impact of shrub expansion on C budgets
17 from alpine regions.

18

1 **Figure 1: Experimental plot combination** of the 2 x 2 factorial design, four treatments replicated
2 eight times in each of three alpine plant communities in Dovre Mountains, Central Norway. The
3 treatments consisted of plots with and without herbivore exclosures, and plots with and without
4 *Salix* introduction with four *Salix* transplants, that were a mixture of *Salix glauca* and *S. lapponum*.
5 Top right photo is an exclosure in the meadow community and lower left photo is a *Salix* transplant
6 in the heath.

7 **Figure 2: Mean standing biomass of functional groups** in plots with and without herbivore exclosure
8 and plots with and without *Salix* transplants. The biomass was estimated from vegetation analysis
9 and harvest performed on harvest plots during mid-growing season for an alpine *Empetrum*-heath,
10 meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway. We used
11 parametric bootstrapping with 1000 replicates to get model estimates of biomass. Model
12 performance and estimates with 95 % confidence intervals are available in Table S1 and Figure S2
13 respectively.

14 **Figure 3: Mean CO₂ flux estimates** ($\mu\text{mol m}^{-2} \text{s}^{-1}$) \pm 96 % confidence interval (CI) on plots with and
15 without herbivore exclosures combined with and without *Salix* transplants during mid-growing
16 season for an alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre
17 Mountains, Central Norway. Estimates based on linear mixed models with plot as a random factor (n
18 = 177). Top: Ecosystem respiration (ER). Middle: Net ecosystem exchange (NEE). Bottom: Gross
19 Ecosystem Photosynthesis (GEP). Within the heath Ecosystem Respiration (ER) was significantly
20 lower with exclosure ($p = 0.021$, Tukey).

21

1 **Additional Files**

2 **Additional File 1.** Location of study site (Figure S1).

3 **Additional File 2.** Supplementary biomass model method (S1), model performance of linear models
4 used to estimate biomass in experimental plots (Table S1), mean biomass model estimates with
5 upper and lower 95 % confidence interval (Figure S2), and a stacked barplot of mean standing
6 biomass in experimental plots illustrating implications of dwarf shrubs categorization (Figure S3).

7 **Additional File 3.** Method for standardization of Gross Ecosystem Photosynthesis (GEP) to 600 PAR
8 (S2) and comparison of GEP to GEP600 (Figure S4).

9 **Additional File 4.** Mean environmental variables during CO₂ flux measurements (Table S2) and
10 during summer and winter (Table S3).

11 **Additional File 5.** Carbon flux model selection (Table S4).

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1 **Declarations**

2 **Ethics approval and consent to participate**

3 Not applicable.

4 **Consent for publication**

5 Not applicable.

6 **Availability of data and materials**

7 The datasets generated and analysed during the current study are [WILL BE UPON ACCEPTANCE]
8 available in the DRYAD repository [PERSISTENT WEB LINK TO DATASETS].

9 **Competing interests**

10 The authors declare that they have no competing interests.

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16 MVS, RS, BJG, KON, DH, BJE participated in the design of the study. MVS performed fieldwork,
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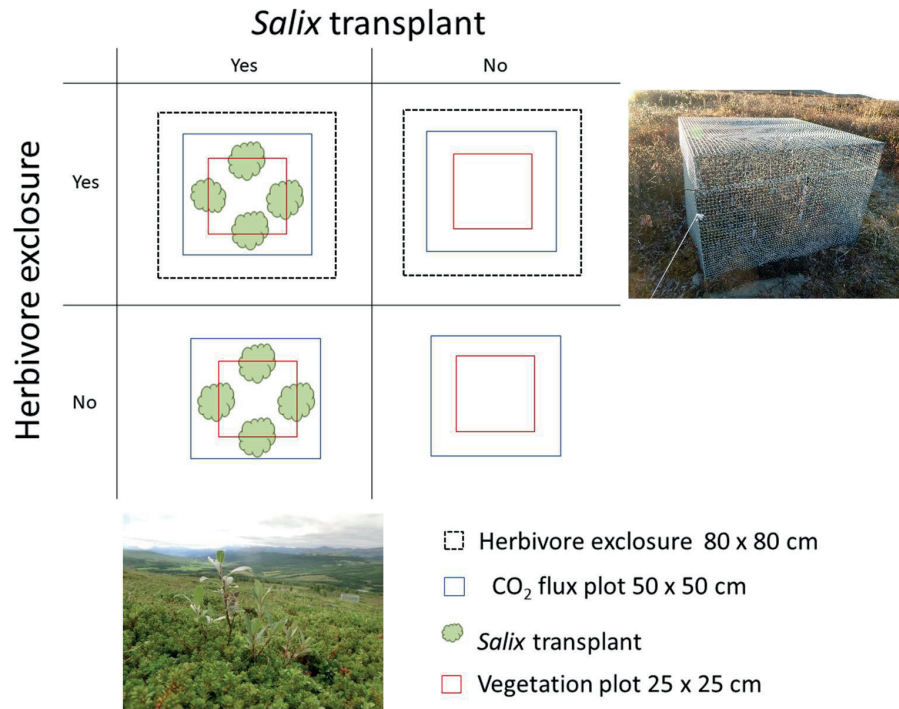
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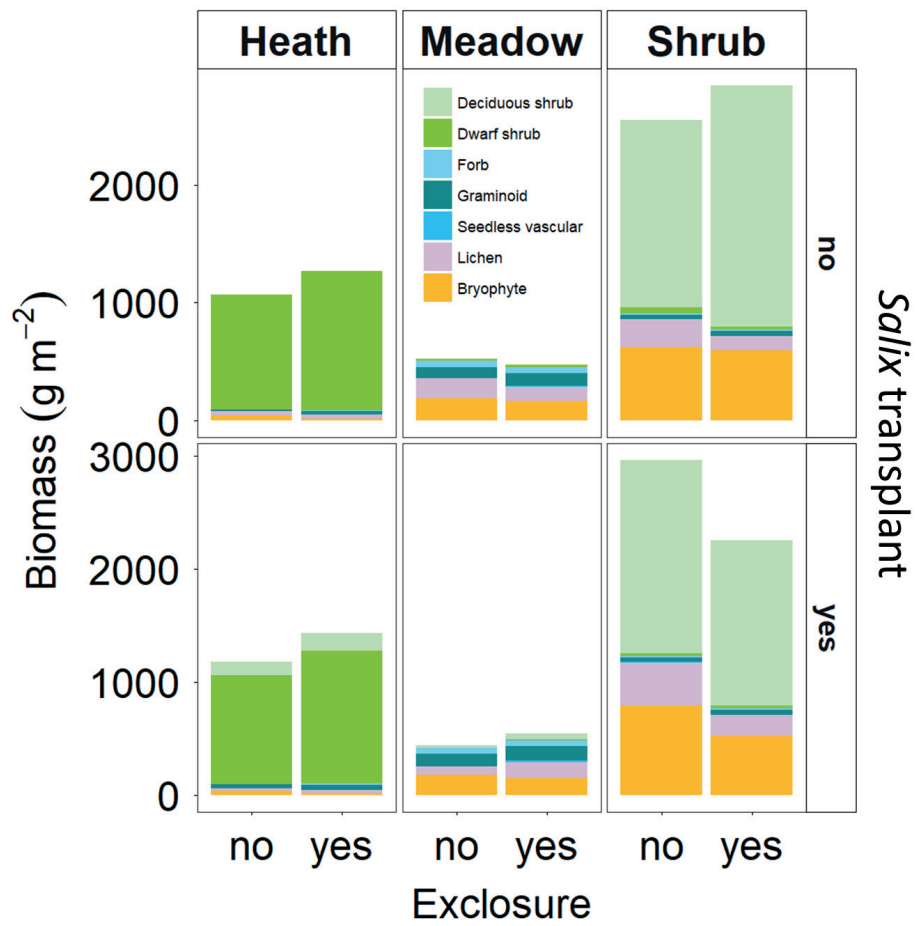
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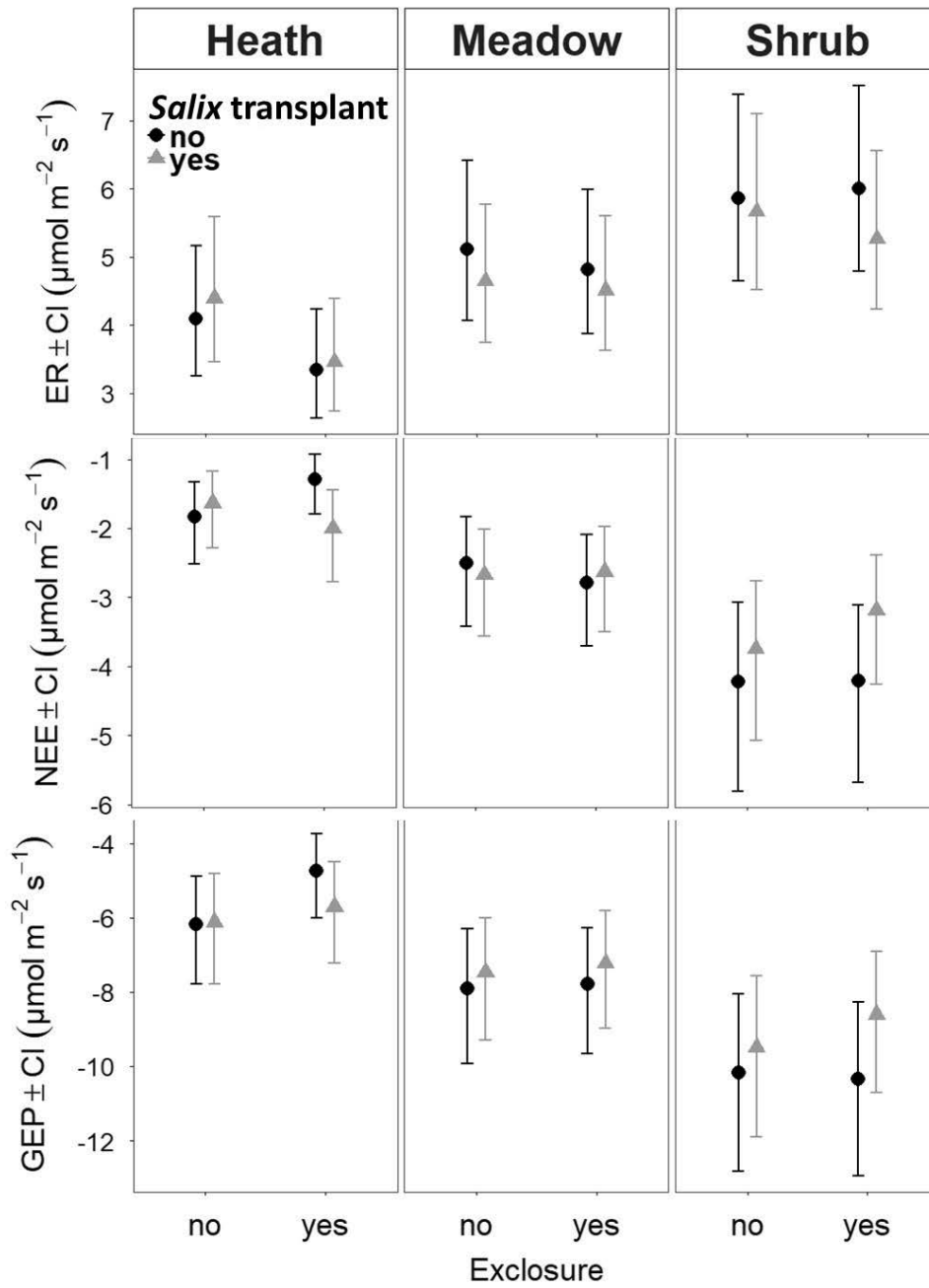
2 **Figure 1.**

3



1

2 Figure 2.



1

2 Figure 3.

1 **Additional file 1**

2 **For**

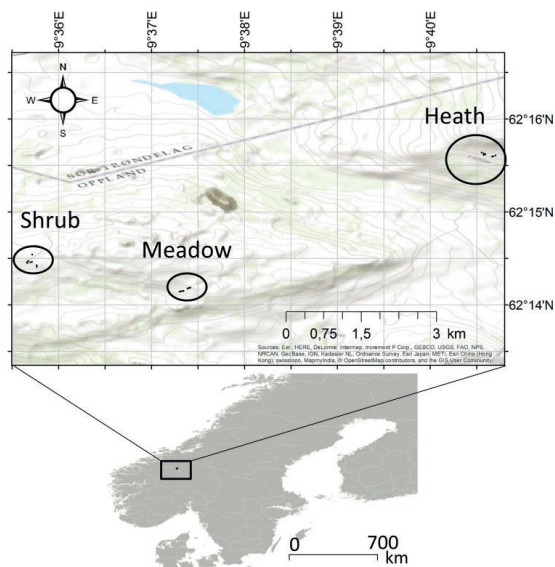
3 Effects of herbivore exclusion and shrub expansion on carbon sequestration in alpine plant
4 communities

5 **Author names:** Mia Vedel Sørensen*, Bente Jessen Graae, Dagmar Hagen, Brian J. Enquist, Kristin
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9



10

11 **Figure S1:** Location of study site and the three plant communities, in Dovre Mountains, Central
12 Norway.

13

14 **S2: Detailed description of community plant species**

15 The heath was dominated by low growing dwarf shrubs (e.g., *Empetrum nigrum hermaphroditum*,
16 *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Loiseleuria procumbens*, *Betula nana*),
17 a few graminoids, especially *Festuca ovina*, and lichens (e.g., *Flavocetraria cucullata*, *Cladonia mitis*,
18 *C. rangiferina*, *C. s.l. gracilis*, *Alectoria ochroleuca*, *Cetraria islandica*) and bryophytes (e.g.,
19 *Polytrichum commune*, *P. juniperinum*, *Dicranum flexicaule*, *Ceratodon purpureus*) were present.

1 The meadow was more species rich and dominated by graminoids (e.g., *Avenella flexuosa*, *Festuca*
2 *ovina*, *Anthoxanthum nipponica*, *Deschampsia cespitosa*, *Carex bigelowii*, *C. vaginata*, *Juncus trifidus*,
3 *Agrostis capillaris*), forbs (e.g., *Thalictrum alpinum*, *Antennaria dioica*, *Leontodon autumnalis*,
4 *Saussurea alpina*, *Campanula rotundifolia*, *Astragalus alpinus*, *Ranunculus acris*, *Potentilla crantzii*,
5 *Galium boreale*, *Sibbaldia procumbens*, *Achillea millefolium*, *Bistorta vivipara*, *Cerastium alpinum*)
6 together with lichens (e.g., *Stereocaulon alpinum*, *Cetraria islandica*) and bryophytes (e.g.,
7 *Hylocomium splendens*, *Barbilophozia lycopodioides*, *Aulacomnium palustre*, *Hylocomiastrum*
8 *pyrenaicum*, *Sanionia uncinata*, *Pleurozium schreberi*). A few dwarf shrubs (*Salix herbacea*) and
9 seedless vascular plants (*Selaginella selaginoides*) were present.

10 The shrub community consisted of a deciduous shrub canopy (*Salix glauca*, *S. lapponum* and some
11 *Betula nana*) with an understory dominated by graminoids (e.g., *Avenella flexuosa*, *Festuca ovina*,
12 *Carex bigelowii*, *C. vaginata*, *Anthoxanthum nipponica*, *Agrostis mertensii*), forbs (*Solidago virgurea*,
13 *Saussurea alpina*, *Thalictrum alpinum*, *Pedicularis lapponica*, *Galium boreale*, *Pyrola minor*, *Trientalis*
14 *europaea*, *Ranunculus acris*), and a thick layer of lichens (*Cladonia mitis*, *C. stellaris*, *C. Stygia*, *C.*
15 *rangiferina*) and bryophytes (*Pleurozium schreberi*, *Polytrichum commune*, *Hylocomium splendens*).
16 A few dwarf shrubs (e.g., *Vaccinium vitis-idaea* L. and *V. myrtillus*) were present.

17 Nomenclature followed Lid and Lid (2007) for vascular plants, Hill et al. (2006) for bryophytes, and
18 Artsdatabanken (2015) for lichens.

19

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29

30

1 **Additional file 2**

2 **For**

3 Effects of herbivore exclusion and shrub expansion on carbon sequestration in alpine plant
4 communities

5 **Author names:** Mia Vedel Sørensen*, Bente Jessen Graae, Dagmar Hagen, Brian J. Enquist, Kristin
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9 **S1: Biomass models method**

10 For each functional group we ran models across community for the harvest plots, to get a
11 relationship between absolute abundance (number of hits) and biomass per each functional group.
12 Biomass was converted to g m², because harvest plots in the heath and meadow was 25 cm x 25 cm
13 and 50 cm x 50 cm in the shrub community.

14 We followed S Jonasson [1] and tested four different linear models for each functional group, and
15 then chose the best model based on r² and normal distribution of model residuals:

16 M1: Biomass per functional group ~ absolute abundance functional group

17 M2: biomass per functional group ~ ln (absolute abundance functional group)

18 M3: ln (biomass per functional group) ~ (absolute abundance functional group)

19 M4: ln (biomass per functional group) ~ ln (absolute abundance functional group)

20 We used parametric bootstrapping with 1000 replicates to get model estimates of biomass and 95%
21 confidence intervals.

22 Models for deciduous shrubs were based on deciduous shrubs present in the *Salix* shrub community
23 only, because there were no hits of deciduous shrubs in the harvest plots in the other communities.
24 In the beginning, there were very high estimated biomass of deciduous shrubs in the heath, but in
25 those plots, quite some *Betula nana* were present. The difference between the heath and the shrub
26 community is the vegetation height, and therefore we chose to categorize *B. nana* in the heath as a
27 dwarf shrub, to get more realistic biomass estimates in the heath community. *B. nana* present in the
28 shrub community was characterized as a deciduous shrub.

29 Models for bryophytes and lichens

30 In the method of vegetation analysis we only counted first hits for those two functional groups. We
31 did not count the amount of hits each pin hit a moss or lichen; there were max 25 hits for those
32 functional groups. So, 24 hits in the meadow and 24 hits in the *Salix* shrub community would result
33 in a very different biomass, because the cryptogam layer was much thicker in the *Salix* shrub
34 community. We therefore chose to ran those models separately for each community.

35 **Bryophytes:** Because there were only two harvest plots in the heath with bryophytes present, and
36 biomass and hit are more similar than biomass and hits in the *Salix* shrub community, we made a
37 model for meadow and heath together and a model for the shrub community.

38 **Lichens:** we made three different models, one for each community. Since 10 hits in the meadow was
39 much higher biomass than 10 hits in the heath.

40

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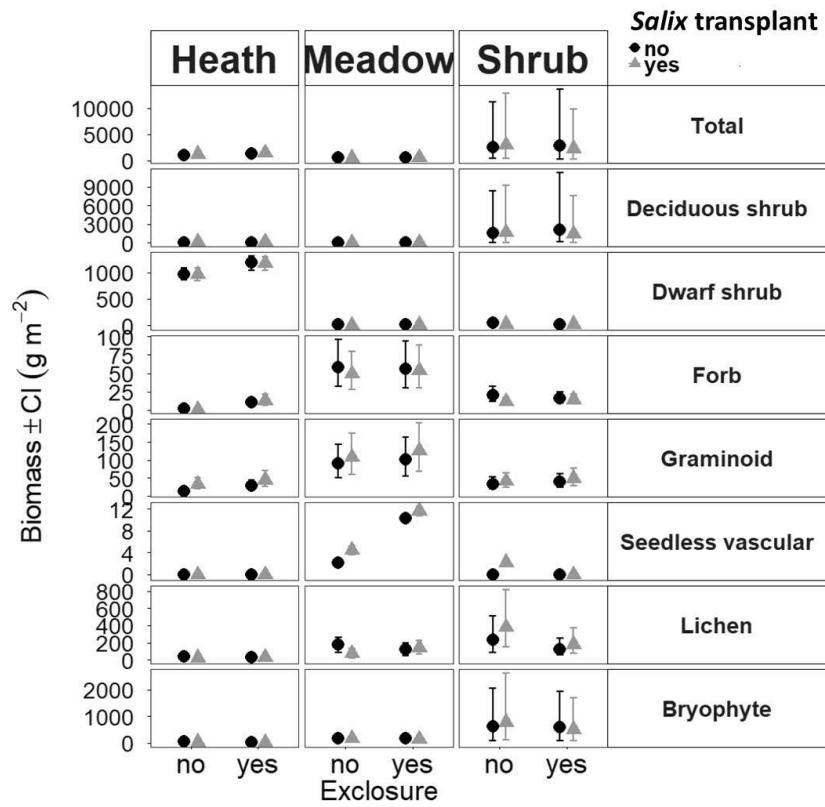
4

5 **Table S1:** Model performance of linear models used to estimate biomass in experimental plots: r^2 ,
6 adjusted r^2 , Akaike information criterion (AIC), F-statistics and degrees of freedom (df). Models were
7 based on total number of hits of each functional group and biomass in harvest plots.

Functional group	r^2	r^2.adj	AIC	F-statistic	df_{num}	df_{den}
Deciduous shrub	0.564	0.455	4	5.17	1	4
Dwarf shrub	0.954	0.951	201	313.26	1	15
Forb	0.933	0.926	12	139.52	1	10
Graminoid	0.954	0.951	18	333.35	1	16
Bryophyte in heath and meadow	0.721	0.674	86	15.50	1	6
Bryophyte in shrub	0.844	0.806	13	21.71	1	4
Lichen in heath	0.695	0.618	53	9.11	1	4
Lichen in meadow	0.804	0.755	63	16.39	1	4
Lichen in shrub	0.962	0.953	8	101.94	1	4
Seedless vascular	0.999	0.999	35	4302.50	1	4

8

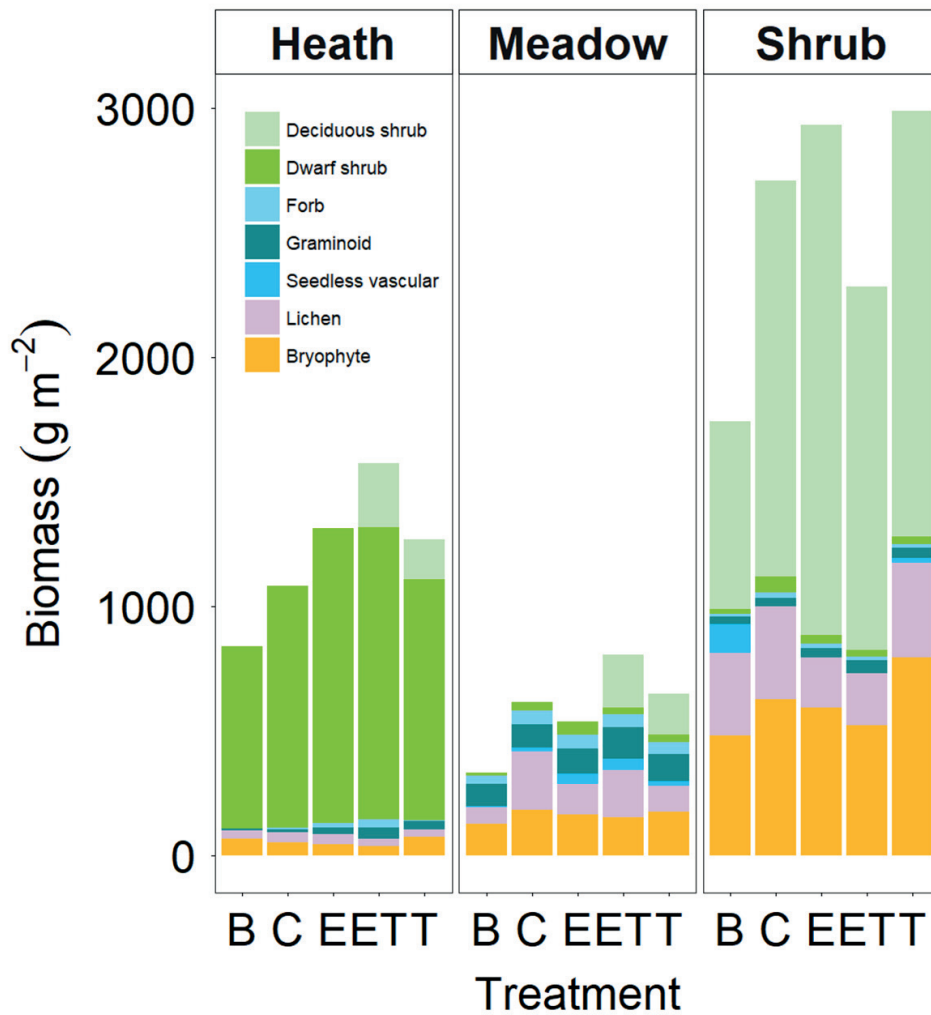
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1

2 **Figure S2:** Mean biomass model estimates with upper and lower 95 % confidence interval (CI) for
 3 total biomass, and all the functional groups in alpine *Empetrum*-heath, meadow and *Salix*-shrub
 4 communities in Dovre Mountains, Central Norway. Only the mean estimates are used in the standing
 5 biomass results in figure 2.

6



1

2 **Figure S3:** Standing biomass in experimental plots (control (C), herbivore exclusion (E), *Salix*
3 transplant (T) and exclusion combined with *Salix* transplant (ET)) compared to harvest plots (B).
4 Here, deciduous shrubs include *Betula nana*, also in the heath. This inclusion was changed in the
5 final models, where we chose to categorize *B. nana* as a dwarf shrub in the heath, to get more
6 realistic biomass estimates in this community. See explanation above in S1.

7

1 **Additional file 3**

2 **For**

3 Effects of herbivore exclusion and shrub expansion on carbon sequestration in alpine plant
4 communities

5 **Author names:** Mia Vedel Sørensen*, Bente Jessen Graae, Dagmar Hagen, Brian J. Enquist, Kristin
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9 **S2: Method GEP standardization to 600 PAR**

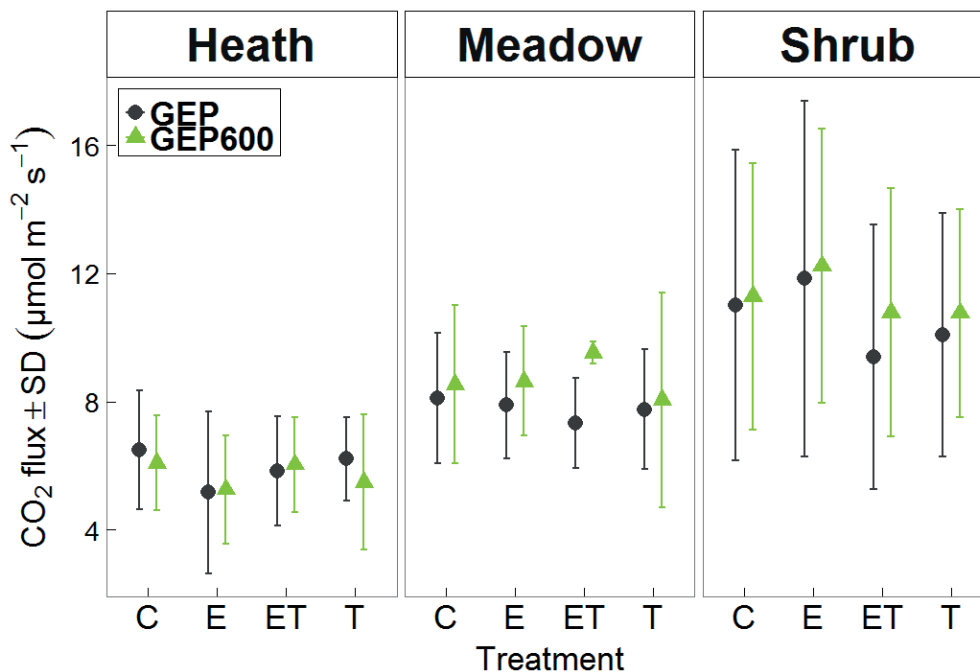
10 Light curve measurements was performed one time during mid-growing season 2015 on all control
11 plots and half of the blocks in each community with all experimental plots (n = 60). One light curve
12 measurement consisted of one measurement in full light, one measurement at three increasing
13 levels of shading, and one measurement in full darkness [1, 2]. The shading was done with three
14 layers of black tulle.

15 Light response curves were derived using the nls functions in R [3] with the following equation:

16
$$GEP = \frac{P_{max} \cdot I}{k + I}$$

17 Where GEP = ER – NEE (ER corresponding to the dark measurements, and NEE corresponding to the
18 four light measurements), I = incident PAR ($\mu\text{mol m}^{-2}\text{s}^{-1}$), P_{max} = rate of light saturated
19 photosynthesis, and k = half saturated constant of photosynthesis.

20 If we did not have any saturation from the light response curve, we used a fixed value of P_{max} , and
21 tried different values, and chose the one with the best fit.



1

2 **Figure S4: GEP compared to GEP600.** Differences between Gross Ecosystem Photosynthesis (GEP)
 3 and GEP standardized to 600 PAR (GEP600) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for the four treatments control (C),
 4 herbivore exclusion (E), *Salix* transplant (T) and exclusion combined with *Salix* transplant (ET) in
 5 alpine *Empetrum*-heath, meadow and *Salix*-shrub communities in Dovre Mountains, Central Norway.
 6 Differences were tested with one-way ANOVA and there was no significant difference between
 7 means of GEP and GEP600 ($F_{1, 22} = 1.3, p = 0.621$).

8

9 **References**

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16

17

1 **Additional file 4**

2 **For**

3 Effects of herbivore exclusion and shrub expansion on carbon sequestration in alpine plant
4 communities

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9 **Table S2: Environmental variables during CO₂ flux measurements:** Moisture = soil moisture (%), T_{air}
10 = air temperature inside chamber (°C), T_{surface} = temperature at 1 cm depth, T_{soil} = soil temperature at
11 8 cm depth (°C), Light = Photosynthetic Active Radiation inside the chamber (μmol m⁻² s⁻¹). For
12 treatments with and without Exclosure and Transplant in alpine *Empetrum*-heath, meadow and
13 *Salix*-shrub communities in Dovre Mountains, central Norway. Estimates and ± 95 % confidence
14 intervals (CI) are from linear mixed effects models fitted with community, Exclosure, Transplant and
15 the interaction of the three as fixed effects, and plot as random effect.
16 In the shrub community moisture was significantly different with and without enclosure ($F_{1,30}=4.35$,
17 $p = 0.046$, ANOVA) as it was drier within the enclosures ($p = 0.037$, Tukey). Air temperature was also
18 significantly different with and without enclosure ($F_{1,58}=5.50$, $p = 0.022$, ANOVA) as it was cooler
19 inside the enclosures ($p = 0.019$, Tukey). In the meadow the surface temperature was significantly
20 different with and without enclosure ($F_{1,30} = 6.2$, $p = 0.018$, ANOVA) as it was cooler inside the
21 enclosures ($p = 0.013$, Tukey).

		Exclosure Transplant		Exclosure Transplant		Exclosure Transplant		Exclosure Transplant	
		No	No	No	Yes	Yes	No	Yes	Yes
		Estimate	CI	Estimate	CI	Estimate	CI	Estimate	CI
Moisture	Heath	19.4	± 6.5	18.5	± 6.3	20.1	± 6.3	19.0	± 6.3
	Meadow	27.4	± 5.2	26.3	± 4.8	27.2	± 4.8	27.2	± 4.8
	Shrub	37.9	± 5.4	28.6	± 5.1	25.9	± 5.0	22.5	± 4.9
Tair	Heath	21.5	± 1.9	21.3	± 2.0	20.9	± 2.0	21.6	± 2.0
	Meadow	21.9	± 1.9	21.6	± 1.7	22.0	± 1.7	21.6	± 1.7
	Shrub	21.1	± 1.9	21.4	± 1.8	19.4	± 1.8	19.3	± 1.7
Tsurface	Heath	15.1	± 1.5	15.5	± 1.7	13.6	± 1.5	13.6	± 1.5
	Meadow	14.1	± 1.5	13.9	± 1.4	12.7	± 1.4	12.3	± 1.4
	Shrub	11.1	± 1.5	10.9	± 1.4	10.0	± 1.4	10.6	± 1.4
Tsoil	Heath	10.7	± 0.8	9.8	± 0.8	10.1	± 0.8	10.3	± 0.8
	Meadow	10.1	± 0.7	9.7	± 0.6	9.2	± 0.6	9.5	± 0.6
	Shrub	8.4	± 0.8	8.9	± 0.7	8.5	± 0.7	8.5	± 0.7
PAR	Heath	609	± 113	662	± 123	587	± 118	671	± 118
	Meadow	539	± 109	599	± 96	610	± 96	621	± 96
	Shrub	607	± 113	580	± 105	576	± 102	544	± 99

22

23

1 **Table S3:** Temperature surface (T_{surface}) summer and winter means \pm SD across 2014 and 2015 and
2 snow depth means \pm SD in 2015, for treatments with and without Exclosure and Transplant in alpine
3 *Empetrum*-heath, meadow and *Salix*-shrub communities in Dovre Mountains, central Norway.
4 Summer reflects the warmest months (July and August) and winter the coldest months (January and
5 February). The surface temperature was measured daily every four hours. Statistical differences
6 were tested within each community, for T_{surface} with ANOVA on linear mixed models where
7 exclosure, transplant, and year were fixed factors, and plot was random factor. Snow depth were
8 measured 4 times per plot in early March 2015. Statistical differences were tested within each
9 community with ANOVA on a linear model.
10 In meadow and heath communities T_{surface} summer was statistically lower with exclosures ($p < 0.05$,
11 Tukey), but there were no difference in the shrub community. In the meadow community T_{surface}
12 winter was significantly higher with exclosures, but there were no significant differences in the heath
13 and shrub communities. Snow depth was significantly ($p < 0.05$, Tukey) deeper within the exclosures
14 in the heath, but there were no significant differences with treatments in the meadow and shrub
15 communities.

Community	Exclosure	Transplant	T_{surface} summer ($^{\circ}\text{C}$)	T_{surface} winter ($^{\circ}\text{C}$)	Snow depth (cm)
Heath	no	no	11.93 \pm 0.54	-3.19 \pm 0.54	0 \pm 0
	no	yes	11.90 \pm 0.57	-2.89 \pm 0.36	0 \pm 0
	Yes	no	11.39 \pm 0.20	-2.83 \pm 0.47	0.96 \pm 1.77
	Yes	yes	11.51 \pm 0.32	-2.98 \pm 0.27	1.08 \pm 1.72
Meadow	no	no	11.50 \pm 0.64	-1.18 \pm 0.27	38.34 \pm 4.41
	no	yes	11.54 \pm 0.43	-1.23 \pm 0.34	42.31 \pm 7.22
	yes	no	11.08 \pm 0.43	-0.88 \pm 0.37	41.41 \pm 8.42
	yes	yes	10.98 \pm 0.49	-0.86 \pm 0.30	47.53 \pm 10.52
Shrub	no	no	10.11 \pm 0.80	-0.92 \pm 0.35	50.88 \pm 23.61
	no	yes	10.11 \pm 0.57	-0.72 \pm 0.39	49.84 \pm 21.16
	yes	no	9.79 \pm 0.71	-0.58 \pm 0.14	49.44 \pm 13.20
	yes	yes	9.72 \pm 0.50	-0.71 \pm 0.32	47.97 \pm 12.43

16

17

1 **Additional file 5**

2 **For**

3 Effects of herbivore exclusion and shrub expansion on carbon sequestration in alpine plant
4 communities

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9 **Table S4: Carbon flux model selection.** Model performance for linear mixed effect models with CO₂
10 fluxes as response variables (ER=Ecosystem Respiration, NEE=Net Ecosystem Exchange, GEP=Gross
11 ecosystem Photosynthesis), plot as random effects, and fixed factors as reported below. Number of
12 observations (n), the proportion of variance explained by fixed factors (R_{marginal}), the proportion of
13 variance explained by both fixed and random factors (R_{conditional}) (Nakagawa & Schielzeth 2013),
14 Akaike information criterion corrected for small sample size (AICc) and delta AIC (dAICc). According
15 to AICc the models with only community were best.

Measurement	Fixed factors	N	R Marginal	R Conditional	AICc	dAICc
ER	Community	177	0.16	0.57	137	0
ER	Community + Exclosure	177	0.17	0.57	141	4
ER	Community + Transplant	177	0.16	0.57	143	5
ER	Community + Transplant + Exclosure	177	0.17	0.57	147	9
NEE	Community	177	0.27	0.45	290	0
NEE	Community + Exclosure	177	0.27	0.45	295	5
NEE	Community + Exclosure + Transplant	177	0.27	0.46	300	10
GEP	Community	177	0.24	0.58	147	0
GEP	Community + Exclosure	177	0.25	0.58	152	4
GEP	Community + Transplant	177	0.24	0.58	153	5
GEP	Community + Exclosure + Transplant	177	0.25	0.58	157	10

16

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18

19

Paper III



Photo: *Campanula* on the heath community, July 2014.

1 Functional group contributions to carbon fluxes in arctic-alpine
2 ecosystems

3 **Journal: Arctic, Antarctic and Alpine Research**

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14

15

16 Keywords

17 Plant functional types, carbon sequestration, plant respiration, soil respiration, net
18 ecosystem exchange

19 Abstract

20 Ongoing responses to climate change in arctic-alpine ecosystems, including increasing
21 dominance of deciduous shrubs, involve major shifts in plant functional group composition.
22 Because rates of photosynthesis and respiration and their responses to temperature may
23 vary among plant functional types, a better understanding of their contributions to carbon
24 fluxes will help improve predictions of how ecosystem changes will affect carbon source-
25 sink relations in globally important tundra regions. We used a sequential harvest method to
26 estimate growing season functional group contributions to net ecosystem exchange (NEE),
27 ecosystem respiration (ER), and gross primary productivity (GPP) in alpine heath, meadow,
28 and *Salix*-dominated shrub communities. We also partitioned ER into above- and
29 belowground components in all three communities. Belowground efflux was the dominant
30 component of ER in the heath and meadow communities (63 and 88% of ER, respectively)
31 but contributed only about 40% of ER in the shrub community. The dominant functional
32 group in each community contributed most to aboveground exchanges. Estimates for
33 cryptogams were uncertain but indicated a minor role for bryophytes and lichens in overall
34 exchange. Unexpected CO₂ efflux after removal of cryptogams or herbs in several plots
35 indicate a possible “lid effect” where dense ground cover traps or utilizes soil-derived CO₂.

36 Introduction

37 Global climate change is expected to result in changes in functional group composition in
38 terrestrial ecosystems around the globe, especially in arctic regions where warming has
39 been greatest and is expected to continue to be so. These changes may be accompanied by
40 changes in ecosystem processes including nutrient cycling and carbon (C) fluxes and storage,
41 as well as effects on energy balance via boundary layer, sensible heat exchange, albedo, and
42 snow cover. These changes may then feedback on global temperature and precipitation
43 patterns (Dormann and Woodin, 2002; Cornelissen et al., 2007; De Deyn et al., 2008; Chapin
44 et al., 2009; Wookey et al., 2009).

45 Arctic and alpine ecosystems cover about 11 million km² or 2 % of the Earth's land surface,
46 with about 5 million km² in arctic tundra, 3 million km² in alpine tundra, and the remainder
47 in intermediate northern highlands (Virtanen et al., 2016). They are critical reservoirs in the
48 global C cycle, with as much as 50 % of the global belowground C pool stored in organic soils
49 and deeper organic deposits in permafrost regions alone (Tarnocai et al., 2009).

50 On a global scale, gross and net productivity in arctic-alpine ecosystems is generally low due
51 primarily to low temperature (Christensen et al., 2000; Grogan and Chapin, 2000; Biasi et al.,
52 2008; Beer et al., 2010; Parker et al., 2015; Sørensen et al., 2018). Low temperature, often
53 combined with water saturated surface conditions due to topography or permafrost, also
54 strongly limits decomposition and ecosystem respiration, resulting in net influx and long-
55 term net C accumulation in organic soils. Shifts in the balance between C uptake and
56 respiration in these systems could result in a strong positive feedback on global warming,
57 and there is evidence that this is already happening (Oechel et al., 2000; Wilmking et al.,
58 2006; Hartley et al., 2012; Parker et al., 2015)

59 A more detailed understanding of how respiration is divided among these sources in
60 different communities and among functional types will help understand and predict the
61 effects of vegetation changes on C balance in arctic-alpine ecosystems.

62 Plants in arctic and northern alpine ecosystems are often grouped into plant functional
63 types based on growth form and functional traits (Chapin et al., 1996; Dormann and
64 Woodin, 2002). Species in these groups are assembled into an array of community types
65 occurring on sites with different microclimate and soil conditions. The dynamics of C
66 exchange, sequestration, and mineralization varies among the functional types and
67 communities composed of them, with relatively high productivity and C turnover in
68 predominantly herbaceous communities as compared to the slower-growing and -
69 decomposing evergreen shrubs and bryophytes (Cornelissen et al., 2007; Lang et al., 2009;
70 Ward et al., 2009; Parker et al., 2015). Shifts in functional group composition, such as the
71 recent and ongoing increases in dominance of deciduous shrubs in arctic-alpine regions
72 (Tape et al., 2006; Cannone et al., 2007; Tommervik et al., 2009; Myers-Smith et al., 2011;
73 Epstein et al., 2012; McManus et al., 2012), may be an important factor in changes in C
74 balance (De Deyn et al., 2008; Wookey et al., 2009).

75 Numerous studies in arctic-alpine ecosystems have explored the dynamics of C exchange at
76 leaf level or in whole communities, but relatively little is known about the middle ground:
77 the relative contributions of the different functional groups to total ecosystem fluxes.
78 Scaling up from leaf level measurements can introduce large errors, while whole system
79 exchange measurements do not yield information on functional group contributions. This
80 gap can be filled by direct measurement of canopy fluxes following experimental
81 manipulation of community composition. For example, Ward et al. (2009) experimentally

82 removed each of the three dominant functional types in a temperate, ombrotrophic
83 peatland over two years and found that removal of dwarf shrubs resulted in dramatic
84 increases in CO₂ fluxes and turnover. Douma et al. (2007) measured gas exchange before
85 and after removal of vascular plants in several arctic community types in plots selected for
86 high bryophyte ground cover and found that bryophytes accounted for a mean of 60% of
87 NEE. To our knowledge, these are the only previous studies that have used this approach.

88 Some studies indicate that variation in respiration rather than primary productivity more
89 strongly affects net C balance in arctic and boreal ecosystems (Jung et al., 2011). Ecosystem
90 respiration is the sum of respiration by leaves, stems, and other aboveground plant parts
91 and belowground activity of plant roots and soil microorganisms. Partitioning of gas
92 exchange by functional group and above and belowground contributions can be used to
93 inform large scale C dynamic models and help resolve questions about, for example, the net
94 effect of well-documented increases in deciduous shrub dominance (Tape et al., 2006;
95 Cannone et al., 2007; Tommervik et al., 2009; Myers-Smith et al., 2011; Epstein et al., 2012;
96 McManus et al., 2012).

97 To provide baseline data on the contributions of deciduous shrubs and other functional
98 groups on C balance in arctic-alpine ecosystems, we used a sequential harvest method to
99 estimate the aboveground contributions of plant functional groups and belowground
100 respiration to ecosystem respiration (ER), net ecosystem exchange (NEE), and gross primary
101 productivity (GPP) in heath, meadow, and *Salix* shrub communities in the Dovre Mountains
102 of Central Norway. We focused on the following questions: 1. What are the relative
103 contributions of below- and aboveground biotic processes to ecosystem respiration in
104 arctic-alpine plant communities? 2. What are the relative contributions of the major

105 functional groups, including cryptogams, to ER, NEE, and GPP in these communities? In
106 addition, we discuss how functional group composition may affect C source-sink activity as
107 arctic-alpine ecosystems respond to global change with increased abundance of deciduous
108 shrubs.

109 Materials and methods

110 Study site

111 Measurements were made in conjunction with a long-term experiment on the effects of
112 grazing and shrub expansion on alpine community composition and C balance (see Sørensen
113 et al., 2018, Sørensen et al. submitted BMC Ecology). The Dovre Mountains in Norway are a
114 high plateau with moderate, rolling relief. We selected study sites on south-facing slopes
115 with representative examples of heath-, herbaceous and *Salix*-dominated communities,
116 designated heath, meadow, and shrub. For further details of the study site and community
117 composition, as well as C pools in the soil and vegetation, see Sørensen et al. (2018). We
118 analyzed six plots within each community. Before harvest, functional group cover and plant
119 height was measured using the point intercept method (Jonasson, 1988) during the 2nd and
120 3rd week of July.

121 Gas exchange measurements were conducted on nine working days during the height of the
122 growing season between July 17 and August 13, 2015. For logistic reasons all the plots in
123 each of the three communities were measured over a period of two to four days. While
124 none of the measurements were made in rain or wet conditions, there was variation in
125 cloud cover and temperature, resulting in variation in environmental conditions at
126 community, plot, and functional group levels (Table 1).

127 Gas exchange measurements and harvest

128 For sequential harvest measurements in the shrub community, we used a collapsible 0.5 x
129 0.5 x 0.6 m gas flux chamber (Sørensen et al., 2018). In the heath and the meadow we used
130 a 0.25 x 0.25 x 0.30 m closed-system Plexiglas chamber with a rubber skirt attached to the
131 base. The chamber skirts were held down and sealed by a length of chain during each
132 measurement. A sampling tube and a return tube entered the center of the chamber roof
133 and sampled 0.2 m above the soil surface. A fan mixed the air inside the chamber 30
134 seconds prior to and during each measurement. Air temperature was measured with a
135 PT100 sensor inside the chamber at a height of 0.2 m above the soil surface, and by a
136 second sensor outside the chamber. Soil temperature was measured at a depth of 8 cm
137 (Digital dial thermometer, Traceable[®] Ultra[™], VWR International). During all flux
138 measurements photosynthetically active radiation (PAR) was measured with a LI-190S
139 quantum sensor (LI-COR Inc., Lincoln, Nebraska, USA) placed within a distance of 1 m from
140 the plexiglass chamber. In the collapsible gas flux chamber, the light sensor was placed 0.2
141 m from the chamber leg and 0.45 m above the soil surface. After measurement under
142 available light conditions (net ecosystem exchange, NEE), the chamber was darkened with
143 an opaque hood for measurement of dark respiration (ecosystem respiration, ER). CO₂
144 concentration was measured every second and the measurement was usually completed
145 within 120 seconds after sealing the chamber.

146 After the initial C flux measurements, the first vegetation compartment was harvested by
147 cutting plants at the base, without taking up roots and soil. This was followed by another
148 pair of C flux measurements, and this procedure continued until all the vegetation
149 compartments were harvested. The vegetation functional types were harvested in the

150 following order 1. Dwarf shrubs (evergreen shrubs and the deciduous shrubs *Vaccinium*
151 *uliginosum*, *V. myrtillus*, *Salix herbacea* and *S. reticulatum*), 2. Herbs (graminoids, forbs, and
152 seedless vascular plants), 3. Cryptogams (bryophytes and lichens), 4. Deciduous erect shrubs
153 (*Betula nana*, *Salix lapponum*, *S. glauca*), 5. Litter (all dead biomass). Finally, a measurement
154 was conducted on the bare soil in both light and dark, to obtain respiration rate from the
155 soil. The sequential harvest was typically completed in four to six hours on a single day, but
156 was interrupted by 1-2 days in five plots due to adverse weather conditions.

157 C flux measurements were also made on four other plots of the same block, and light curve
158 measurements were done on the control plot for each block during the growing season.

159 One light curve measurement consisted of one measurement in full light, measurements at
160 three increasing levels of shading, and one measurement in full darkness (Williams et al.,
161 2006; Street et al., 2007). The shading was done with three layers of black tulle.

162 In the lab, samples were sorted into more detailed functional groups (deciduous shrubs,
163 evergreen shrubs, forbs, graminoids, bryophytes, lichens). The biomass was oven-dried at
164 70 °C for 72 h before weighing to an accuracy of 0.001 g. After drying, deciduous shrubs
165 were sorted into stems and leaves.

166 Data analysis

167 CO₂ fluxes were calculated by linear regression (Jasoni et al., 2005), usually based on the last
168 90 seconds of the measurement period, and are expressed on a plot surface area basis in
169 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In this article, net respiration is expressed as a negative value and net
170 photosynthesis is positive. In principle, removal of a vegetation compartment should result
171 in reduced respiration as measured in the dark, and reduced net photosynthesis in the light,

172 since vegetation contributes to both processes. Subtracting the ER and NEE measurements
173 after removal of a compartment from those made before removal gives a raw estimate of
174 the contribution of the removed compartment to the total measured at the outset.
175 However, this was not always the case, so we made adjustments to the raw data as
176 described below to compensate for some of these anomalous results as well as for
177 variations in light and temperature during measurement.

178 We modified the data and calculated estimates of gas exchange for the functional group
179 layers in the following steps:

180 1. Inspection of the raw data for each plot showed unexpected increases in respiration after
181 removal of cryptogams or herbaceous plants in some plots (Figure S1). Due to the
182 sequential harvest subtraction algorithm, these measurements affect gas exchange
183 estimates for both the removed and the subsequent layer. To provide better estimates for
184 the latter, we replaced these anomalous values with the mean of the measurements on
185 either side. This method was also applied to a single case where removal of a layer was
186 followed by a large increase in NEE. In two plots in the meadow, ER was greater after
187 removal of all biomass than in the intact vegetation (Figure S1). Other than the temperature
188 correction described below, we did not attempt to correct for this anomaly.

189 2. There was little difference in ER or NEE before and after removal of the litter layer or in
190 light and dark (Figure S1). We used the mean of these four measurements as a robust
191 estimate of belowground respiration and the mean soil temperatures for these four
192 measurements as the reference temperature for this initial estimate of belowground
193 respiration.

194 3. In cases where the amount of biomass removed in a layer was less than 5 g m⁻² we used
195 the mean of the values before and after removal to provide a more robust estimate of gas
196 exchange before removal of the next layer. We then set all gas exchange estimates for the
197 low biomass layer to 0, but included these null estimates in calculation of community
198 means.

199 4. Because temperature has a direct effect on respiration and varied between about 5 and
200 10°C in the soil and 10 and 25°C in the canopy during measurement of different blocks
201 (Table 1), we used an assumed Q₁₀ of 2 (Tjoelker et al 2001) to adjust belowground
202 respiration estimates to a common temperature of 10°C and plant canopy respiration
203 measurements to 20°C, the approximate average soil and aboveground temperatures across
204 all three communities in 2015, respectively. The mean value calculated in step 2 gives a
205 straightforward estimate of soil respiration. Temperature-corrected estimates of
206 belowground respiration at the soil temperature during measurement of each layer (R_{Tbelow})
207 and at the common soil temperature (R_{10below}) were calculated using the Q₁₀ formula:

$$208 \quad R_{adj} = R_{below} Q_{10}^{\left(\frac{10-T_{soil}}{10}\right)}$$

209 where R_{adj} is R_{Tbelow} or R_{10below}, R_{below} is the measured ER for bare soil, and T_{soil} is the
210 respective soil temperature.

211 5. R_{Tbelow} for each harvest step was subtracted from the corresponding ER measurement to
212 give an estimate of respiration due to plants only (R_{above}). For each layer, R_{above} after removal
213 was subtracted from that before removal to give an estimate of aboveground respiration
214 attributed to each functional group. Using the air temperature in the chamber and the Q₁₀
215 equation, these estimates were then adjusted to 20°C, designated R_{dec}, R_{eve}, R_{her}, and R_{cry} for

216 deciduous shrubs, evergreen and dwarf shrubs, graminoids and other herbaceous plants,
217 and cryptogams, respectively.

218 6. As described above, a raw estimate of NEE for each layer was obtained by subtracting the
219 NEE after layer removal from that before layer removal. Layer NEE – Layer R gives an initial
220 estimate of layer GPP. PAR during NEE measurements varied between about 200 and 1700
221 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 1). To correct GPP for these variations, a single light response curve was
222 fitted to data for eight control plots in each community using nls functions in R:

$$223 \quad GPP = \frac{P_{max} \cdot I}{k + I}$$

224 Where $GPP = NEE - R$, $I =$ incident PAR ($\mu\text{mol m}^{-2}\text{s}^{-1}$), P_{max} = rate of light saturated
225 photosynthesis, and $k =$ half saturated constant of photosynthesis.

226 The expected community GPP at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ and at the measurement PAR for each
227 layer were calculated, and the ratio of these was used as a correction factor. GPP estimates
228 were corrected for temperature using a Q_{10} of 2 and then multiplied by the correction factor
229 to give an estimate of layer GPP at 20°C and $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR.

230 7. The temperature and light-corrected estimates of ER and GPP were summed to give a
231 revised estimate of NEE for each layer.

232 All gas exchange estimates obtained after data modification and temperature adjustment
233 are designated “adjusted”, while those obtained from the original data are designated
234 “raw”. We present summaries of both in order to discuss how the adjustments affect
235 interpretation of the results.

236 The productivity per biomass for each functional group in each community was calculated as
237 GPP/biomass, using leaf biomass only for deciduous shrubs and total biomass for the other
238 functional groups.

239 We tested for differences among communities in raw and adjusted ER, NEE, and GPP using
240 one way ANOVA and Tukey's HSD. All data processing and analysis was carried out in R (R
241 Core Team, 2017).

242 Results

243 Overall ecosystem fluxes

244 As in our previous study (Sørensen et al., 2018), pre-harvest rates of NEE and initial
245 estimates of GPP differed significantly among communities (NEE: $F_{2,15}=4.77$; GPP: $F_{2,15}=3.8$,
246 $p < 0.05$, ANOVA). NEE in the shrub community was significantly higher ($p < 0.05$) than in the
247 heath community, and marginally higher ($p=0.06$, TukeyHSD) than the meadow community.
248 However, pairwise comparisons were not significantly different for initial estimates of GPP,
249 as values were only marginally higher in the shrub community than in the other two
250 communities ($p < 0.10$, TukeyHSD) (Figure 1). Raw ER did not differ significantly among
251 communities ($F_{2,15}=1.85$, $p = 0.19$, ANOVA). Estimates based on the adjusted and summed
252 functional group contributions show increased variability in NEE and GPP in some cases
253 (Figure 1). As estimated for similar temperature and light conditions, gross and net
254 productivity in the meadow is intermediate, lower than in the shrub community and higher
255 than in the heath community. There were no significant differences among communities in
256 adjusted ER, NEE, and GPP.

257 Based on the pre-harvest measurements of NEE and ER, the mean proportion of GPP
258 consumed by ER was about 73% in the heath, 66% in the meadow, and 55% in the shrub
259 community. In the adjusted estimates for common temperature and light conditions, these
260 become 78, 46, and 49%, respectively (Table 2). The differences between these estimates
261 are largely a result of adjustments for excess respiration after removal of herb or cryptogam
262 layers in several plots (Figure S1). The effects of adjustments for temperature and light are
263 relatively minor.

264 Based on the adjusted estimates, aboveground respiration contributed about 37, 13, and
265 60% of total ER in the heath, meadow, and shrub communities, respectively, with the
266 remainder as belowground respiration (Table 2). In the heath and meadow communities,
267 most of the aboveground respiration was attributed to the respective dominant functional
268 type, while in the shrub community aboveground respiration was more evenly divided
269 among all four functional types. In the heath and meadow, belowground respiration
270 consumed about 49 and 41% of GPP, respectively, while in the shrub community this is
271 about 20%. Aboveground respiration consumed about 29% of GPP in the heath and shrub
272 communities and about 6% of GPP in the meadow.

273 Functional group contributions

274 Plant contributions to ER, NEE, and GPP were dominated by the respective dominant
275 functional type in each ecosystem (Figure 2). The remaining vascular plant functional types
276 contributed proportionally more to gas exchange in the shrub community than in the heath
277 and meadow (about 30 vs. 10 and 14% of plant NEE, respectively). The adjustments to the
278 data did not affect this general picture (Figure S2), with the exception of a reduction in NEE
279 and GPP in deciduous shrubs in the shrub community, which was a result of the correction

280 for the strong increase in efflux after removal of cryptogams in four of the six shrub plots
281 (Figure S1).

282 Because our data adjustments involved changing the flux estimates after removal of
283 cryptogams in several plots, we do not think the adjusted estimates for cryptogams in
284 Figure 2 are reliable. However, the raw NEE results indicate a minimal contribution of
285 cryptogams to overall gas exchange, even though they comprise a large portion of total
286 biomass in the meadow and shrub communities. Mean cryptogam NEE was negative (net
287 efflux) in the raw data for the meadow and shrub communities (Figure S2).

288 Most of the deciduous shrub (willow) biomass and a substantial proportion of dwarf shrub
289 biomass was in woody parts (Figure 2 D). Using the GPP estimates and biomass data, we
290 calculated productivity as $\mu\text{mol CO}_2$ fixed per dry weight of leaf tissue for all functional
291 groups present in the three communities. Estimates based on only a few grams of leaf tissue
292 were highly variable, presumably due to error propagation based on the very small amounts
293 of tissue. The estimates (in $\mu\text{mol kgDW}^{-1} \pm \text{sd}$) for the dominant functional group in each
294 community are as follows: 13.6 ± 5.2 for dwarf shrub leaves in the heath; 83.6 ± 28.8 for
295 herbaceous plants in the meadow, and 71.0 ± 33.4 for deciduous leaves in the shrub
296 community.

297

298 Discussion

299 Our results highlight potentially important differences in C dynamics in three widespread
300 arctic-alpine community types. We provide a first look at the relative contributions of the
301 major functional groups in these communities to growing season gas exchange, and

302 partition ecosystem respiration into above- and belowground components. As climate
303 change and changes in grazing practices result in shifts in community composition in arctic
304 and alpine regions, our results can be used to inform predictions about the potential for
305 shifts in C source-sink balance.

306 Our pre-harvest rates of ER, NEE, and GPP are within the broad range defined by previous
307 studies of diurnal growing season CO₂ fluxes in arctic-alpine ecosystems (Johnson et al.,
308 2000; Shaver et al., 2007; Street et al., 2007; Nobrega and Grogan, 2008). In these studies,
309 *Betula* or *Salix*-dominated deciduous shrub communities are most productive with NEE at
310 around 10 μmol m⁻² s⁻¹, moist sedge meadows are intermediate at about 8 μmol m⁻² s⁻¹, and
311 heaths are on par with or sometimes considerably lower than the meadows depending on
312 type and perhaps moisture status (Shaver et al., 2007; Susiluoto et al., 2008). Fluxes
313 modeled or integrated over longer periods, from days to full seasons via small scale closed
314 chamber methods or eddy covariance, are one to two orders of magnitude lower when
315 expressed in μmol m⁻² s⁻¹, with some sites showing net loss of C to the atmosphere over a
316 growing season or year (Jones et al., 1998; Natali et al., 2011; Kittler et al., 2017).

317 Under growing season daytime conditions, in moderate light and at average summer
318 temperatures, over 75% of the primary production in the heath was consumed by ER, while
319 this is more on the order of 45 to 50% in the meadow and shrub communities (Table 2). The
320 remaining proportions as represented by NEE are available for growth, reproduction,
321 storage, or respiratory consumption at night under more disadvantageous conditions.

322 Respiratory losses were dominated by belowground processes in the heath and meadow,
323 while aboveground layers consumed a greater proportion of GPP in the willow shrub
324 community. Because respiration continues in low light and during night hours, 24-hour and

325 longer-term respiratory losses are likely much greater, with the possibility that any of the
326 three systems may be net C sources on an annual basis. Our previous work suggests that
327 shrub invasion of heath or meadow communities could result in a net loss of soil C that
328 exceeds aboveground biomass gains, resulting in a long term net loss of C that could
329 aggravate global warming (Sørensen et al., 2018).

330 The respective dominant functional group in each community dominates aboveground
331 ecosystem exchanges. In the heath and meadow the non-dominant vascular plant groups
332 account for less than 10% of total ER. However, in the shrub community, the non-dominant
333 herbs and dwarf shrubs together account for roughly 40% and 45% of NEE and GPP
334 respectively, but about 56% of aboveground respiration and 34% of total ER (Figure 2), and
335 thus have a disproportionate role in overall respiratory losses in this system.

336 Despite lower productivity than vascular plants, bryophytes and lichens are important
337 components of boreal and arctic ecosystems. Explicit consideration of cryptogam fluxes may
338 help improve the accuracy of regional and global models of GPP and NEE (Yuan et al., 2014).
339 Miller et al. (1980) reported that cryptogams contribute an average of about 30% of total
340 NEE over a broad range of arctic community types at Barrow, Alaska, ranging from less than
341 5% in a *Dupontia* meadow to 48% in a *Carex-Poa* meadow. Despite the problems arising
342 from unexpected efflux after cryptogam removal, our results indicate that cryptogams are
343 minor players in overall C fluxes in our communities, presumably due to intrinsically low
344 productivity (Frolking, 1997; Goulden and Crill, 1997).

345 The large increases after ground cover removal may indicate a “lid effect” involving release
346 of belowground CO₂. In an experiment involving removal of all vascular plants in a single

347 step, Douma et al. (2007) found that mosses may account for an average of 60% of NEE in a
348 range of heath, meadow, and deciduous shrub (*Betula nana*) dominated plots, all selected
349 for nearly 100% moss cover at ground level. They attributed increases in efflux after
350 removal of vascular plants to “wound respiration”, and consequently based their estimates
351 of moss productivity on changes in GPP rather than NEE after vascular plant removal. In our
352 study, increases in efflux occurred mainly after removal of cryptogams or in some cases
353 graminoids rather than other vascular plant layers, and so cannot be attributed to
354 respiration from cut stems or roots, at least in the former case. Possible reasons for the lid
355 effect include soil disturbance, reduced resistance to efflux from the soil surface, and
356 reduced photosynthetic absorption (“recycling”) of soil-derived CO₂ (Smolders et al., 2001).
357 The latter process is an intriguing possibility. Uptake of soil-derived CO₂ would not be
358 reflected in NEE measurements, but would result in higher cryptogam biomass productivity
359 than predicted from in situ estimates of moss NEE. This could be resolved by repeated,
360 season-long measurement and integration of NEE and biomass accumulation. It would also
361 be of interest to measure CO₂ concentrations within the cryptogam layer.

362 Estimates of leaf productivity for the dominant functional group in each community show
363 that herbaceous plants fixed most CO₂ per leaf mass, whereas this was intermediate for
364 deciduous shrubs and least for dwarf shrubs. This corresponds to expectations based on
365 community weighted means of specific leaf area, which were highest in the meadow,
366 intermediate in the shrub community and lowest in the heath community (Sørensen et al
367 submitted in AAAR in June). This overall fit with the leaf economic spectrum (Reich et al.,
368 1997; Wright et al., 2004), confirms that the use of functional groups based on growth form
369 can be useful in relation to C studies and potentially for future predictions as was suggested

370 by Chapin et al. (1996). Future studies could measure the temperature responses of C fluxes
371 in the specific groups to predict responses to future climate change (Dormann and Woodin,
372 2002; Dorrepaal, 2007). A preliminary study of leaf level temperature responses in our sites
373 showed decreases in net photosynthesis at temperatures above 17 °C in three *Salix* species,
374 *Betula nana*, *Empetrum nigrum*, and *Vaccinium vitis-idaea* (Eckert, 2015).

375 To the extent that our sites are representative of other arctic-alpine community types, our
376 results illustrate the differing roles of the main arctic-alpine plant functional types in this
377 shifting carbon balance. In this study, we quantified relative contributions of above-and
378 below-ground processes and of the main functional groups in three alpine plant
379 communities. Other studies have indicated that the ongoing expansion of deciduous shrubs
380 into heath and graminoid-dominated communities in arctic-alpine regions may already be
381 altering source-sink relations in these regions (Oechel et al., 2000; Wilmking et al., 2006;
382 Hartley et al., 2012; Parker et al., 2015). In our sites, we have also found lower total
383 ecosystem C due to lower organic soil C pools in the shrub than in the heath and meadow
384 (Sørensen et al., 2018). Our results indicate that this soil C loss most likely does not happen
385 during the summer growing season, because the soil C released from belowground
386 respiration in the meadow was much greater than that released from the shrub and the
387 heath communities. The released C from belowground respiration is likely recently fixed C
388 during the growing season (Illeris et al., 2003) and any soil loss might rather be due to
389 recalcitrant soil C being broken down in shrub communities during winter (Hartley et al.,
390 2013). Differences in root density and soil microbial communities between the three
391 communities could also contribute to these altered source-sink relations outside of growing
392 season in these regions (Bardgett et al., 2005; Blume-Werry et al., 2015; Sloan et al., 2015).

393 In order to understand the response of C cycling to climate and vegetation changes, future
394 studies should unravel the influence of plants, microbes, and soil processes on C cycling in
395 both growing and dormant seasons.
396

Table 1. Environmental conditions during CO₂ flux measurement. Mean \pm SD, n = 6 plots in each community.

Parameter	Heath	Meadow	Shrub
Measurement period	12 - 13 August	15 - 17 July	19 - 22 July
Chamber temperature NEE	20.3 \pm 4.8	18.7 \pm 3.3	17.5 \pm 3.3
Temperature span NEE*	8.1 \pm 2.6	7.6 \pm 2.1	7.8 \pm 3.2
Chamber temperature ER	18.3 \pm 4.4	16.6 \pm 3.1	17.3 \pm 3.5
Soil temperature NEE	8.3 \pm 0.5	7.3 \pm 1.8	8.0 \pm 1.0
Soil temperature ER	8.4 \pm 0.5	7.9 \pm 1.5	8.0 \pm 1.0
PAR NEE	1187 \pm 537	493 \pm 561	464 \pm 227

*difference between highest and lowest chamber temperature among functional group measurements in each plot

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399

400 **Table 2.** Partitioning of growing season daytime ecosystem respiration (ER) and gross
 401 primary productivity (GPP) into above- and belowground respiration (R) and net ecosystem
 402 exchange (NEE) in three arctic-alpine communities, expressed as mean CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
 403 ¹) and as mean proportion of ER (%ER) or GPP (%GPP), based on adjusted estimates (n=6).

	CO ₂ flux($\mu\text{mol m}^{-2} \text{s}^{-1}$)	%ER	%GPP
Heath			
Aboveground R	-1.78	36.8	28.6
Belowground R	-3.05	63.2	49.0
ER	-4.83		77.6
NEE	1.39		22.4
Meadow			
Aboveground R	-0.56	12.5	5.8
Belowground R	-3.91	87.5	40.5
ER	-4.47		46.3
NEE	5.19		53.7
Shrub			
Aboveground R	-3.65	59.9	29.3
Belowground R	-2.44	40.1	19.6
ER	-6.09		48.9
NEE	6.35		51.1

404

405

406

407 **Figure 1.** Total CO₂ fluxes in three arctic-alpine plant communities calculated from raw
408 measurements and after adjustment for anomalous measurements and differences in
409 temperature and light conditions during measurement. Mean ± standard deviation of 6
410 plots per community.

411 **Figure 2.** A-C: Adjusted soil and functional group contributions to ecosystem CO₂ fluxes in
412 three arctic-alpine plant communities based on sequential harvest and closed system
413 measurements in light and dark after removal of each functional group. D: Functional group
414 biomass, with deciduous and dwarf shrub leaf and woody stem biomass separated and
415 herbaceous plants and cryptogams divided into subgroups. Means of 6 plots per
416 community, including null values for plots where a functional group was absent.

417 **Figure S1.** Closed system CO₂ exchange measurements of plot ER and NEE and initial
418 estimates of plot GPP during sequential removal of functional groups from three arctic-
419 alpine plant communities. None - undisturbed plot; eve - evergreen dwarf shrubs; her -
420 herbaceous plants; cry – cryptogams; dec – deciduous shrubs; lit – litter layer. Colors
421 represent individual plots.

422 **Figure S2.** Uncorrected estimates of soil and functional group contributions to ecosystem
423 CO₂ fluxes in three arctic-alpine plant communities, based on sequential harvest and closed
424 system measurements in light and dark after removal of each functional group. Means of 6
425 plots per community, including null values for plots where a functional group was absent.

426

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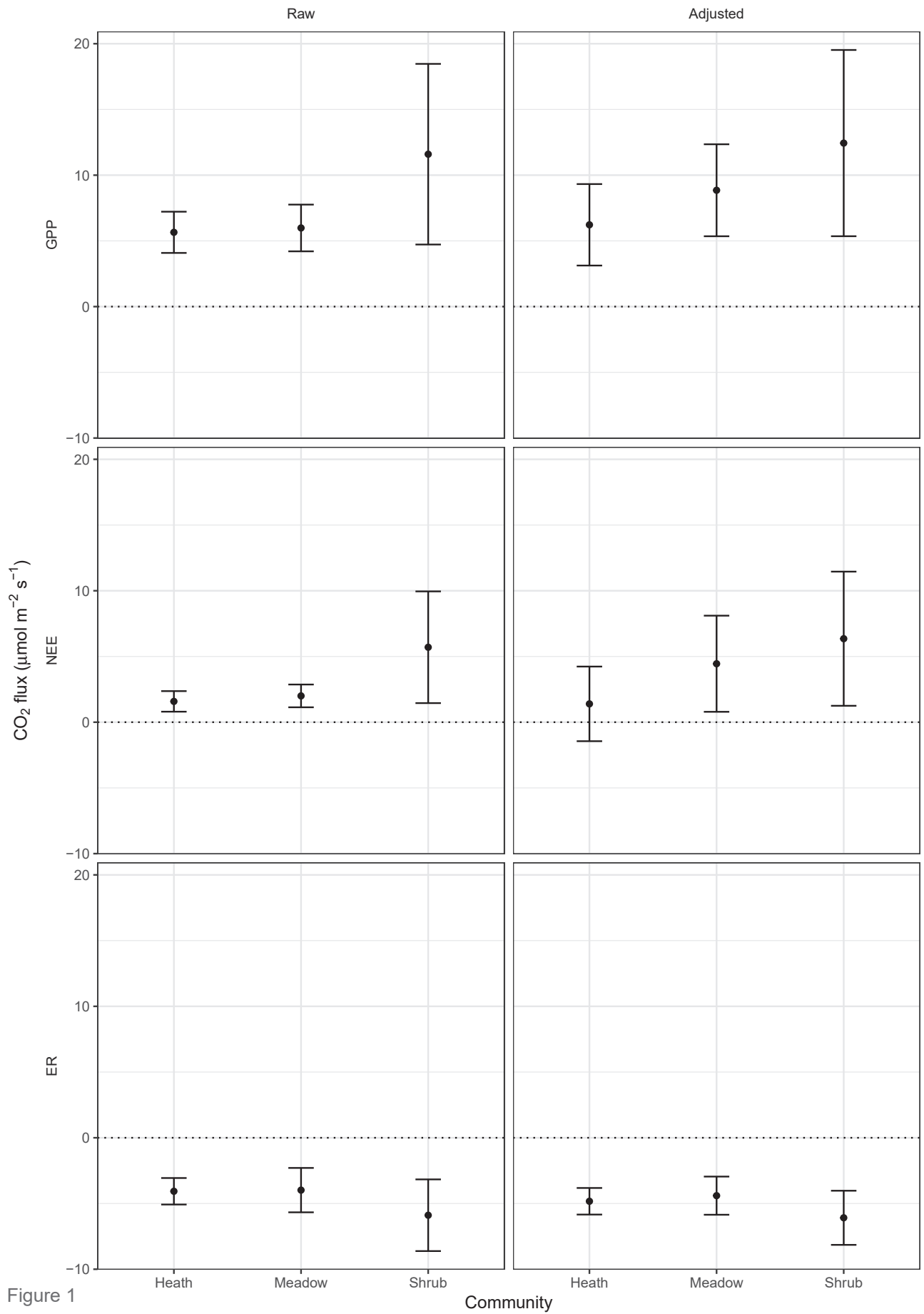


Figure 1

Community

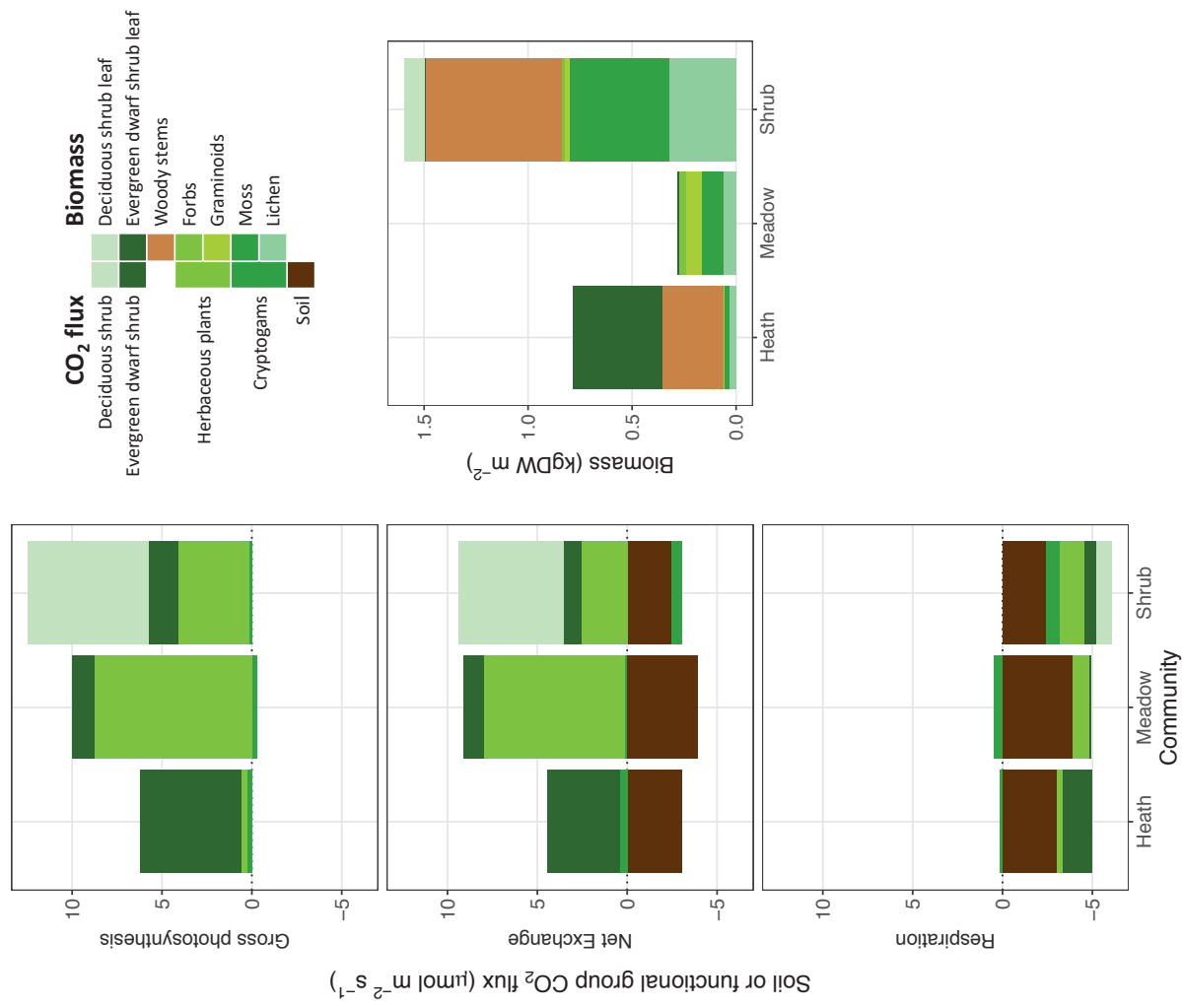


Figure 2

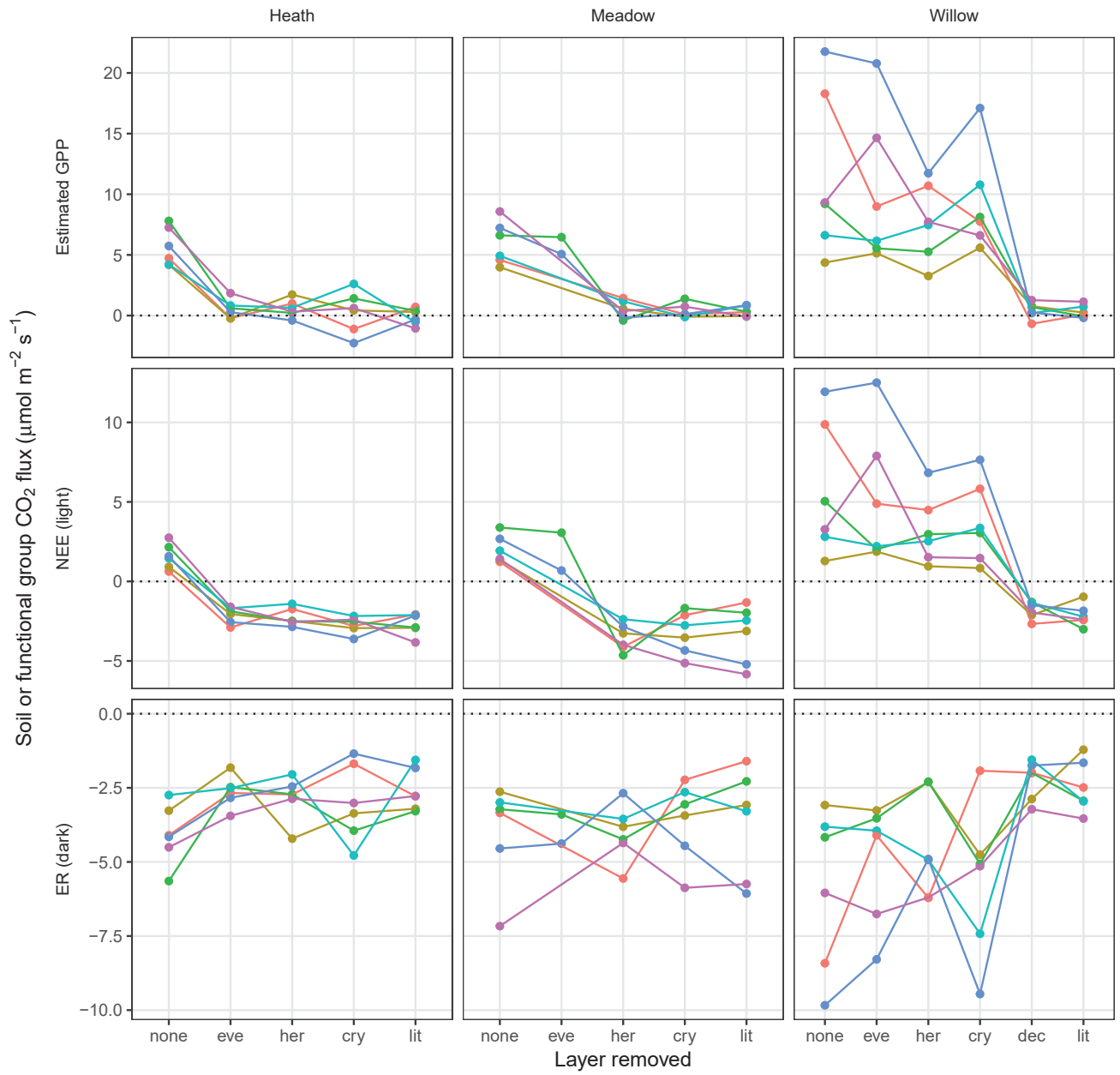


Figure S1

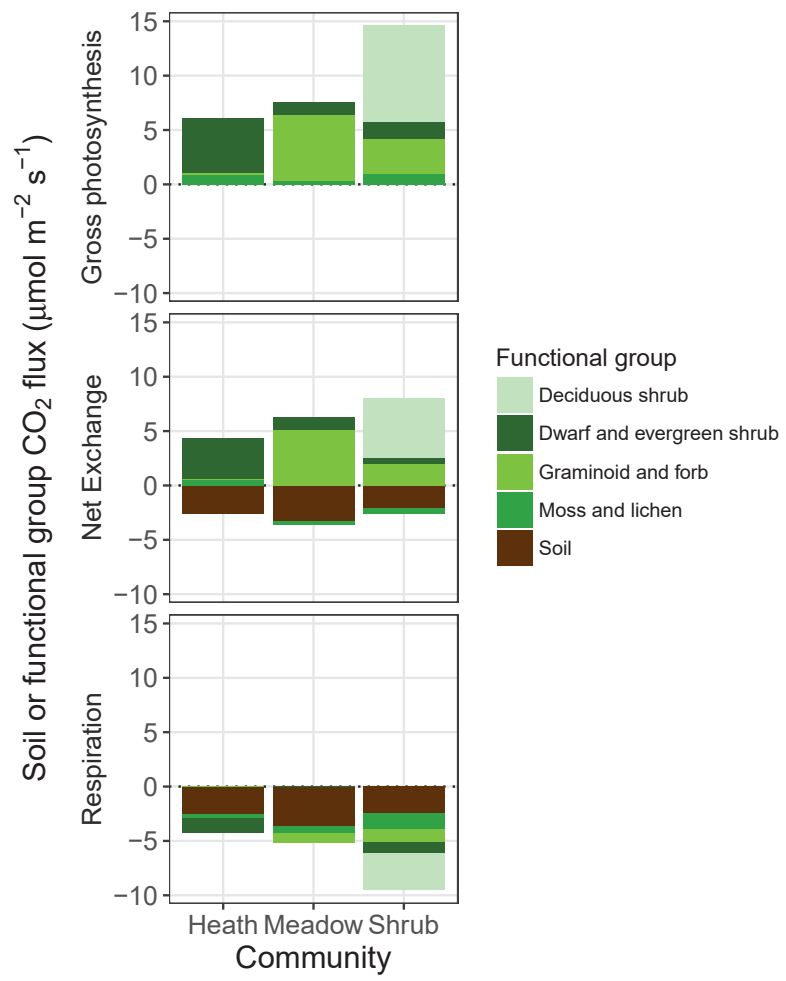


Figure S2

Paper IV

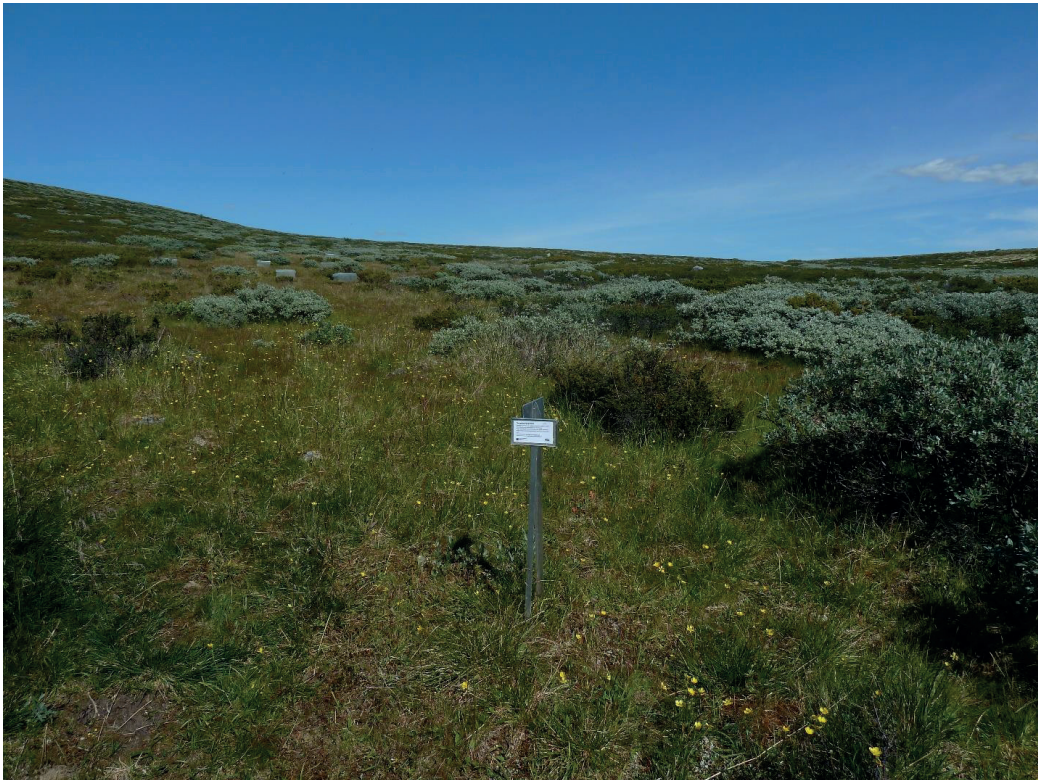


Photo: The meadow community July 2013

1 **Title:**

2 **Biotic and abiotic drivers of C cycling in three arctic-alpine**
3 **tundra plant communities: potential mechanisms**

4 **Journal Arctic, Antarctic and alpine research**

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18

19

1 **Abstract**

2 Recent vegetation changes in arctic-alpine tundra ecosystems may affect several ecosystem
3 processes that regulate microbe and soil functions. Such changes can alter ecosystem C cycling
4 with positive feedback to the atmosphere if plant uptake of C is lower than the amount of soil C
5 released. Here, we examine how differences in plant functional traits, microbial activity, and soil
6 processes within and across *Salix*-dominated shrub, dwarf-shrub-dominated heath, and herb-and
7 cryptogam-dominated meadow communities influence C cycling. We test a hypothesized
8 framework using an *a priori* model selection that emphasizes predicting variation in day-time
9 growing season ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP).
10 GEP was closely related to soil moisture and secondarily to plant functional traits and above-
11 ground biomass. While the above-ground respiration was not related to variation in above-
12 ground biomass, variation in below-ground respiration was dependent on the community
13 weighted mean of SLA (SLA_{CWM}). Similarly, microbial activity was linked with SLA_{CWM} and
14 was highest in the meadow, and carbon degrading microbial activity decreased with vegetation
15 woodiness. These results indicate how shrub expansion into alpine tundra communities may
16 influence the summer C cycling (ER) differently depending on plant community, as ER might
17 increase in the heath, and decrease in the meadow communities.

18 **Keywords**

19 Gross ecosystem photosynthesis, ecosystem respiration, shrub expansion, plant functional traits,
20 enzyme activity.

21

22

23

1 **Introduction**

2 Due to climate change, fluctuations in herbivory, and human land use changes, the rate of shrub
3 expansion and cover is predicted to increase with future climate change (Settele et al. 2014,
4 Myers-Smith et al. 2015, Martin et al. 2017, Normand et al. 2017, Post and Pedersen 2008,
5 Speed et al. 2013, Ravolainen et al. 2011). Indeed, over the last several decades shrub cover has
6 increased in high-latitude arctic and alpine tundra ecosystems (Tape, Sturm, and Racine 2006,
7 Cannone, Sgorbati, and Guglielmin 2007, Tømmervik et al. 2009, Myers-Smith et al. 2011,
8 Epstein et al. 2012, Epstein et al. 2015). An open question is how will shrub expansion impact
9 the carbon balance of these ecosystems (Virkkala et al. 2017)? While high-latitude tundra
10 ecosystems currently store more than half of global soil carbon (C) (Tarnocai et al. 2009), these
11 systems are predicted to be highly sensitive to climate warming with projections of some of the
12 greatest C losses (Crowther et al. 2016). Plant-microbial-soil feedbacks regulate soil C (Wardle
13 et al. 2004, De Deyn, Cornelissen, and Bardgett 2008). If shrub expansions leads to more soil C
14 is released than plant uptake is enhanced, these vegetation changes may alter ecosystem C
15 cycling with potential positive feedback to the atmosphere (Bardgett 2011, Parker, Subke, and
16 Wookey 2015, Cahoon et al. 2012a, Wilmking, Harden, and Tape 2006, Crowther et al. 2016,
17 Wookey et al. 2009). However, understanding the response of C cycling to climate and
18 vegetation changes requires unraveling the influence of plants, microbes, and soil processes on C
19 cycling (Bardgett 2011), and these links are largely unknown in tundra ecosystems (Myers-Smith
20 et al. 2011).

21

22 Arctic and alpine tundra vegetation is a mosaic of plant communities created by variations in
23 microclimate (snow-depth, moisture, temperature) and underlying bedrock types that form major

1 gradients in soil pH and soil nutrients and quality (Sonesson, Wielgolaski, and Kallio 1975,
2 Sundqvist et al. 2011, Eskelinen, Stark, and Männistö 2009). Two communities that are subject
3 to shrub expansion are the dwarf shrub-dominated heath and herb-dominated meadow (Björk and
4 Molau 2007, Molau and Alatalo 1998, Cannone, Sgorbati, and Guglielmin 2007). In a previous
5 study in alpine tundra vegetation, we found that the soil C stocks in meadow and heath
6 communities were much larger than in a *Salix* shrub community (Sørensen et al. 2017).
7 Among the abiotic drivers, variation in soil moisture influences leaf photosynthesis and below-
8 ground respiration (Sjögersten and Wookey 2002, Sjögersten et al. 2012, Illeris, Michelsen, and
9 Jonasson 2003, Volk et al. 2000). The influence of soil moisture on photosynthesis can be
10 through plant nutrient availability (Körner 2003, Berdanier and Klein 2011). Respiration,
11 however, might be indirectly influenced via microbial activity.

12 Soil temperature and moisture under a shrub canopy may differ from neighboring tundra plant
13 communities (Sturm et al. 2005, Myers-Smith et al. 2011). Changes in the shrub canopy cover
14 affects evapotranspiration and the timing of spring snow-melt. Shrub branches trap and
15 accumulate snow increasing snow depths in shrub communities (Sturm et al. 2005), and shrubs
16 (*Salix* in particular) might also thrive in places with intermediate to deep snow in winter and
17 higher soil moisture during summer. Alpine meadow vegetation is often found in lee sites with
18 deep snow cover during winter (Björk and Molau 2007) whereas heath vegetation usually is
19 more wind-exposed, well-drained, and the winter snow cover is shallower (Sturm et al. 2001a).
20 Shrub expansion into heath may thus increase snow depth and hence increase winter soil
21 temperatures, and potentially also alter winter soil respiration and spring soil moisture (Myers-
22 Smith and Hik 2013, Grogan and Jonasson 2006, Sturm et al. 2001a).

23

1 An increase in shrub cover also increases total above-ground biomass. Increases in vegetation
2 biomass in turn has been linked to greater productivity and respiration on global, regional, and
3 local scales (Gould, Reynolds, and Walker 2003, Wookey et al. 2009, Cahoon et al. 2012a,
4 Sørensen et al. 2017, Michaletz, Kerkhoff, and Enquist 2018). Vegetation changes also can
5 influence the composition of functional groups and alter above- and below-ground plant traits
6 that in turn may affect ecosystem productivity, decomposition, and nutrient availability
7 (Cornelissen et al. 2007, Veen, Sundqvist, and Wardle 2015, Freschet et al. 2013, Freschet,
8 Aerts, and Cornelissen Johannes 2011, Chapin 2003, De Deyn, Cornelissen, and Bardgett 2008,
9 Wookey et al. 2009). Changes in ecosystem carbon sequestration due to altered community
10 structure have been analyzed using plant community effect traits (Klump and Soussana 2009),
11 and the mass-ratio hypothesis underlies these analyses (Lavorel and Garnier 2002, Grime 1998).
12 According to the mass-ratio hypothesis, ecosystem properties (e.g., energy pools and fluxes)
13 depend on the most dominant trait value (the abundance weighted means) of effect traits at the
14 level of community (Garnier et al. 2004, Garnier, Navas, and Grigulis 2016). Currently there is
15 strong evidence for the mass-ratio hypothesis and using community weighted means (CWM) of
16 leaf traits to analyze ecosystem properties (Garnier et al. 2004, Lavorel 2012, Garnier, Navas,
17 and Grigulis 2016, Enquist et al. 2015). Still, not many studies have tested the relationships
18 between ecosystem C fluxes and community weighted leaf traits (but see Klump and Soussana
19 2009, Enquist et al. 2015).

20

21 Net and gross photosynthesis differ among functional plant groups due to differences in plant
22 resource economy (Ward et al. 2009, Strimbeck et al. *in prep* will be submitted to AAAR). For
23 example forbs and graminoids in meadow vegetation are adapted to rapid growth, short leaf life

1 span and high leaf level photosynthesis, and usually these plants have thin leaves (high specific
2 leaf area (SLA)), low leaf dry matter content (LDMC), and moderate to high rates of
3 photosynthesis on an area or mass basis (Wright et al. 2004, Díaz et al. 2015, Pierce et al. 2016).
4 In contrast, evergreen dwarf shrubs typically dominating heath vegetation are relatively slow
5 growing, with long leaf life span, low leaf photosynthetic rates and thick and small leaves (low
6 SLA) containing many defense compounds (high LDMC) (Wright et al. 2004, Díaz et al. 2015).
7 Specific leaf area often correlates closely with LDMC, and SLA can therefore represent leaf
8 recalcitrance and hereby leaf decomposability. Specific leaf area is also highly correlated with
9 leaf nitrogen (Wright et al. 2004), and leaf nitrogen is a very good indicator of nitrogen
10 availability (Cornelissen et al. 1997, Hodgson et al. 2011). Since specific leaf area (SLA) is
11 strongly related to relative growth rate, leaf photosynthesis, decomposability, and nitrogen
12 availability (Wright et al. 2004), we will test how the community weighted mean of SLA affects
13 gross ecosystem photosynthesis and ecosystem respiration. In addition, the woodiness of
14 vegetation is important for C cycling in plant communities. Indeed, deciduous shrubs have thin
15 and annual leaves, but they produce abundant woody stems and roots, which affect
16 decomposition and the C:N ratio, and thereby the C pool and C cycling (Cornelissen et al. 2007,
17 Freschet et al. 2013, Rasse, Rumpel, and Dignac 2005, Dietzel, Liebman, and Archontoulis
18 2017).

19

20 In comparison to other ecosystems, arctic-alpine tundra ecosystems are nutrient poor, and within
21 tundra plant communities, heath vegetation is more nutrient poor than meadow vegetation (Björk
22 and Molau 2007, Makarov et al. 2003). Microbes play an important role in supplying and
23 regulating various limiting nutrients such as nitrogen (N) and phosphorous (P) (Van Der Heijden,

1 Bardgett Richard, and Van Straalen Nico 2007). By stimulating productivity, microbes can act as
2 a vector for plant C build-up in the soil. Biotic interactions with organisms such as mycorrhiza
3 can influence C cycling locally and globally (Averill and Hawkes 2016, Phillips, Brzostek, and
4 Midgley 2013). The plant symbiosis also appear to be very important in arctic-alpine
5 ecosystems, where they are associated with priming and C loss in shrub tundra but not in heath
6 tundra communities (Parker, Subke, and Wookey 2015, Hartley et al. 2012, Clemmensen et al.
7 2015). Evergreen dwarf shrubs are primarily being associated with ericoid mycorrhiza (ERM),
8 whereas several arctic-alpine deciduous shrubs are associated with ectomycorrhiza (ECM), and
9 forbs and graminoids in meadows are generally more associated with arbuscular mycorrhiza
10 (AM) (Becklin, Pallo, and Galen 2012, Becklin and Galen 2009, Cornelissen et al. 2001,
11 Michelsen et al. 1998, Väre, Vestberg, and Euroala 1992). Recent studies suggest that ECM
12 contribute to the loss of soil C from ecosystems by acting as decomposers, especially in arctic
13 and boreal systems (Talbot, Allison, and Treseder 2008, Lindahl and Tunlid 2015, Clemmensen
14 et al. 2015, Hartley et al. 2012, Parker, Subke, and Wookey 2015).

15 Potential microbial activity is an instantaneous measure of decomposition, and can represent
16 heterotrophic soil respiration, as extracellular enzymes are produced by bacteria, archaea and
17 fungi (Burns et al. 2013, Hernández and Hobbie 2010, Kjøller and Struwe 2002). Besides being
18 affected by abiotic properties (Burns et al. 2013, Karhu et al. 2014, Schinner 1983, Koyama et al.
19 2013, Sinsabaugh, Carreiro, and Alvarez 2002), microbial activity is affected by litter and leaf
20 quality (De Deyn, Cornelissen, and Bardgett 2008, Hernández and Hobbie 2010, Bardgett 2017,
21 Sinsabaugh, Carreiro, and Alvarez 2002, Sinsabaugh, Moorhead, and Linkins 1994).

22

1 The aim of this study is to explore how ecosystems controls, such as plant functional traits,
2 microbial activity and abiotic properties, affect C cycling (Figure 1). We measured day-time
3 growing season ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP) in a
4 *Salix*-dominated shrub community, a dwarf-shrub-dominated heath, and a herb-and cryptogam-
5 dominated meadow in Central Norway and hypothesized (see Figure 1) that:

- 6 1) GEP across communities is primarily controlled by the community weighted mean of
7 SLA (SLA_{CWM}), total above-ground biomass ($Biomass_{above}$), and soil moisture with
8 SLA_{CWM} being the strongest driver (Hypothesis 1).
- 9 2) ER can be separated into above- and below-ground respiration. Above-ground respiration
10 is influenced by SLA_{CWM} and $Biomass_{above}$ with $Biomass_{above}$ having the greatest effect
11 (Hypothesis 2a). Below-ground respiration is controlled by root biomass ($Biomass_{roots}$),
12 microbial activity, and SLA_{CWM} . We expect microbial activity to have most effect in the
13 meadow and SLA_{CWM} most effect in the heath and shrub communities (Hypothesis 2b).
- 14 3) Carbon degrading microbial activity related to cellulose and lignin degradation decrease
15 with vegetation woodiness represented by C:N ratio of above-ground vegetation and
16 decrease with leaf recalcitrance represented by SLA_{CWM} (hypothesis 3).

17 **Materials and Methods**

18 **Study area and sampling design**

19 The field sites were located above the forest line in the low-alpine vegetation zone around 1100
20 m a.s.l. in Dovrefjell, Central Norway (62°N, 9°E), in an *Empetrum*-dominated heath, an herb-
21 and cryptogam-dominated meadow, and a *Salix*-dominated shrub community (Figure S1). The
22 climate in the area is continental (Moen 1998) with annual and summer mean temperatures of -
23 1°C and 7.1 °C and precipitation 700 mm and 298 mm for the period from 1960 to 1990 (New,

1 Hulme, and Jones 2000). The plant communities were chosen to have a large area with
2 homogeneous vegetation and were therefore situated on different but neighboring mountain
3 slopes, whilst keeping variation in other abiotic variables to a minimum, i.e. aspect and slope.
4 The three communities differed in the surrounding topography, as the heath was more wind-
5 exposed and the meadow and shrub communities were more sheltered, presumably influencing
6 the vegetation composition (Table 1). For a more detailed list of dominant species see table S1 in
7 Sørensen et al. (2017).

8 Soils were podzolic in all sites, with a partial albic horizon in the shrub community and a well-
9 developed albic horizon in the heath (Sjögersten and Wookey 2009). Soils were developed from
10 glacial moraines, over metavolcanic rock in the heath and shrub community and shale in the
11 meadow (NGU 2015). At present, the area undergoes low-intensity (25 sheep per km²) summer
12 grazing by domestic white sheep (*Ovis aries*). Other herbivores in the area are voles (*Microtus*
13 *agrestis*, *M. oeconomus*, and *Myodes rufocanus*), lemmings (*Lemmus lemmus*), ptarmigan
14 (*Lagopus lagopus* and *L. muta*), hare (*Lepus timidus*), moose (*Alces alces*), and occasionally wild
15 reindeer (*Rangifer tarandus*).

16

17 The sampling design of this study was part of a larger experiment with four different treatments
18 in each of eight blocks for each community (Sørensen et al. In revision BMC ecology) (Figure
19 S1). In the present study, six replicate blocks from each community were randomly selected for
20 measurements. The average distance among blocks within community was 23.0 m in the shrub
21 community, 21.7 m in the meadow community, and 28.1 m in the heath community. Across
22 communities the average distance \pm SD between nearest control plot was 24.4 ± 3.4 m, thus
23 reducing spatial autocorrelation of factors controlling C fluxes (Marriott et al. 1997).

1

2 In each block, C fluxes, microclimate, and leaf traits were measured on the control plots ($0.5 \times$
3 0.5 m) and above-ground biomass was harvested for chemical analysis in neighboring harvest
4 plots (0.25×0.25 m in heath and meadow and 0.5×0.5 m in shrub community to catch the
5 heterogeneity of woody biomass). Additionally, the below-ground properties microbial activity,
6 root biomass, pH, and soil C:N ratios were measured in a soil pit in early September 2015
7 (details below). Six blocks were studied in the meadow and heath communities, whereas only
8 five blocks were included in the shrub community due to logistics. The total number of samples
9 across communities was 17.

10

11 **Flux measurements and microclimate**

12 During mid-growing season in 2015, on sunny days only, CO₂ fluxes were measured in control
13 plots, using a closed system composed of a collapsible 0.5 m \times 0.5 m \times 0.6 m (L \times W \times H)
14 polyethylene chamber and a LI-840A CO₂/H₂O infrared gas analyzer (LI-COR Inc., Lincoln,
15 Nebraska, USA). The chamber was sealed with a 5 m long chain weighing 5 kg.
16 Each measurement consisted of a light and a dark measurement. Net Ecosystem Exchange (NEE)
17 and Ecosystem Respiration (ER) were calculated from those measurements, respectively, via
18 linear regression (Jasoni, Smith, and Arnone 2005). Gross Ecosystem Photosynthesis (GEP) was
19 calculated by subtracting ER from NEE. We performed light curve measurements one time on all
20 control plots. One light curve measurement consisted of one measurement in full light,
21 measurements at three increasing levels of shading, and one measurement in full darkness
22 (Williams et al. 2006, Street et al. 2007). The shading was done with three layers of black tulle.
23 For dark measurements, we used an opaque hood to block out the light (Street et al. 2007). For

1 more details on the flux measurement methods see Sørensen et al. (2017).
2 During all flux measurements, we measured light (PAR) with a LI-190S quantum sensor (LI-
3 COR Inc., Lincoln, Nebraska, USA), air temperature with a PT100 sensor inside (at 40 cm
4 height) and outside the chamber (at a height of 60 cm), soil temperature at 8 cm depth, and soil
5 moisture at 5 cm depth with a TRIME-PICO32 sensor (IMKO, Germany). Additionally, soil
6 moisture was measured in early, mid, and late growing season. Surface temperature (at 1 cm
7 depth) was recorded every four hours with temperature sensors (iButtons, Maxim Integrated
8 Products, Sunnyvale, CA, USA). The surface temperatures during the flux measurements were
9 estimated by interpolation. Snow depth was measured four times per plot with an avalanche
10 probe in March 2015 and April 2016; if marking sticks were not visible plots were located by a
11 handheld GPS receiver (3 m precision).

12

13 **Above-ground plant traits**

14 *Leaf traits*

15 Samples for specific leaf area (SLA) and leaf dry matter content (LDMC) of the dominant
16 vascular species were collected in each block outside of the experimental plots in each plant
17 community during peak growing season 2013, 2014 and 2016. Dominant species were those that
18 collectively made up 80 % of cumulative relative abundance in each plant community (Pérez-
19 Harguindeguy et al. 2013), based on vegetation analysis performed in 2013. Between 3 and 20
20 leaves per species from two individuals per block were sampled. Leaves (on twigs when
21 possible) were sampled and placed in plastic bags with moist paper towels and stored at 4 °C
22 (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). Fresh leaves including petioles were
23 weighed to an accuracy of 0.1 mg, scanned at 600 dpi, and the area was measured with Image J

1 software (National Institutes of Health, Bethesda, Maryland, USA). The leaves were then oven
2 dried at 70°C for 72 h and weighed again (Cornelissen et al. 2003).
3 Community weighted means (CWM) were calculated (Garnier et al. 2004, Violle et al. 2007) for
4 SLA (SLA_{CWM}) and LDMC (LDMC_{CWM}) for each control plot in each community, based on the
5 mean trait value per species per block in each community and the relative abundance in control
6 plots. The relative abundances of species were recorded with the point intercept method
7 (Jonasson 1988) in July 2015 during mid-growing season with a 25 × 25 cm quadrat and 25 pins
8 (Figure 1).

9 *Above-ground biomass harvest*

10 Above-ground biomass (Biomass_{above}) was destructively sampled from harvest plots during the
11 mid-growing season in July 2015. All plant material was oven-dried at 70 °C for 72 h before
12 weighing to an accuracy of 0.001 g. Above-ground plant and litter C and N pools (g C m⁻²) were
13 estimated by multiplying the oven-dry weight (g) by the average C concentration (mg⁻¹ g) per
14 functional group. The C concentration per functional group was determined from plant material
15 harvested in an earlier study in 2013 from the same sites (See appendix 2 in Sørensen et al.
16 2017).

17

18 **Below-ground properties**

19 Each soil pit was dug to bedrock or the BC horizon. Mean total depth of the soil pits was 56 ± 8
20 cm and ranged from 42 to 70 cm. Duplicate soil samples were extracted from each horizon,
21 identified by color and texture. Each sample was extracted for a defined volume (5 × 5 × 5 cm)
22 using a knife. The duplicate samples were analyzed in two different laboratory locations. One
23 sample was used for measurements of microbial activity, root biomass, and soil pH and the other

1 was used to determine soil and root C and N content. The samples were stored at 4 °C for a
2 maximum of five days before being processed.

3 *Root biomass, carbon, and nitrogen*

4 To determine root biomass ($Biomass_{roots}$), all visible roots (living and dead) were manually
5 extracted from fresh soil samples for 15 min per samples. In nearly all samples this meant
6 extracting every single root visible to the naked eye. The collected roots were oven-dried at 60
7 °C for 48 h and weighed. To determine root C and N content from the other duplicate sample,
8 roots were washed, and oven-dried, and homogenized by grinding (MF 10 basic IKA Werke)
9 prior to elemental combustion (ECS 4100, Costech).

10 *Soil properties*

11 To determine total soil C and N content, soils were oven-dried at 60 °C for 48h. Roots and stones
12 (> 2 mm) were removed by sieving the soil. Soil organic matter was determined for each soil
13 sample from all horizons via loss on ignition (LOI) in a furnace at 550 °C for 5 h. Soil samples
14 were then bulked per horizon to determine C and N concentrations via elemental combustion
15 (ECS 4100, Costech). Average LOI per horizon (FractionLOI (%)) was significantly correlated
16 with bulked soil C concentration (C concentration (%): $C \text{ concentration (\%)} = 0.43575 * \text{FractionLOI (\%)} - 0.25687$, $p < 0.0001$, $r^2 = 0.918$, $n = 74$). This relationship between
17 FractionLOI (%) and C concentration (%) was used to extrapolate C concentrations for eight soil
18 horizons that were not included in our soil C concentration determination. For all soil samples
19 we found no evidence of inorganic C in the form of carbonates determined by effervescence
20 following the addition of 1 M HCl (see Hodgson 1997). Soil organic carbon (SOC) (kg C m^{-2})
21 was calculated by multiplying the C concentration (%) per horizon by horizon thickness (m) and
22 bulk density (kg m^{-3}). Following these calculations, horizons were then pooled into organic
23

1 versus mineral based upon a threshold of 80 % LOI for organic soils (Hodgson 1997). Soil pH
2 was measured using 0.01 M CaCl₂ in a 1:3 soil-to-solution mixture for each soil horizon in each
3 soil pit.

4 *Microbial activity*

5 We assessed the activity of the soil community by assaying the potential extracellular enzyme
6 activity of extracellular α -glucosidase (a-gluc), β -glucosidase (b-gluc), cellobiohydrolase, β -
7 xylosidase (xylo), cellobiohydrolase (cbh), and N-acetylglucosaminidase (NAG) for each soil
8 horizon in all of the soil pits. Enzymes that are important in C degradation (a-gluc, b-gluc, cbh
9 and xylo) break down carbohydrates and polysaccharides. NAGase mineralizes nitrogen from
10 chitin, and thus is produced by fungi to acquire N (Read and Perez-Moreno 2003, Bell et al.
11 2013).

12 One to two grams of soil from each sample was mixed in 125 mL 0.5 M sodium acetate buffer
13 (pH 5) on a stir plate. We added substrates for enzymes to act on in eight analytical replicates in
14 96-well plates: 4-MUB- α -D-glucoside, 4-MUB- β -D-glucoside, 4-MUB- β -D-cellobioside, 4-
15 MUB- β -D-xyloside, and 4-MUB-N-acetyl- β -D-glucosaminide, respectively. The plates were
16 incubated in a dark environment at room temperature before the activity was analyzed with a
17 fluorimeter/spectrophotometer (Synergy HT; Biotek Inc, Winooski, VT, USA). Fluorescence of
18 the enzymes was measured at an excitation of 365 nm and an emission of 450 nm. Potential
19 enzyme activity is expressed in the units of nmol h⁻¹ g⁻¹ dry soil. To get the total enzyme activity
20 for the full soil depth, as recommended by Hernández and Hobbie (2010), we used soil bulk
21 density to convert the activity per horizon from nmol g⁻¹ h⁻¹ to nmol h⁻¹ m⁻² and then summed up
22 the enzyme activity across all horizons (microbes_{sum}).

1 *Hyphal ingrowth*

2 Mycorrhizal ingrowth bags were buried 2-11 cm below the soil surface between the organic and
3 mineral soil horizon for 13 weeks from mid June to September in each block in the three
4 communities. The size of the ingrowth bags was 5×3.5 cm and the material was 50 μ m nylon to
5 allow hyphal ingrowth but too fine for plant roots. Each bag contained approximately 30 g
6 autoclaved quartz sand (Moore et al. 2015). Mycorrhizal hyphal biomass was measured by
7 extracting hyphae from the ingrowth bags within two weeks after collection, using standard
8 floating techniques (Wallander, Göransson, and Rosengren 2004). The extracted hyphae were
9 freeze dried at -20 °C prior to weighing (Moore et al. 2015) and the biomass reported as mg of
10 hyphal biomass per g sand (Wallander, Göransson, and Rosengren 2004). These data were not fit
11 for analysis as there were poor ingrowth in some plots, but the data are reported in Table 1 as
12 background data.

13

14 **Data analysis**

15 *Flux analysis*

16 GEP was standardized to $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, and ER was separated into above-ground
17 (R_{above}) and below-ground respiration (R_{below}). In order to reduce variance and due to reduced
18 degrees of freedom we standardized respiration to temperature by using standardized Q10
19 relationship. Since we know from earlier studies that shrub expansion has an effect on canopy
20 and soil temperature (Sturm et al. 2005, Myers-Smith and Hik 2013, Sørensen et al. 2017) and to
21 reduce degrees of freedom, we standardized ER to a specific temperature (ER_{temp}) by using a
22 Q10 relationship (Tjoelker, Oleksyn, and Reich 2001):

23
$$ER_{\text{temp}} = R_{\text{above}} + R_{\text{below}}$$

1
$$R_{above20} = f_{above_{community}} ER Q10^{\left(\frac{20-T_{air}}{10}\right)}$$

2
$$R_{below10} = f_{below_{community}} ER Q10^{\left(\frac{10-T_{soil}}{10}\right)}$$

3 Ecosystem Respiration (ER) was separated into above- and below-ground components by
 4 multiplying with fractions specific for each community ($f_{above_{community}}$ and $f_{below_{community}}$). The
 5 specific fractions were means across community identified by flux measurement before and after
 6 biomass harvest in Strimbeck et al. (*in prep* will be submitted to AAAR). Above-ground
 7 respiration was standardized to 20 °C (R_{above}), corresponding to mean air temperature inside the
 8 chamber during flux measurements (T_{air}), whereas below-ground respiration was standardized to
 9 10 °C (R_{below}), corresponding to mean soil temperature at 8 cm depth during the measurements
 10 (T_{soil}). The ratio of rates given a 10 °C change in temperature (Q10), was set to 2 (Tjoelker,
 11 Oleksyn, and Reich 2001).

12 To standardize GEP to a photosynthetically active radiation (PAR) of 600 ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
 13 (GEP_{600}), we used light response curves for each plot derived by using the nls functions in R (R
 14 Core Team 2017)

15
$$GEP = \frac{P_{max} \cdot I}{k + I}$$

16 Where $GEP = ER_{temp} - NEE$, $I =$ incident PAR ($\mu\text{mol m}^{-2}\text{s}^{-1}$), $P_{max} =$ rate of light saturated
 17 photosynthesis, and $k =$ half saturated constant of photosynthesis. If we did not have any
 18 saturation from the light response curve, we used a fixed value of P_{max} , tried different values, and
 19 chose the one with the best fit. Even though GEP_{600} was not significantly different from non-
 20 standardized GEP measurements (Sørensen et al. 2017), we chose to use GEP_{600} in order to
 21 reduce the variance between the plots.

22

1 *Hypothesis testing*

2 To test the hypothesized framework of ecosystem controls of C fluxes, we used multiple linear
3 models with z-standardized variables $(x - \text{mean}(x)) / \text{sd}(x)$. Variables included in the final full
4 models followed the a priori models described in hypothesis 1-3 and were SLA_{CWM} ,
5 $\text{Biomass}_{\text{above}}$, soil moisture, $\text{Biomass}_{\text{roots}}$, and $\text{microbes}_{\text{sum}}$. Variables excluded due to collinearity
6 (following Zuur, Ieno, and Elphick 2010) were LDMC_{CWM} and Community. The fluxes were ln-
7 transformed to meet model assumptions. We used backward model selection (drop1 function in
8 R) to identify the significance of each predictor variable. Additionally, we used exhaustive
9 model selection on the a priori models (Burnham and Anderson 2002), with AICc as the
10 selection criterion (glmulti package and MuMIn package) (Grueber et al. 2011). We visualized
11 the different ecosystem controls across and within the three communities by keeping two
12 variables constant by their means and plotting the third variable against the C fluxes.
13 Due to limited degrees of freedom, we did not test interaction effects in the model selection.
14 To test if microbial activity beneath woody vegetation differed from that in non-woody
15 vegetation (the meadow) we summed up the activity of enzymes degrading recalcitrant litter (b-
16 gluc, cbh, xylo). The activity of those C degrading enzymes were tested for correlation with C:N
17 ratios of total ecosystem, above-ground vegetation, soil, and roots and SLA_{CWM} , respectively.
18 We used one-way ANOVA to test for community differences in microbial activity and tested
19 significance using multiple comparisons with a Tukey's honest significant difference test ($p <$
20 0.05).
21 The enzyme activities were estimated per m^2 , but to test if it was driven by the content of C in
22 the soil, we also converted the enzyme activity to per g soil C per m^2 (Stone, DeForest, and
23 Plante 2014). There were some outliers in the enzyme data which we decided to keep due to the

1 small sample size, except for one, agluc H4_P1B1 (Figure S4).

2 All analyses were performed in R programming environment (R Core Team 2017).

3 **Results**

4 **Soil moisture has the greatest effect on gross ecosystem photosynthesis**

5 Soil moisture was the most important and only significant predictor with the greatest effect on
6 GEP (Table 2, Figure 2c). Across community, there was a positive relationship with GEP and
7 moisture (Figure 2c). Biomass_{above} and SLA_{CWM} had less effect on GEP but made strong
8 contributions to explanation of variance (Table 3). The model with lowest AICc contained only
9 soil moisture and Biomass_{above} and explained 52 % of the variance, whereas the full model
10 containing all three variables SLA_{CWM}, moisture and Biomass_{above} explained a bit more variation
11 ($R^2 = 0.55$) (Table 3).

12 Within communities, models were overall very poor, with high uncertainty due to the few data
13 points. Soil moisture and SLA_{CWM} were significant predictors in the shrub community only
14 (Figure 2a-c, Table S1).

15

16 **Above-ground biomass was the best predictor of above-ground respiration**

17 Above-ground respiration (R_{above}) was highest in the shrub community, intermediate in the heath
18 community and lowest in the meadow community (Figure 2d-e). Biomass_{above} had the greatest
19 effect on R_{above} , but was non-significant in backwards model selection (Table 2). Alone,
20 Biomass_{above} constituted the best model with lowest AICc, explaining 32 % of the variance. The
21 full model with both Biomass_{above} and SLA_{CWM} was second best and explained slightly more (R^2
22 = 0.36; Table 4). The effect of SLA_{cwm} on R_{above} across community was non-significant (Table 2,
23 Figure 2d).

1 Within community, we expected Biomass_{above} to have the greatest effects on R_{above}, though this
2 effect was only marginally significant ($p = 0.055$) and only in the heath community (Table S1).

3

4 **Specific leaf area (SLA) underpins below-ground respiration**

5 Below-ground soil respiration (R_{below}) was highest in the meadow, and lowest in the heath and
6 shrub communities. Specific Leaf Area (SLA_{CWM}) had the greatest and a positive effect and was
7 the only significant predictor of R_{below} (Figure 2f, Table 2). The best model with lowest AICc
8 scores only contained SLA_{CWM} ($R^2 = 0.45$) (Table 5). However, slightly more variation was
9 explained when the model also contained microbial activity ($R^2 = 0.51$) or Biomass_{roots} ($R^2 =$
10 0.50) (Table 2 and 5).

11 Within the shrub community, both SLA_{CWM}, Biomass_{roots}, and microbes_{sum} were significant, but
12 SLA_{CWM} had the greatest effect on R_{below} (Table s1). Unexpectedly, there was a negative
13 relationship between R_{below} and Biomass_{roots} and microbes_{sum} in the shrub community (Figure 2g-
14 h).

15

16 **Carbon degrading microbial activity was highest in the meadow and related to specific leaf** 17 **area**

18 Microbial activity was mostly similar in the woody heath and shrub communities, and the carbon
19 degrading enzyme activity related to cellulose and lignin degradation (cbh and xylo) in the soils
20 was lowest in the woody communities and highest in the meadow ($p < 0.05$, TukeyHSD) (Figure
21 3a, Table 6). In the organic horizon all enzymes except a-gluc were highest in the meadow
22 community ($p < 0.001$, TukeyHSD) (Table 6, Figure S2a). We tested if this could be due to the
23 high carbon content in the meadow soil, by controlling for amount of SOC. We then found that

1 the only significant differences that remained was the potential activities of the a-gluc enzymes
2 per gram C were marginally higher in the heath community (mineral horizon: $p \leq 0.05$, total
3 horizon: $p \leq 0.07$, TukeyHSD), and potential enzyme activity of b-gluc per gram C were
4 marginally higher in the heath than the shrub community (mineral horizon: $p = 0.05$, Total
5 horizon: $p = 0.06$, TukeyHSD) (Figure 3b, Figure S2d, Table S2).

6
7 The vegetation woodiness represented by the C:N ratio of above-ground vegetation was
8 negatively related to carbon degrading microbial activity ($R^2 = 0.28$, $p < 0.05$). However more
9 variation was explained by SLA_{CWM} ($R^2 = 0.34$, $p < 0.01$), which was positively related to
10 carbon degrading microbial activity (Figure 4). The C:N ratio of soil, roots and total ecosystem
11 were also negatively related to carbon degrading microbial activity, though the relationships
12 were weak (C:N ratio_{soil}: $R^2 = -0.0075$, $p = 0.36$; C:N ratio_{roots}: $R^2 = 0.059$, $p = 0.18$; C:N ratio_{total}
13 ecosystem: $R^2 = 0.15$, $p = 0.07$).

14

15 **Discussion**

16 This study demonstrates the varying importance of ecosystem controls of C cycling in three
17 alpine plant communities when calculations are controlled for temperature and light (Figure 5 a,
18 b, c). Gross Ecosystem Photosynthesis (GEP) was least driven by plant functional traits whereas
19 soil moisture and above-ground biomass were more important. Also above-ground respiration
20 was driven by the amount of above-ground biomass, whereas below-ground respiration was
21 dependent on the community weighted mean of SLA (SLA_{CWM}). Potential microbial activity was
22 highest in the meadow, and carbon degrading microbial activity decreased with vegetation

1 woodiness and increased with SLA_{CWM} .

2

3 **Soil moisture and above-ground biomass controls above-ground C fluxes**

4 Soil moisture was the best predictor of GEP and the effect is probably related to the shift in
5 vegetation composition along the moisture gradient with heath vegetation in the driest end and
6 shrub communities in the wettest (Westergaard-Nielsen et al. 2017, Martin et al. 2017). Soil
7 moisture was even more important than above-ground standing biomass ($Biomass_{above}$) of the
8 system. Other studies also identified soil moisture as limiting GEP in arctic-alpine ecosystems
9 (Dahl et al. 2017, Sjögersten, van der Wal, and Woodin 2006). A direct effect of soil moisture on
10 GEP could be through drought stress limiting stomatal conductance. On exposed sites in alpine
11 regions, the selective pressure for dealing with drought stress events is clearly seen in many
12 plants that have low growth, small leaves, and high content of leaf dry matter (Körner 2003). A
13 more indirect effect could be the importance of soil moisture for nutrient mineralization and
14 availability. Desiccation of soils limits the flow of nutrients to the roots and also microbial
15 activity and nutrient mineralization (Körner 2003, Berdanier and Klein 2011).

16 Contrary to expectation (Klumpp and Soussana 2009, Lavorel and Garnier 2002), SLA_{CWM}
17 turned out a less important predictor of GEP across communities. Community weighted means of
18 SLA for vascular plants do not capture the amount of leaf area in a community, and may
19 therefore be inferior to LAI that is often used to predict GEP (Street et al. 2007, Chapin 2003).

20 The high fraction of cryptogams in the communities (Sørensen et al. 2017) could also have
21 affected both the importance of soil moisture and the lack of importance of leaf traits for the
22 GEP. Cryptogam traits vary considerably and cryptogam photosynthesis has been reported to be
23 important in arctic-alpine ecosystems (Sancho et al. 2016, Jonsson et al. 2015, Douma et al.

1 2007). The importance of soil moisture on GEP may have been related to the poikilohydric
2 strategies of cryptogams regulated by soil moisture (Chadburn et al. 2017, Sancho et al. 2016).
3 On the other hand, the biomass of the cryptogams may have obscured the patterns between GEP
4 and Biomass_{above}. In another study, we investigated the role of cryptogams in our sites, and
5 showed minimal contributions to gas exchange (Strimbeck et al. *in prep* will be submitted to
6 AAAR).
7 Above-ground respiration followed the same trend as Biomass_{above}, highest in the shrub
8 community, intermediate in the heath, and lowest in the meadow, but the relationship was not a
9 linear fit (figure 2e). The non-significant influence of Biomass_{above} could potentially be explained
10 by the relatively large woody biomass component in the shrub community and heath
11 communities. In the shrub community, deciduous shrub leaves made up only 8 to 18 % of the
12 deciduous biomass, whereas evergreen leaves in the heath community made 52 to 65 % of total
13 evergreen shrub biomass. Also, the high biomass and low productivity of cryptogams in some of
14 our sites may contribute to the lack of correlation between Biomass_{above} and R_{above}.

15

16 **Specific leaf area drives soil respiration across community**

17 Community weighted means of specific leaf area had the greatest effect on below-ground
18 respiration (R_{below}). High SLA_{CWM} indicates labile leaves that decompose fast and has thereby
19 been suggested to increase heterotrophic respiration (De Deyn, Cornelissen, and Bardgett 2008,
20 Questad et al. 2007, Garnier et al. 2004, Bardgett 2017), but few studies have actually confirmed
21 this impact of leaf traits on ecosystem respiration. Secondly, SLA is strongly correlated with leaf
22 nitrogen (Wright et al. 2004), and can be a surrogate for nitrogen availability (Hodgson et al.

1 2011). Nitrogen availability may relate to microbial activity and thereby heterotrophic
2 respiration, see more in the section below.

3 Hypothesis 2a was confirmed for the shrub community, as all three variables SLA_{CWM} ,
4 $Biomass_{roots}$ and $microbes_{sum}$ were significantly important for R_{below} . Across communities there
5 was a positive relationship between SLA_{CWM} and R_{below} within the shrub community (Figure 2f),
6 and this variable showed the strongest effect on R_{below} . Unexpectedly, there was a negative
7 relationship between R_{below} and $microbes_{sum}$ and $Biomass_{roots}$ in this community. We suspect
8 however, that the significance of these relationships could be due to Type 1 error, caused by the
9 very small sample size in this community. Given the high variability of the systems, in the shrub
10 community in particular, higher intensity sampling is required for full delineation of these
11 relationships. Ideally, sampling of fluxes and potential enzyme activity should also be measured
12 concurrently in the same point in time and space (German, Chacon, and Allison 2011), but this
13 was prevented by logistics in our study.

14 In this study, R_{below} was not separated into autotrophic and heterotrophic respiration, but since
15 SLA_{CWM} and not $Biomass_{roots}$ had the greatest effect, this could imply that the difference among
16 communities consists primarily in the heterotrophic respiration compartment and not so much in
17 the autotrophic respiration.

18

19 **Microbial activity was related to SLA and was highest in the meadow**

20 Mycorrhizal fungi should be common members of the microbial community in all the plant
21 communities we studied, and we found hyphal growth in both the ERM heath and ECM shrub
22 community, but not in the AM-dominated meadow community (Table 1). We predicted that
23 microbial enzyme activity would be highest where plant root and fungal production were also the

1 highest because an increase in inputs should increase microbial activity overall (e.g., priming).
2 We found that the C:N ratio in plant material, here an indication of woodiness, was negatively
3 correlated with potential microbial enzyme activity (Figure 2, Figure 3a). Interestingly, we found
4 that the function of the microbial community was more related to a key functional plant trait, as
5 the C degrading microbial activity was positively correlated with SLA_{CWM}. This finding is
6 supported by the proposed Mycorrhizal Associated Nutrient Economy Framework that was
7 suggested for AM- and ECM-dominated temperate forests, as they here state that AM-dominated
8 vegetation has higher rates of decomposition and high chemical quality litter, as compared to
9 ECM dominated vegetation with lower chemical quality litter (Phillips et al 2013). Indeed, the
10 microbial activity was highest in the meadow ecosystem and likely reflects the more labile inputs
11 and higher root production found in meadow ecosystems relative to the woody heath and shrub
12 ecosystems (Stark and Väisänen 2014, German, Chacon, and Allison 2011, Iversen et al. 2015)
13 together with higher nitrogen availability (Garnier et al 2004, Hodgson et al 2011). Additionally,
14 the meadow had twice as much soil organic carbon (SOC) and total soil nitrogen as well as
15 higher minimum pH compared to in the heath and shrub communities (Table 1) (Sørensen et al.
16 2017). Yet an alternative source of N in both the meadow and the shrub communities could
17 further be provided by cryptogams (*Pleurozium schreberi*, *Hylocomium splendens*, and
18 *Peltigera*) that are associated with N fixing cyanobacteria (Knowles, Pastor, and Biesboer 2006,
19 Jonsson et al. 2015). When we corrected our measured activities for SOC, the differences among
20 the three communities dismissed, suggesting that the enzyme activities were positively related to
21 total soil carbon.

22

23

1 **Prediction of mechanisms for changes of C cycling under shrub expansion**

2 Understanding ecosystem processes of alpine plant communities is important for predicting the
3 impacts of the ongoing deciduous shrub expansion. Figure 5 synthesizes the knowledge gained
4 from our and others' studies (e.g., Wookey et al. 2009, Clemmensen et al. 2015, Veen,
5 Sundqvist, and Wardle 2015, Parker, Subke, and Wookey 2015, Becklin, Pallo, and Galen 2012)
6 on how shrub expansion may affect growing season C cycling in alpine heath and meadow
7 vegetation.

8 Shrub expansion into heath and meadow could increase mid-growing season C sequestration
9 (GEP), in the heath most likely due to increased SLA, and in both the meadow and heath due to
10 increased soil moisture (Figure 5d). In Norway, the climate is expected to rise in temperature
11 with increased precipitation and growing season lengths in the coming 100 years (Hanssen-
12 Bauer et al. 2015). We chose to standardize respiration to a fixed temperature, due to reduced
13 degrees of freedom. However, arctic-alpine summer soil temperatures decrease with shrub
14 expansion (Table 1) (Sturm et al. 2005, Myers-Smith and Hik 2013). Some studies have found
15 that shrub expansion therefore conserves soil moisture (Naito and Cairns 2011, Mann et al. 2002,
16 Myers-Smith et al. 2015), while others found soil moisture decreased as evapotranspiration
17 increased (Christiansen et al. 2018). We need studies to predict changes in moisture due to
18 species-specific shrub expansion into different plant communities.

19 Shrub expansion might also shorten the local growing season length and lower accumulated
20 temperature in heaths due to deeper snow cover and increased shading (Table 1). This might
21 limit soil C build-up when deciduous shrubs outcompete evergreen dwarf shrubs that could have
22 photosynthesized outside of the summer growing season and even under shallow snow (see
23 discussion in Sørensen et al. 2017).

1 We suggest that ecosystem respiration might change differently with shrub expansion into heath
2 and meadow ecosystems. As shrubs expand, above-ground respiration might increase in both
3 heath and meadow, because of increased above-ground biomass. However, in heath
4 communities, below-ground respiration may increase with shrub expansion (Figure 5d) due to
5 increased decomposability of the litter (reflected by higher SLA) whereas, in meadow below-
6 ground respiration may decrease (Figure 5e), due to lower root productivity and lower
7 decomposability of leaf, woody stems and roots (Cornelissen et al. 2007, Veen, Sundqvist, and
8 Wardle 2015, Christiansen et al. 2018, Iversen et al. 2015). This might seem counter-intuitive
9 since we previously found greater soil C pools in the meadow than in the shrub community
10 (Table 1) (Sørensen et al. 2017), but shrubs could easily reduce these pools due to seasonal
11 changes in below-ground respiration (Bardgett et al. 2005, Grogan and Jonasson 2006, see
12 further discussion Sørensen et al. (2017)). Also, more knowledge is needed on how C cycling
13 and stocks relate to mycorrhizal abundance of ECM, ERM and AM in arctic-alpine ecosystems
14 (Soudzilovskaia et al 2015).

15 In this study we suggested a hypothesized framework, however further studies are needed to test
16 it and corroborate the predicted C budget consequences into specific plant communities.

17 We demonstrated that the use of plant traits related to the leaf economic spectrum is useful when
18 analyzing C cycling, and we have demonstrated the importance of both including above-and
19 below-ground processes and as well as pools when looking at ecosystem properties and
20 processes related to carbon dynamics. Taken together these results indicate how shrub expansion
21 into alpine tundra communities may influence the summer C cycling (ER) differently depending
22 on plant community, as ER might increase in the heath, and decrease in the meadow
23 communities.

1 **Author contributions**

- 2 MVS, ATC, BJB, RS conceived and designed study
3 MVS performed fieldwork, lab work, and statistical analysis
4 ATC analyzed enzyme and hyphal data
5 BJE and ATC contributed to new methods
6 MVS wrote the paper with input from all coauthors.

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20

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1 **Tables with captions**

2 **Table 1:** Community means \pm SD for alpine *Empetrum*-dominated heath, meadow and *Salix*-
3 shrub plant communities in Dovre Mountains, Central Norway. The three most dominant species
4 within each community are based on total number of hits in each community, recorded on each
5 plot with the point intercept method 25 \times 25 cm quadrat and 25 pins (n = 96). Snow depth is
6 maximum depth across March 2015 and April 2016 (n=17). Soil moisture was measured on June
7 10th in the shrub, and 11th in the meadow and heath communities, and in July it was measured
8 on the 21st in the heath, 22nd in the shrub, and 23rd in the meadow. In September, soil moisture
9 was measured on the 28th in all three communities (n = 17). Temperature inside the CO₂ chamber
10 (T_{air}), surface temperature (T_{surface}), and soil temperature (T_{soil}) was obtained during CO₂
11 measurements. Summer T_{surface} is surface temperature across the warmest months July and
12 August 2015S, and winter T_{surface} is across the coldest months, January and February, in 2015 (n
13 = 24). Growing degree hours are the sum of hours where surface temperature were > 5 °C (sensu
14 Graae et al 2012) (n = 24). Minimum pH, soil organic carbon, and soil total nitrogen was from
15 throughout the full soil pit with mean depth 56 ± 8 cm (n = 17). Amount of above-ground
16 vegetation of total vegetation biomass is reflected in proportion of vegetation carbon above- and
17 below-ground (n = 17). Leaf traits representative of the community are represented as community
18 weighted means of Specific Leaf Area (SLA_{CWM}), Leaf Dry Matter content (LDMC_{CWM}), and
19 Leaf Area (LA_{CWM}) (n = 17). Hyphal ingrowth (mg g⁻¹) was for 5 x 3.5 cm sand bags made of 50
20 μ m nylon with placed in each community (n = 24).

21

Table 1

Community	Heath	SD	Meadow	Shrub	SD
Three most dominating species	<i>Arctostaphylos uva-ursi</i> (L.) Spreng. <i>Empetrum nigrum hermaphroditum</i> L. <i>Festuca ovina</i> L.		<i>Avenella flexouosa</i> (L.) Drejer <i>Festuca ovina</i> L. <i>Anthoxanthum nipponicum</i> Honda	<i>Avenella flexouosa</i> (L.) Drejer <i>Salix lapponum</i> L. <i>Salix glauca</i> L.	
Snow depth maximum (cm)		2.41 ± 2.10	39.56 ± 4.76	58.50 ± 18.59	
Soil moisture June (%)		18.65 ± 2.41	28.45 ± 3.29	60.11 ± 31.19	
Soil moisture July (%)		22.51 ± 2.27	53.06 ± 14.97	46.23 ± 25.86	
Soil moisture September (%)		28.95 ± 3.44	39.25 ± 5.78	37.33 ± 7.81	
T _{air} (°C)		22.80 ± 3.77	23.08 ± 2.79	22.26 ± 2.42	
T _{surface} (°C)		15.65 ± 5.13	13.65 ± 2.82	12.20 ± 2.60	
T _{soil} (°C)		10.23 ± 1.35	8.90 ± 1.53	8.95 ± 0.80	
T _{surface} summer mean		10.30 ± 0.74	10.09 ± 0.54	9.08 ± 1.12	
T _{surface} summer minimum		2.50 ± 0.80	2.00 ± 0.76	2.00 ± 0.93	
T _{surface} summer maximum		15.00 ± 6.22	18.00 ± 3.87	13.00 ± 5.64	
T _{surface} winter mean		-3.03 ± 0.49	-1.05 ± 0.23	-0.76 ± 0.42	
T _{surface} winter minimum		-6.75 ± 0.55	-3.25 ± 0.61	-2.75 ± 0.71	
T _{surface} winter maximum		-0.50 ± 0.33	-0.50 ± 0.23	-0.50 ± 0.16	
Growing degree hours		9040 ± 1709	8403 ± 1056	6663 ± 1801	
PH minimum		3.53 ± 0.40	4.38 ± 0.27	3.51 ± 0.27	
Soil organic carbon (kg C m ⁻²)		7.387 ± 2.59	10.713 ± 2.88	4.90 ± 2.26	
Soil total nitrogen (kg N m ⁻²)		0.38 ± 0.15	0.80 ± 0.23	0.43 ± 0.18	
SLA _{CWM} (mm ² mg ⁻¹)		6.78 ± 0.69	16.28 ± 2.37	11.50 ± 1.90	
LDM _{CWM} (mg g ⁻¹)		462.19 ± 14.04	345.62 ± 23.17	378.6	5 ± 33.06
LA _{CWM} (mm ²)		37.67 ± 7.25	196.23 ± 67.62	268.1	8 ± 131.88
Hypheal ingrowth (mg g ⁻¹)		0.022 ± 0.031	-	0.028 ± 0.053	

Table 2: Effects ($\mu\text{mol m}^{-2} \text{s}^{-1}$) SD^{-1} of each variable in full models across community. Explanatory variables were z-standardized $(x - \text{mean}(x))/\text{sd}(x)$ so one unit change corresponds to one SD. Models were run without log transformation to ease understanding of the effects. Sum of squares (χ^2) and p -values were derived from a likelihood-ratio test (Chi square test) performed on backward model selection (drop1 function in R) ($n = 17$). Significant effects are bold.

Response	Explanatory variables	Effect ($\mu\text{mol m}^{-2} \text{s}^{-1}$) SD^{-1}	SE	$\chi^2(1)$	p -value
GEP ₆₀₀	Intercept	9.51	± 0.58		
	zSLA _{CWM}	0.60	± 0.60	3.72	0.256
	zMoisture	2.93	± 1.05	28.16	0.005
	zBiomass _{above}	-0.74	± 0.59	5.66	0.165
R _{above}	Intercept	1.29	± 0.20		
	zSLA _{CWM}	-0.09	± 0.21	0.12	0.644
	zBiomass _{above}	0.34	± 0.22	1.69	0.108
R _{below}	Intercept	3.86	± 0.32		
	zSLA _{CWM}	1.19	± 0.36	18.85	0.001
	zBiomass _{roots}	0.17	± 0.40	0.31	0.626
	zMicrobes _{sum}	0.04	± 0.45	0.01	0.923

Table 3: Gross Ecosystem Photosynthesis (GEP) model selection based on AICc on multiple linear models, testing hypothesis 1. GEP were standardized to 600 PAR (GEP₆₀₀) and log-transformed. Soil moisture (%), Specific Leaf area (SLA_{CWM}) (mm² mg⁻¹), and above-ground biomass (Biomass_{above}) (g DW m⁻²) were z-standardized. Akaike weight values (w) is the probability a model is best, given the set of models considered. R²-adjusted were calculated for each model (n = 17).

Model rank	Model parameters	Intercept	zSLA _{CWM}	zBiomass _{above}	zMoisture	df	logLik	AICc	ΔAICc	w	R ² adjusted
m1	$\ln(\text{GEP}_{600}) \sim 1 + \text{zBiomass}_{\text{above}} + \text{zMoisture}$	2.24	NA	-0.12	0.42	4	3.19	4.95	0	0.68	0.52
m2	$\ln(\text{GEP}_{600}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zBiomass}_{\text{above}} + \text{zMoisture}$	2.21	0.09	-0.07	0.32	5	4.36	6.73	1.79	0.28	0.55
m3	$\ln(\text{GEP}_{600}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zBiomass}_{\text{above}}$	2.1	0.2	0.03	NA	4	0.46	10.41	5.47	0.04	0.33
m4	$\ln(\text{GEP}_{600}) \sim 1 + \text{zBiomass}_{\text{above}}$	2.09	NA	-0.05	NA	3	-3.92	15.69	10.74	0	-0.04
m5	$\ln(\text{GEP}_{600}) \sim 1 + \text{zMoisture}$	2.12	NA	NA	0.14	3	-8.25	23.83	18.88	0	0.09
m6	$\ln(\text{GEP}_{600}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zMoisture}$	2.11	0.07	NA	0.12	4	-7.83	26	21.06	0	0.08
m7	$\ln(\text{GEP}_{600}) \sim 1 + \text{zSLA}_{\text{CWM}}$	2.06	0.16	NA	NA	3	10.88	28.95	24.01	0	0.1
m8	$\ln(\text{GEP}_{600}) \sim 1$	2.06	NA	NA	NA	2	12.67	29.92	24.97	0	0

Table 4: Above-ground respiration (R_{above}) model selection based on AICc on multiple linear models, testing hypothesis 2a. R_{above} was standardized to 20 °C and log-transformed. Specific Leaf area (SLA_{CWM}) (mm² mg⁻¹) and above-ground biomass (Biomass_{above}) (g DW m⁻²) were z-standardized. Akaike weight values (w) is the probability a model is best, given the set of models considered. R²-adjusted were calculated for each model (n = 17).

Model rank	Model parameters	Intercept	zSLA _{CWM}	zBiomass _{above}	df	logLik	AICc	ΔAICc	w	R ² adjusted
m1	$\ln(\text{R}_{\text{above}}) \sim 1 + \text{zBiomass}_{\text{above}}$	0.05	NA	0.41	3	-13.08	34.01	0	0.55	0.32
m2	$\ln(\text{R}_{\text{above}}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zBiomass}_{\text{above}}$	0.04	-0.19	0.33	4	-11.96	35.25	1.24	0.29	0.36
m3	$\ln(\text{R}_{\text{above}}) \sim 1 + \text{zSLA}_{\text{CWM}}$	0.04	-0.31	NA	3	-14.68	37.21	3.21	0.11	0.18
m4	$\ln(\text{R}_{\text{above}}) \sim 1$	0.05	NA	NA	2	-16.92	38.69	4.68	0.05	0

Table 5: Below-ground respiration (R_{below}) model selection based on AICc on multiple linear models, testing hypothesis 2b. R_{below} was standardized to 10 °C and log-transformed. Specific Leaf area (SLA_{CWM}) ($\text{mm}^2 \text{mg}^{-1}$), the sum of microbial activity ($\text{Microbes}_{\text{sum}}$) ($\text{nmol h}^{-1} \text{m}^{-2}$), and standing root biomass ($\text{Biomass}_{\text{roots}}$) (g DW m^{-2}) were z-standardized. Akaike weight values (w) is the probability a model is best, given the set of models considered. R^2 adjusted were calculated for each model ($n=17$).

Model rank	Model parameters	Intercept	zSLA_{CWM}	$\text{zBiomass}_{\text{roots}}$	$\text{zMicrobes}_{\text{sum}}$	df	logLik	AICc	ΔAICc	w	R^2 adjusted
m1	$\ln(R_{\text{below}}) \sim 1 + \text{zSLA}_{\text{CWM}}$	1.24	0.28	NA	NA	3	-4.19	15.57	0	0.44	0.45
m2	$\ln(R_{\text{below}}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zMicrobes}_{\text{sum}}$	1.26	0.28	NA	0.07	4	-2.61	16.55	0.98	0.27	0.51
m3	$\ln(R_{\text{below}}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zBiomass}_{\text{roots}}$	1.26	0.3	0.05	NA	4	-2.77	16.88	1.3	0.23	0.5
m4	$\ln(R_{\text{below}}) \sim 1 + \text{zSLA}_{\text{CWM}} + \text{zMicrobes}_{\text{sum}} + \text{zBiomass}_{\text{roots}}$	1.26	0.28	0.02	0.06	5	-2.59	20.63	5.05	0.04	0.48
m5	$\ln(R_{\text{below}}) \sim 1 + \text{zMicrobes}_{\text{sum}}$	1.25	NA	NA	0.22	3	-7.44	22.72	7.15	0.01	0.2
m6	$\ln(R_{\text{below}}) \sim 1 + \text{zMicrobes}_{\text{sum}} + \text{zBiomass}_{\text{roots}}$	1.25	NA	0	0.22	4	-7.44	26.21	10.64	0	0.14
m7	$\ln(R_{\text{below}}) \sim 1 + \text{zBiomass}_{\text{roots}}$	1.25	NA	0.12	NA	3	-9.19	26.23	10.66	0	0.01
m8	$\ln(R_{\text{below}}) \sim 1$	1.24	NA	NA	NA	2	-11.99	28.55	12.98	0	0

1 **Table 6:** F-value, degrees of freedom and *p*-value from one-way ANOVA tests of differences
 2 among enzyme activities (nmol h⁻¹ m⁻²) between communities. The enzymes were from
 3 organic and mineral horizons, and total across the soil pit. The significant differences are
 4 bold. In the organic horizon b-gluc, ch, xylo, and nag were significantly higher in the
 5 meadow than in the heath and shrub communities (*p* < 0.001, TukeyHSD). Activity of a-gluc
 6 in the meadow were only higher than the shrub community (*p* < 0.05, TukeyHSD).

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Horizon	Enzyme	F-value	df _{num}	df _{den}	<i>p</i> -value
Organic	ln(a-gluc)	12.36	2	13	0.00
	ln(b-gluc)	5.19	2	13	0.02
	ln(cbh)	18.97	2	13	0.00
	ln(xylo)	15.03	2	13	0.00
	ln(nag)	23.58	2	13	0.00
Mineral	ln(a-gluc)	0.31	2	15	0.74
	ln(b-gluc)	2.63	2	15	0.11
	cbh	0.52	2	15	0.60
	xylo	0.20	2	15	0.82
	nag	0.92	2	15	0.42
Total	ln(a-gluc)	0.73	2	15	0.50
	ln(b-gluc)	2.76	2	15	0.10
	ln(cbh)	7.56	2	15	0.01
	xylo	6.28	2	15	0.01
	nag	4.90	2	15	0.02

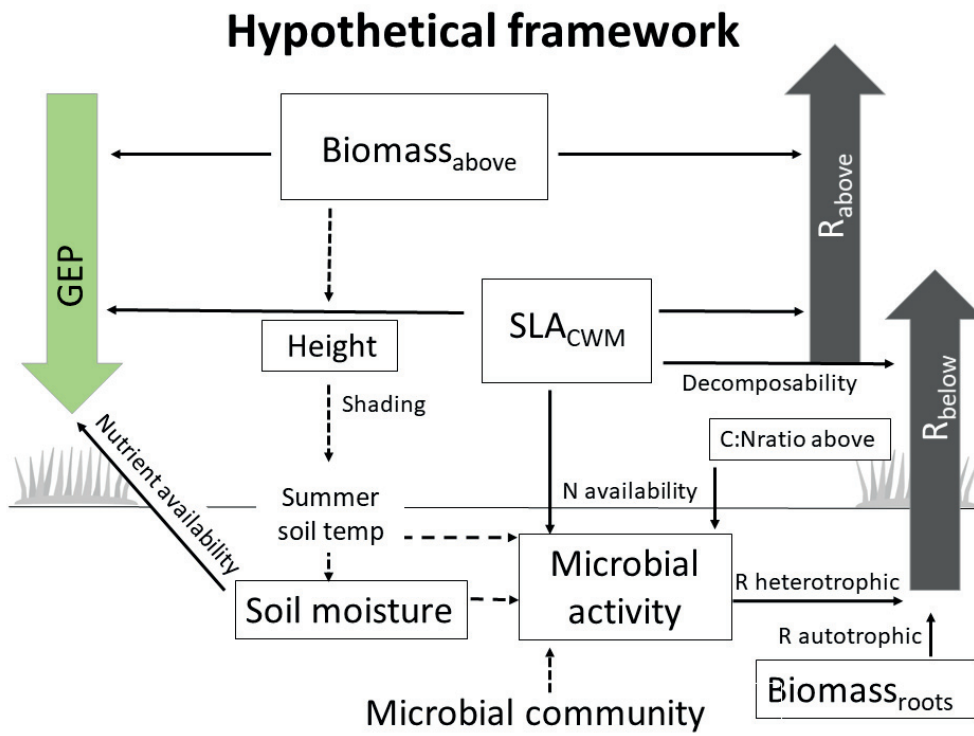
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1 Figures

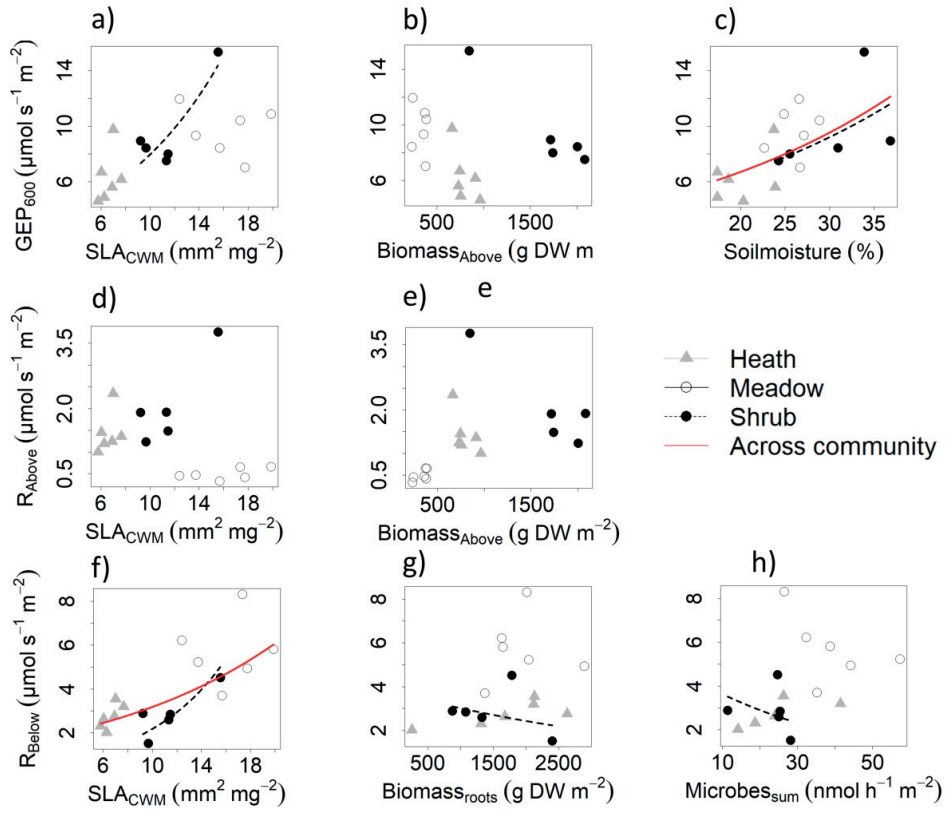
2 Figure 1



3

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1 **Figure 2**

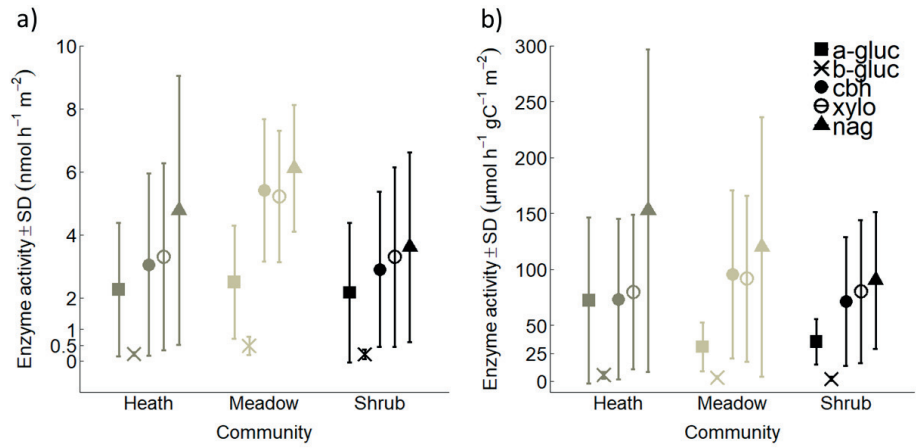


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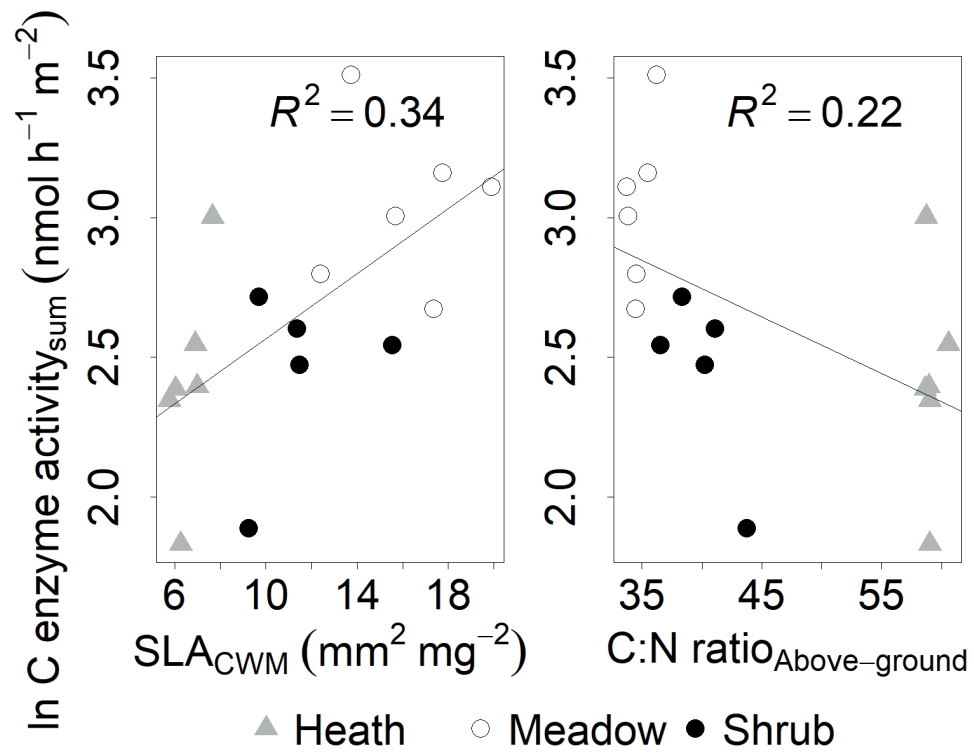
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1 **Figure 3**



2

3 **Figure 4**



4

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Figure Captions:

Figure 1: The hypothesized framework for growing season carbon fluxes: Gross Ecosystem Photosynthesis (GEP) depends on total above-ground biomass ($Biomass_{above}$), community weighted mean of specific leaf area (SLA_{CWM}), and on soil moisture (Hypothesis 1). Above-ground respiration (R_{above}) depends on $Biomass_{above}$ and SLA_{CWM} (Hypothesis 2a). Below-ground respiration (R_{below}) depends on root biomass ($Biomass_{roots}$), microbial activity, and SLA_{CWM} , where SLA_{CWM} in this context represents leaf decomposability (Hypothesis 2b). Microbial activity depends on vegetation woodiness, represented by C:N ratio of above-ground vegetation (C:Nratio above), and on nutrient availability and leaf recalcitrance as represented by SLA_{CWM} (Hypothesis 3). Stippled lines between variables indicate presumable important relationships not tested in this study. The framework is based on Wookey et al. (2009), Clemmensen et al. (2015), Veen, Sundqvist, and Wardle (2015), Parker, Subke, and Wookey (2015), and Becklin, Pallo, and Galen (2012).

Figure 2: Full model variable relationships when plotting one variable, and keeping the others constant by the means. Relationships are across community and within community, based on growing season measurements in an alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway (n = 17). Lines drawn are only for significant variables across (red line) and within community (stippled line), tested with a likelihood-ratio test (Chi-square test) performed on backward model selection (drop1 function in R).

Top (a, b, c): Gross ecosystem photosynthesis standardized to 600 PAR (GEP_{600}) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and the variables community weighted means of specific leaf area (SLA_{CWM}) ($\text{mm}^{-2} \text{mg}^{-1}$), total above-ground biomass ($Biomass_{above}$) (g DW m^{-2}), and soil moisture (%).

Middle (d, e): Above-ground respiration standardized to 20 °C (R_{above}) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and the

variables SLA_{CWM} and $Biomass_{Sabove}$ (g DW m⁻²).

Bottom (f, g, h): Below-ground respiration standardized to 10 °C (R_{below}) and the variables SLA_{CWM} , root biomass (g DW m⁻²), sum of microbial activity (nmol h⁻¹ m⁻²).

Figure 3: Mean enzyme activity \pm SD a) in nmol h⁻¹ m⁻² and b) in μ mol h⁻¹ gC⁻¹ m⁻² for alpine *Empetrum*-dominated heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway. Activity for each enzyme is the sum across the total soil pit with mean depth 56 \pm 8 cm (n = 17). See activities in organic and mineral horizons in figure S2, and statistical differences in Table 6 and Table S2.

Figure 4: Total enzyme activity of b-gluc, cbh and xylo (C enzyme activity_{sum}) (nmol h⁻¹ m⁻²) correlated with “vegetation woodiness” across alpine *Empetrum*-dominated heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway. Left, community weighted mean of SLA ($p = 0.009$) and right, C:N ratio of above-ground vegetation (n= 17).

Figure 5: Summary of hypothesized mechanisms (a, b, c) based on results and (d, e) suggested implications of shrub expansion on growing season summer C fluxes in heath and meadow communities based on measurements in an alpine *Empetrum*-heath, meadow and *Salix*-shrub plant communities in Dovre Mountains, Central Norway. Up-arrows indicate high values (a, b, c) or an increase (d, e). Downward arrows indicate low values (a, b, c) or a decrease in variables due to shrub expansion in the respective community. Red arrows indicate a variable significant in the full model across community, red stippled line indicate variable significant in simple correlation, black arrows indicate a variable significant within community, black stippled lines presumed relationships not tested in this study, and grey arrow variable not significant in full model. The flux arrow width is proportional to its flux size transformed to gC m⁻² h⁻¹. The transparent arrows (d, e) corresponds to the flux in the community invaded by shrubs.

Supplementary Information

Title: Biotic and abiotic drivers of C cycling in three arctic-alpine tundra plant communities:
potential mechanisms

Journal Arctic, Antarctic and Alpine Research

Authors: Mia Vedel Sørensen*, Bente Jessen Graae, Aimee Classen, Brian J. Enquist, Richard
Strimbeck

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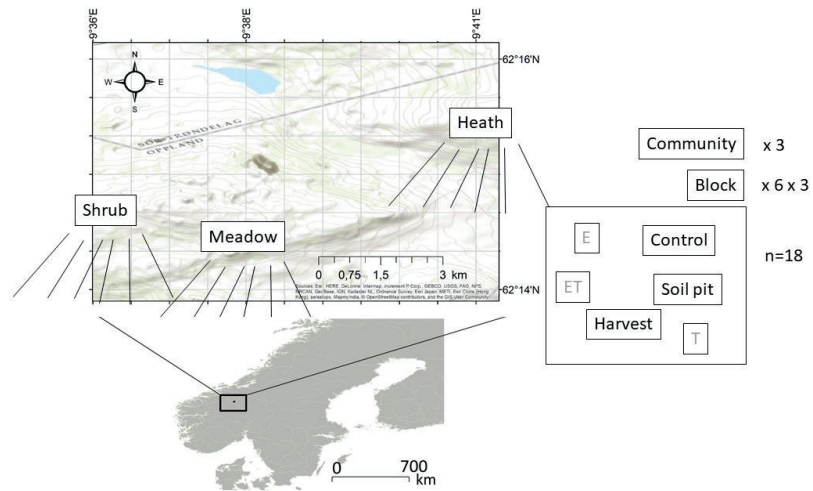
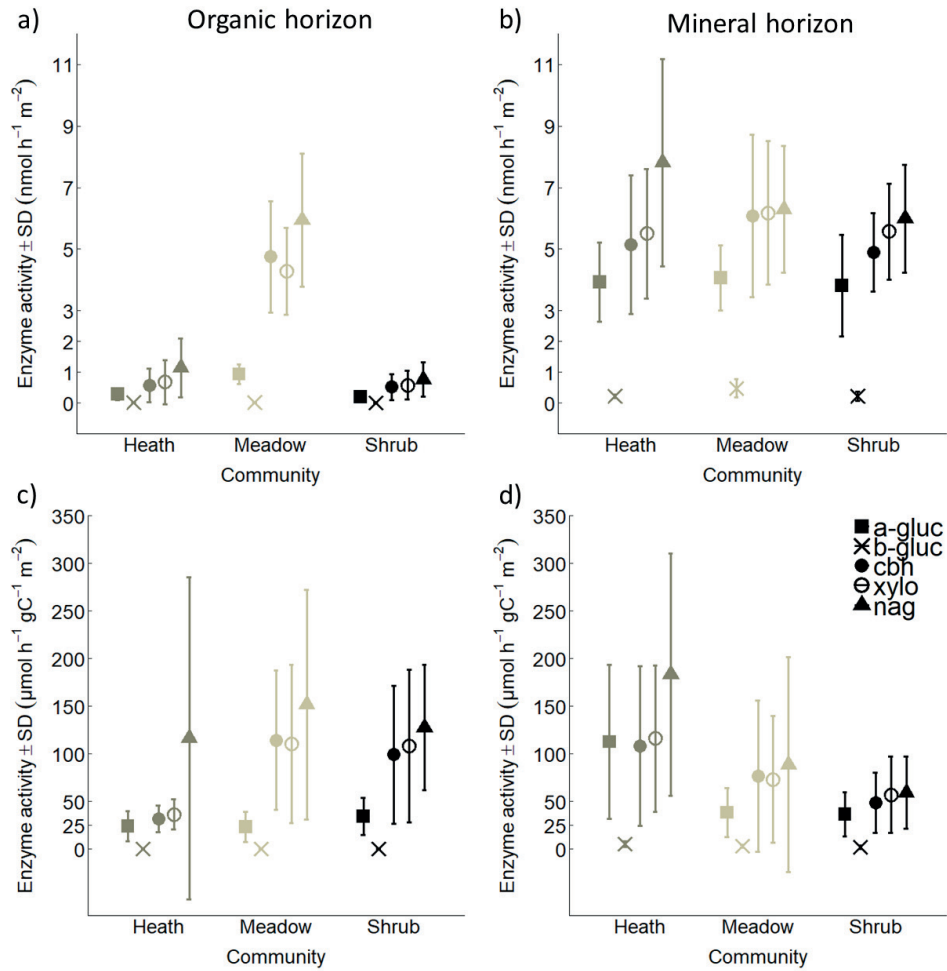


Figure S1: Sampling design and location of study area. In Dovre Mountains, Central Norway, we sampled in six blocks within each of a shrub, meadow and heath community. The sampling design of this study was part of a larger experiment that included herbivore exclusion (E) and willow transplant (T) treatments. Carbon fluxes, microclimate, and leaf traits were measured on control plots, above-ground C to N ratio was measured in harvest plots, and root biomass, microbial activity and pH was measured in samples from a separate soil pit.

Table S1: Effects ($\mu\text{mol m}^{-2} \text{s}^{-1}$) SD^{-1} of each variable in full models within community. Explanatory variables were z-standardized ($(x - \text{mean}(x))/\text{sd}(x)$) so one unit change corresponds to one SD. Models were run without log transformation to ease understanding of the effects. Sum of squares (χ^2) and p -values were derived from a likelihood-ratio test (Chi square test) performed on backward model selection (drop1 function in R). Significant effects are bold.

Response	Heath (n = 6)				Meadow (n = 6)			Shrub (n = 5)		
	Explanatory variable	Effect ($\mu\text{mol m}^{-2} \text{s}^{-1}$) SD^{-1}	SE	$\chi^2(1)$ p-value	Effect ($\mu\text{mol m}^{-2} \text{s}^{-1}$) SD^{-1}	SE	$\chi^2(1)$ p-value	Effect ($\mu\text{mol m}^{-2} \text{s}^{-1}$) SD^{-1}	SE	$\chi^2(1)$ p-value
GEP ₆₀₀	(Intercept)	10.16	6.65		-4.76	21.86		7.98	2.65	
	zSLA _{cwm}	3.32	5.86	1.33 0.345	1.37	3.27	0.99 0.478	5.74	2.28	2.41 0.002
	zMoisture	1.01	3.17	0.42 0.586	6.91	8.95	3.38 0.211	3.49	1.42	2.29 0.002
	zBiomass _{above}	-5.24	5.18	4.24 0.116	-16.23	22.80	2.88 0.244	0.85	1.90	0.08 0.340
R _{above}	(Intercept)	2.25	1.34		1.02	0.64		2.98	0.74	
	zSLA _{cwm}	0.93	1.14	0.11 0.276	0.04	0.11	0.00 0.604	0.70	0.77	0.19 0.190
	zBiomass _{above}	-1.57	0.99	0.43 0.057	0.62	0.62	0.015 0.190	-0.71	0.56	0.38 0.085
R _{below}	(Intercept)	4.17	2.56		6.54	2.06		2.38	0.09	
	zSLA _{cwm}	1.22	2.37	0.06 0.389	-0.16	1.49	0.05 0.853	1.94	0.11	4.28 < 0.001
	zBiomass _{roots}	0.20	0.22	0.18 0.157	0.62	1.23	0.99 0.401	-0.12	0.09	0.03 0.022
	zMicrobe _{sum}	0.10	0.51	0.01 0.742	-1.01	1.05	3.72 0.129	-0.87	0.15	0.48 < 0.001

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4 **Figure S2:** Mean enzyme activity ± SD (a, c) in organic and (b, d) in mineral horizons for
5 alpine *Empetrum*-dominated heath, meadow and *Salix*-shrub plant communities in Dovre
6 Mountains, Central Norway. Activity for each enzyme is the sum across the total soil pit with
7 mean depth 56 ± 8 cm (n = 17). Note different units top: (nmol h⁻¹ m⁻²), and bottom: μmol h⁻¹
8 gC⁻¹ m⁻². Mineral soil is defined as LOI < 20 %. See statistical differences in Table 6 and
9 Table S2.

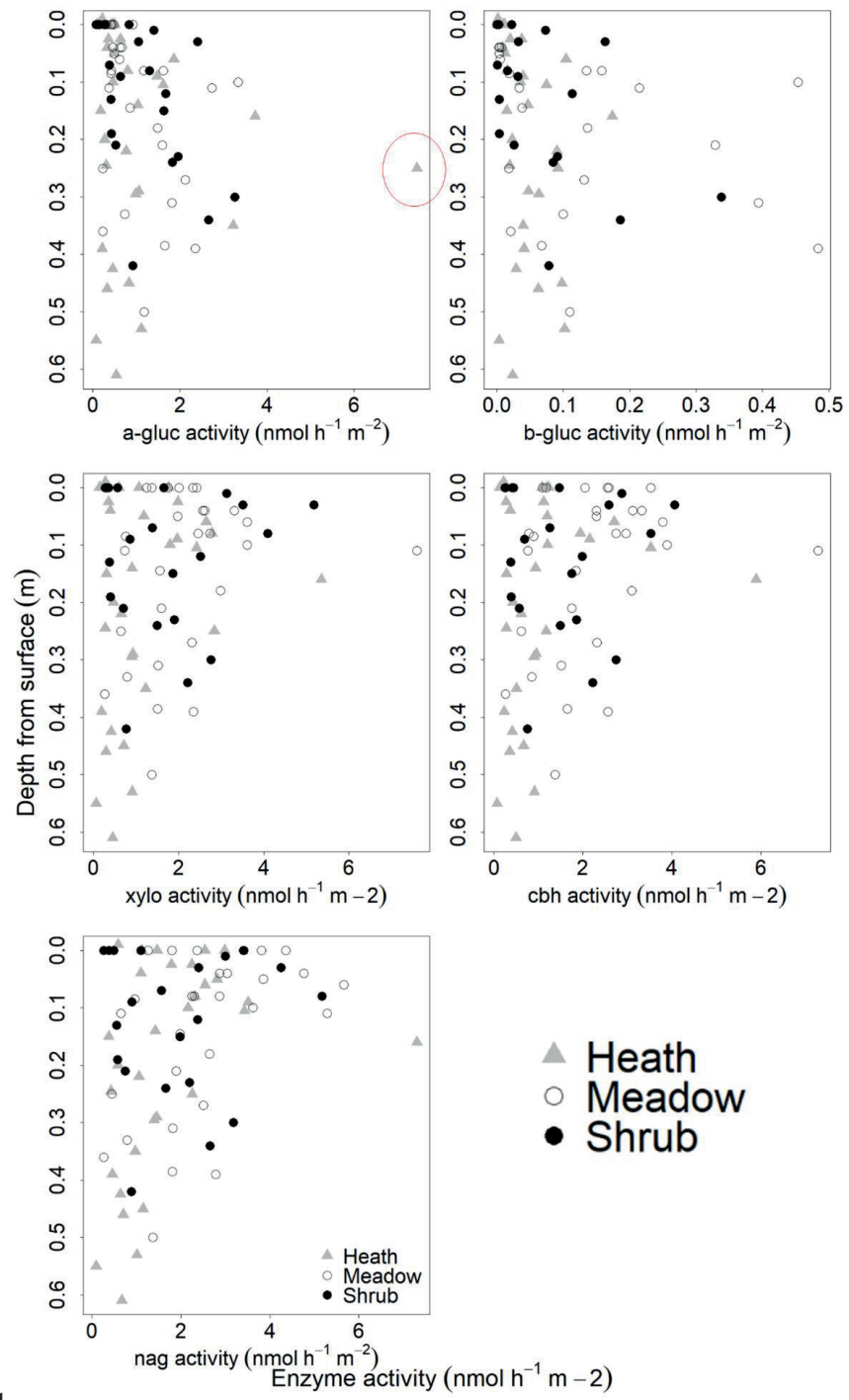
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1 **Table S2:** F-value, degrees of freedom and *p*-value from one-way ANOVA tests of
 2 differences among enzyme activities (nmol h⁻¹ gC⁻¹ m⁻²) between communities. The enzymes
 3 were from organic and mineral horizons, and total across the soil pit. The significant
 4 differences are bold.

Horizon	Enzyme	F-value	df_{num}	df_{den}	<i>p</i>-value
Organic	a-gluc	0.67	2	13	0.53
	b-gluc	0.24	2	13	0.79
	cbh	2.73	2	13	0.10
	xylo	1.94	2	13	0.18
	nag	0.11	2	13	0.89
Mineral	a-gluc	4.36	2	15	0.03
	b-gluc	3.44	2	15	0.06
	cbh	1.12	2	15	0.35
	xylo	1.41	2	15	0.28
	nag	2.49	2	15	0.12
Total	a-gluc	3.99	2	15	0.04
	b-gluc	3.35	2	15	0.06
	cbh	1.43	2	15	0.27
	xylo	0.56	2	15	0.58
	nag	1.23	2	15	0.32

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1 **Figure S4**
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1 **Figure S4:** Enzyme activity ($\text{nmol h}^{-1} \text{m}^2$) sampled over depth from surface (m). In activity
2 of a-gluc, H4 the sample circled out was removed (from block 4 in the heath) since it was
3 driving the pattern in the PCA and because it was inexplicably high. We decided not to
4 remove other outliers, due to the small sample sizes.

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Appendix V



Photo: The heath community early morning September 2014.

Appendix V

Supplementary information for thesis

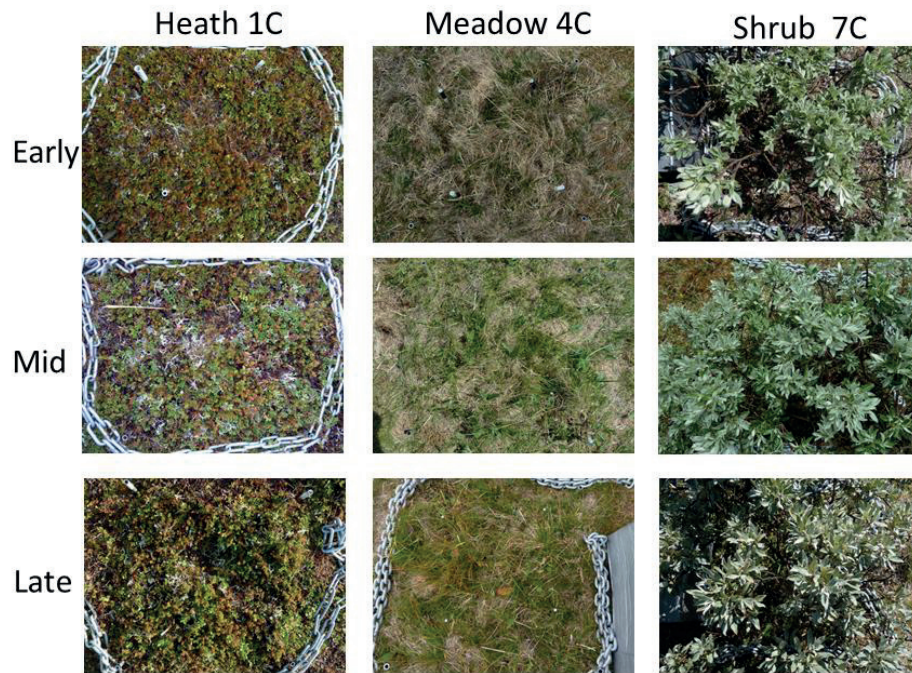


Figure S1: Seasonal phenology during early, mid, and late growing season in 2014 exemplified by one control plot from each community.

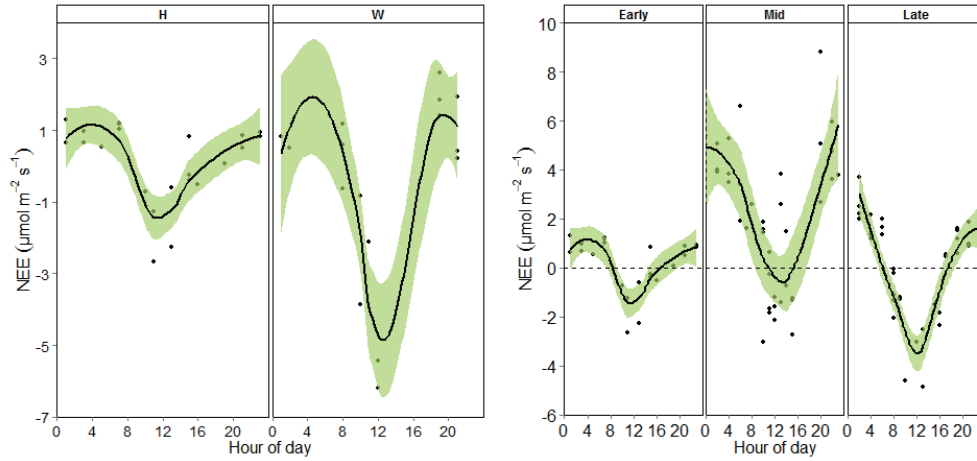


Figure S2: Diurnal measurements of net ecosystem exchange (NEE) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) Left: early growing season measurements in heath (H) (26.-27. June) and willow shrub (W) (2.-3. July) Right: Across the growing season during early, mid, and late growing season in an arctic-alpine heath plant community in central Norway. The green shadow is 75 % confidence interval around the mean, based on a local polynomial regression fit (loess fit). N varies, see details in Table S2-S4.

Table S1: Rieman integral of diurnal NEE measurements, based on a local polynomial regression fit (loess fit).

Growing season	Shrub		Heath	
	Early	Early	Mid	Late
Rieman integral of loess fit ($\text{mgCO}_2 \text{ m}^{-2} \text{ day}^{-1}$)	-0.45	0.13	2.37	-0.42
Rieman integral of loess fit ($\text{mg C m}^{-2} \text{ day}^{-1}$)	-0.12	0.036	0.65	-0.11

Table S2: Replicates Early season diurnal measurements from heath.
Night and day measurements from block 1-4 from 26.-27. June.

Hour	1	3	5	7	10	11	13	15	16	19	21	23
n	2	2	1	3	1	2	2	3	1	1	2	2

Table S3: Replicates Mid growing season diurnal measurements from Heath.
Night measurements from block 1-3, 14. And 15th of July, day measurements from 17., 21., and 24. of July from block 1, 2, 3, 4, 5, 6, 7, 8.

Hour	0	2	4	6	7	8	10	11	12	13	14	15	20	22	23
n	2	3	3	3	1	1	4	4	3	3	2	3	3	3	1

Table S4: replicates from Late growing season diurnal measurements.
Night measurements from 11-12. July block 1-3. Day measurements from 4.th July block 1, 2, 3, 4, 5, 6.

Hour	2	4	6	8	9	10	12	13	15	16	17	19	21	23
n	4	3	3	5	2	2	1	2	1	2	3	4	3	4

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympatric species of newts (<i>Triturus</i> , <i>Amphibia</i>) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i>
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (<i>Trichoptera</i>) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i>
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (<i>Salmo salar</i>): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (<i>Mytilus edulis</i>)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (<i>Salmo salar</i> L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i>
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two workplaces with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (<i>Salmo salar</i>) and brown trout (<i>Salmo trutta</i>): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i>
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (<i>Lynx lynx</i>) in Norway
1991	Jan Henning L'Abée Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods

1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torggrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (<i>Phleum pratense</i> L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O ⁶ -methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (<i>Gallinago media</i>): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i>
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (<i>Rubus idaeus</i> L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers

1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i>
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cuckoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i>
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjörg Einarsdóttir	Dr. scient Zoology	Production of Atlantic salmon (<i>Salmo salar</i>) and Arctic charr (<i>Salvelinus alpinus</i>): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters

1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (<i>Hyllobius abietis</i>), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i>
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (<i>Salvelinus alpinus</i> (L.)) and brown trout (<i>Salmo trutta</i> L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (<i>Salmo salar</i>) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (<i>Alces alces</i>) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach

1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i>
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (<i>Gadus morhua</i> L.) and Halibut (<i>Hippoglossus hippoglossus</i> L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (<i>Micromisistius poutassou</i>), haddock (<i>Melanogrammus aeglefinus</i>) and cod (<i>Gradus morhua</i>) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokuus</i>
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (<i>Salmo salar</i>) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (<i>Salmo salar</i> L.) and Brown trout (<i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (<i>Cuculus canorus</i>) and its host: adaptations and counteradaptations in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (<i>Loxodonta africana</i>)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (<i>Salvelinus alpinus</i>), with emphasis on the high Arctic Diesel charr on Spitsbergen, Svalbard

2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (<i>Salmo trutta</i>) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (<i>Symphodus melops</i> L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (<i>Castor fiber</i>)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A ₂ in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i>
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatus</i> L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (<i>Syncerus caffer</i>) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (<i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i>)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>

2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (<i>Salmo Salar</i> L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (<i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i>)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (<i>Fragaria x ananassa</i>): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelién	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (<i>Halichoerus grypus</i>) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations

2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds, Retinoids and α -tocopherol – potential biomarkers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i>
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (<i>Salmo trutta</i>) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i>
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (<i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography

			Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod (<i>Gadus morhua</i> L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (<i>Struthio camelus massaicus</i>) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (<i>Taeniopygia guttata</i>)
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (<i>Gadus morhua</i>): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	<i>Arabidopsis thaliana</i> Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes

2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches
2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (<i>Panthera leo</i>) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (<i>Rachycentron canadum</i>) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinčov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brønne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (<i>Gobiusculus flavescens</i>)
2011	Ann-Iren Kittang	PhD Biology	<i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity

2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i>
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (<i>Poecilia reticulata</i>): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (<i>Salmo salar</i>): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (<i>Elephas maximus</i>) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in <i>Arabidopsis</i>
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (<i>Mytilus edulis</i>): Feed requirements, storage and integration with salmon (<i>Salmo salar</i>) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (<i>Salmo trutta</i> L) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in <i>Calanus finmarchicus</i>
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect <i>Heliothis virescens</i> .

2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in <i>Emiliania huxleyi</i> Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in <i>Arabidopsis thaliana</i>
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (<i>Salmo salar</i>) farming
2013	Ingrid Ertsbus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in <i>Calanus finmarchicus</i> – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in <i>Arabidopsis thaliana</i>
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom <i>Phaeodactylum tricorutum</i>
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog (<i>Lycaon pictus</i>) habitat selection and ranging behaviour: conservation and management implications

2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (<i>Salmo salar</i> L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose (<i>Alces alces</i>) habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite <i>Syngamus trachea</i> in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (<i>Rissa tridactyla</i>)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms <i>Phaeodactylum tricornutum</i> and <i>Seminavis robusta</i>
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in <i>Arabidopsis thaliana</i>
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (<i>Sphagnum</i>)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (<i>Gadus morhua</i> L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod <i>Calanus finmarchicus</i> in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod <i>Calanus finmarchicus</i>

2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (<i>Gadus morhua</i> L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (<i>Somateria mollissima</i>)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (<i>Giraffa camelopardalis tippelskirchi</i>) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Environmental Mapping and Monitoring: A Methodological approach for endusers.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (<i>Lycaon pictus</i>) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of <i>Tanytarsus van der Wulp, 1874</i> (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (<i>Sphagnum</i>)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on <i>Arabidopsis thaliana</i>
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania