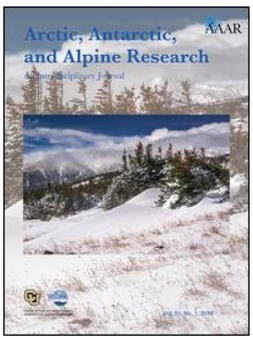

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Drivers of C cycling in three arctic-alpine plant communities

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ABSTRACT

Recent vegetation changes in arctic-alpine tundra ecosystems may affect several ecosystem processes that regulate microbe and soil functions. Such changes can alter ecosystem carbon (C) cycling with positive feedback to the atmosphere if plant C uptake is less than the amount of soil C released. Here, we examine how differences in plant functional traits, microbial activity, and soil processes within and across *Salix*-dominated shrub, dwarf shrub–dominated heath, and herb- and cryptogam-dominated meadow communities influence C cycling. We develop a hypothesized framework based on a priori model selection of variation in daytime growing season gross ecosystem photosynthesis (GEP) and above- and belowground respiration. The fluxes were standardized to light and temperature.

Gross ecosystem photosynthesis was primarily related to soil moisture and secondarily to plant functional traits and aboveground biomass, and belowground respiration was dependent on the community weighted mean of specific leaf area (SLA_{CWM}). Similarly, microbial activity was linked with SLA_{CWM} and was highest in meadows, and carbon-degrading microbial activity decreased with vegetation woodiness. These results suggest that shrub expansion may influence summer C cycling differently depending on plant community, as belowground respiration might increase in the heath and decrease in the meadow communities.

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Gross ecosystem photosynthesis; respiration; shrub expansion; plant functional traits; enzyme activity

Introduction

In response to climate change, fluctuations in herbivory, and human land-use changes, shrub cover is increasing in high-latitude arctic and alpine tundra ecosystems, and the rate of shrub expansion is predicted to increase (Tape, Sturm, and Racine 2006; Post and Pedersen 2008; Tømmervik et al. 2009; Ravolainen et al. 2011; Speed et al. 2013; Settele et al. 2014; Epstein et al. 2015; Myers-Smith et al. 2015; Martin et al. 2017; Normand et al. 2017). It is unclear how shrub expansion will affect the carbon balance of these ecosystems (Virkkala et al. 2017). While high-latitude tundra ecosystem soils currently store more than half of global soil carbon (C; Tarnocai et al. 2009), these systems are predicted to be highly sensitive to climate warming, with the potential for some of the greatest C losses globally (Crowther et al. 2016). Plant-microbial-soil feedbacks regulate soil C (Wardle et al. 2004; De Deyn, Cornelissen, and Bardgett 2008). If shrub expansion leads to more soil C release than plant C uptake, these vegetation changes may alter ecosystem C cycling with potential positive feedback to the atmosphere (Wilmking, Harden, and Tape 2006; Cahoon et al. 2012; Parker, Subke, and Wookey 2015). Understanding the response of C cycling to climate and vegetation changes requires unraveling the influence of plants, microbes, and soil processes on C cycling (Bardgett 2011), and these links are largely unknown in tundra ecosystems (Myers-Smith et al. 2011).

Arctic and alpine tundra vegetation is a mosaic of plant communities created by variations in microclimate (snow depth, moisture, temperature) and underlying bedrock types that form major gradients in soil pH and soil nutrient availability (Sonesson, Wielgolaski, and Kallio 1975; Eskelinen, Stark, and Männistö 2009; Sundqvist et al. 2011). Dwarf shrub–dominated heath and herb-dominated meadow are two common tundra communities that are subject

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Supplementary data for this article can be accessed here.

to shrub expansion via both colonization and increased canopy dominance (Molau and Alatalo 1998; Björk and Molau 2007; Cannone, Sgorbati, and Guglielmin 2007). In a previous study on alpine tundra vegetation, we found that the soil C stocks in meadow and heath communities were much larger than in a *Salix* shrub community, even though gross ecosystem photosynthesis (GEP) was similar in the meadow and shrub communities (Sørensen et al. 2017).

The balance between the competing processes of photosynthesis and total respiration will determine if an ecosystem is a net carbon absorber or emitter. Net ecosystem exchange of CO_2 can be divided into three dynamic processes: GEP, aboveground respiration, and belowground respiration. All of these may be affected by the changes in plant and soil microbial community composition associated with shrub expansion via effects on both the abiotic environment and biotic processes.

Photosynthesis is carried out by vascular plant leaves and cryptogam thalli. Shrub expansion involves increases in leaf biomass and is generally expected to increase primary production (Gould, Raynolds, and Walker 2003; Wookey et al. 2009; Cahoon et al. 2012; Sørensen et al. 2017; Michaletz, Kerkhoff, and Enquist 2018). Photosynthetic rate may be directly affected by air temperature and soil moisture (Körner 2003; Berdanier and Klein 2011), which may in turn be affected by changes in community composition via effects on albedo, evapotranspiration, winter snow accumulation, and spring and summer snowmelt (Sturm et al. 2001; Grogan and Jonasson 2006; Myers-Smith and Hik 2013). Photosynthetic rates in leaves are tightly linked to leaf traits, including specific leaf area (SLA) and leaf nitrogen (N) content according to the well-documented leaf economic spectrum (Wright et al. 2004). These traits vary among the main functional groups in arctic-alpine ecosystems, with deciduous leaves and graminoids generally having higher rates of photosynthesis, SLA, and leaf nitrogen as compared to evergreen dwarf shrub leaves. The overall trait composition of a community can be summarized using community weighted means (CWM) of the various leaf traits (Grime 1998; Lavorel and Garnier 2002; Garnier et al. 2004; Lavorel 2012; Enquist et al. 2015; Garnier, Navas, and Grigulis 2016). Increasing dominance of deciduous shrubs might shift leaf trait CWMs toward higher photosynthetic rates. Soil nutrient availability and dynamics, discussed further on, may also affect aboveground productivity by affecting the availability of N or other nutrients for the production of leaves and their photosynthetic machinery.

All aboveground plant parts respire, including living cells in wood and bark, so that aboveground respiration depends on the aboveground biomass of both leaves and herbaceous and woody stems, which increase during shrub expansion. Respiration rates are directly affected by temperature, which is affected by community composition as noted earlier. Rates of respiration in leaves also vary in concert with leaf economic traits (Wright et al. 2004).

Because most of the carbon in arctic-alpine systems is stored belowground as soil organic matter that may either accumulate or decompose, belowground respiration is a critical component of overall gas exchange. In principle, belowground respiration can be further divided into plant root and microbial respiration, but given the tight coupling of roots and soil microflora independent measurement of these two sources is difficult if not impossible to achieve in practice. Changes in aboveground plant community composition may be accompanied by changes in litter quality, temperature, soil moisture, and soil pH and aeration, all of which may affect respiration more or less directly or via changes in soil microflora (Schinner 1983; Sinsabaugh, Moorhead, and Linkins 1994; Illeris, Michelsen, and Jonasson 2003; De Deyn, Cornelissen, and Bardgett 2008; Karhu et al. 2014). In comparison to other ecosystems, tundra ecosystems are nutrient poor, and heath vegetation in particular is more nutrient poor than meadow vegetation (Makarov et al. 2003; Björk and Molau 2007). The dominant plants in heath, meadow, and deciduous shrub communities associate with ericoid (ERM), arbuscular-vesicular (AM), and ectomycorrhiza (ECM), respectively (Väre, Vestberg, and Eurola 1992; Michelsen et al. 1998; Becklin and Galen 2009). These different mycorrhizal types may differ in biomass, respiration rates, and nutrient delivery to plant roots, affecting primarily belowground respiration and secondarily the aboveground gas-exchange processes. Recent studies suggest that ECM contribute to the loss of soil C from ecosystems by acting as decomposers, especially in arctic and boreal systems (Talbot, Allison, and Treseder 2008; Lindahl and Tunlid 2015). It is reasonable to expect shifts in soil microbial communities during shrub expansion as well. Relative soil microbial activity can be assessed by measuring the activities of extracellular enzymes in soil samples (Hernández and Hobbie 2010).

The aim of this study was to explore how plant functional traits, microbial activity, and abiotic properties affect C cycling (Figure 1). We measured daytime growing-season ecosystem respiration (ER) and GEP in

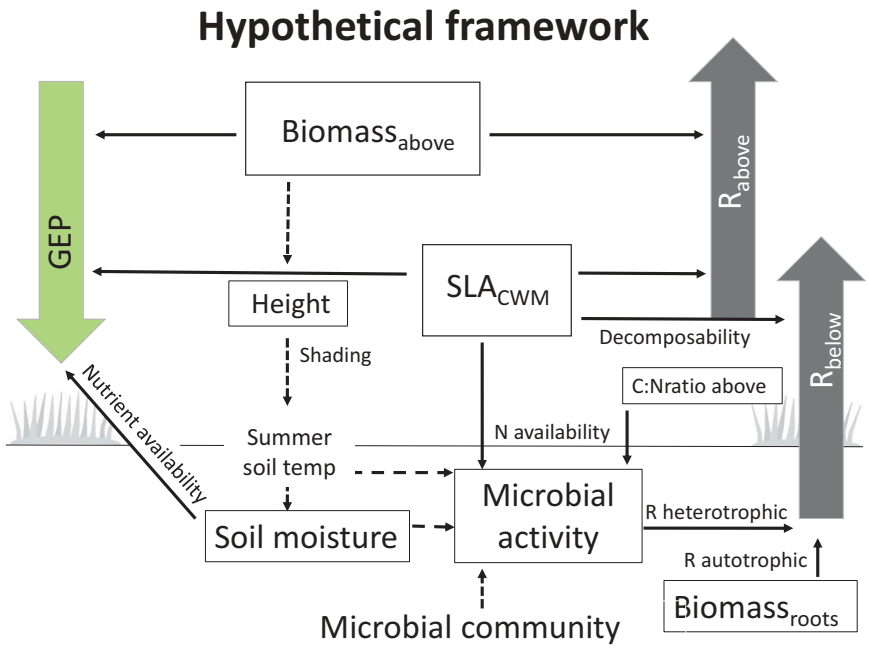

Figure 1. Hypothesized framework for growing-season C fluxes: gross ecosystem photosynthesis depends on total aboveground biomass ($Biomass_{above}$), community-weighted mean of specific leaf area (SLA_{CWM}), and soil moisture (Hypothesis 1). Aboveground respiration (R_{above}) depends on $Biomass_{above}$ and SLA_{CWM} (Hypothesis 2a). Belowground 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 the C:N ratio of aboveground vegetation (C:Nratio above), and on nutrient availability and leaf recalcitrance as represented by SLA_{CWM} (Hypothesis 3). Dashed lines between variables indicate 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).

a *Salix*-dominated shrub community, a dwarf shrub–dominated heath, and an herb-, bryophyte-, and lichen-dominated meadow in central Norway, and hypothesized (see Figure 1) that:

Hypothesis 1: GEP across communities is primarily controlled by the community-weighted mean of SLA (SLA_{CWM}), total aboveground biomass ($Biomass_{above}$), and soil moisture with SLA_{CWM} being the strongest driver.

Hypothesis 2: (a) The aboveground component of ER is influenced by SLA_{CWM} and $Biomass_{above}$ with $Biomass_{above}$ having the greatest effect. (b) Belowground respiration is controlled by root biomass ($Biomass_{roots}$), microbial activity, and SLA_{CWM}. We expect microbial activity to be the strongest driver in the meadow and SLA_{CWM} to be the strongest driver in the heath and shrub communities.

Hypothesis 3: Carbon-degrading microbial activity related to cellulose and lignin degradation decreases with vegetation woodiness, represented by C:N ratio of aboveground vegetation, and decreases with leaf recalcitrance, represented by SLA_{CWM}.

Materials and methods

Study area and sampling design

The field sites were located above the forest line in the low-alpine vegetation zone approximately 1,100 m a.s.l. in Dovrefjell, central Norway (62°N, 9°E) in an *Empetrum*-dominated heath; an herb-, bryophyte-, and lichen-dominated meadow; and a *Salix*-dominated shrub community (Figure S1). The climate in the area is continental (Moen 1998), with annual and summer mean temperatures of −1°C and 7.1°C and 700 mm and 298 mm of precipitation for the period from 1960 to 1990 (New, Hulme, and Jones 2000). In 2015, the annual and growing-season mean temperatures were 1.58°C and 8.15°C, respectively, and the total precipitation for the same periods was 667 mm and 265 mm at the closest weather station at Hjerkinn, 1,012 m a.s.l. (Norwegian Meteorological Institute, eklima.met.no). Large areas of homogeneous vegetation were chosen for each community and therefore situated on different but neighboring mountain slopes, while keeping variation in other abiotic variables to a minimum; that is, aspect and slope. The three communities differed in the surrounding

topography, as the heath was more wind exposed and the meadow and shrub communities were more sheltered, presumably influencing the vegetation composition (Table 1). For a more detailed list of dominant species see Table S1 in Sørensen et al. (2017).

Soils were podzolic in all sites, with a partial albic horizon in the shrub community and a well-developed albic horizon in the heath (Sjögersten and Wookey 2009). Soils were developed from ground moraine over metavolcanic rock in the heath and shrub community and shale in the meadow (NGU 2015).

The sampling design of this study was part of a larger experiment with four different treatments in each of eight blocks for each community (Sørensen et al. 2018; Figure S1). In the present study, six replicate blocks from each community were randomly selected for measurements. The average distance among blocks within community was 23.0 m in the shrub community, 21.7 m in the meadow community, and 28.1 m in the heath community. Across communities the average distance ±SD between neighboring plots was 24.4 ± 3.4 m.

In each block, C fluxes, microclimate, and leaf traits were measured on 0.5 × 0.5 m plots and aboveground biomass was harvested for chemical analysis in neighboring harvest plots, measuring 0.25 × 0.25 m in the heath and meadow communities and 0.5 × 0.5 m in the shrub community, to capture the heterogeneity of woody biomass in the latter. Additionally, the belowground properties microbial activity, root biomass, pH, and soil C:N ratios were measured in a soil pit in early September 2015 (details further on). Six blocks were studied in the meadow and heath communities, whereas only five blocks where included in the shrub community because of logistics, resulting in a total of seventeen across the three communities.

Table 1. Community means ± SD for alpine *Empetrum*-dominated heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, central Norway.

Community	Heath	SD	Meadow	SD	Shrub	SD
Three most dominant species	*Arctostaphylus uva-ursi* (L.) Spreng. *Empetrum nigrum hermaphroditum* L. *Festuca ovina* L.		*Avenella flexousa* (L.) Drejer *Festuca ovina* L. *Anthoxanthum nipponicum* Honda		*Avenella flexousa* (L.) Drejer *Salix lapponum* L. *Salix glauca* 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
$LDMC_{CWM}$ (mg g^{-1})	462.19	± 14.04	345.62	± 23.17	378.65	± 33.06
LA_{CWM} (mm^2)	37.67	± 7.25	196.23	± 67.62	268.18	± 131.88
Hyphal ingrowth (mg g^{-1})	0.022	± 0.031	-		0.028	± 0.053

Note. The three most dominant species within each community are based on total number of hits in each community, recorded on each plot with the point intercept method 25 × 25 cm quadrat and twenty-five pins (n = 96). Snow depth is maximum depth across March 2015 and April 2016 (n = 17). Soil moisture was measured on June 10 in the shrub and June 11 in the meadow and heath communities, and it was also measured on July 21 in the heath, July 22 in the shrub, and July 23 in the meadow. Soil moisture was measured on September 28 in all three communities (n = 17). Temperature inside the CO_2 chamber (T_{air}), surface temperature ($T_{surface}$), and soil temperature (T_{soil}) was obtained during CO_2 measurements. Summer $T_{surface}$ is surface temperature across the warmest months, July and August 2015, and winter $T_{surface}$ is across the coldest months, January and February 2015 (n = 24). Growing degree hours are the sum of hours where surface temperature was greater than 5°C (sensu Graae et al. 2012; n = 24). Minimum pH, soil organic carbon, and soil total nitrogen was from throughout the full soil pit with a mean depth of 56 ± 8 cm (n = 17). Amount of aboveground vegetation of total vegetation biomass is reflected in proportion of vegetation carbon above- and belowground (n = 17). Community-weighted means of specific leaf area (SLA_{CWM}), leaf dry matter content ($LDMC_{CWM}$), and leaf area (LA_{CWM}; n = 17). Hyphal ingrowth (mg g^{-1}) was for 5 × 3.5 cm sand bags made of 50 µm nylon with placed in each community (n = 24).

Flux measurements and microclimate

In mid-growing season in 2015, on sunny days only, CO_2 flux was measured in a closed system composed of a collapsible 0.5 m × 0.5 m × 0.6 m (L × W × H) polyethylene chamber and a LI-840A CO_2/H_2O infrared gas analyzer (LI-COR Inc., Lincoln, NE, USA). The chamber was sealed with a canvas skirt along the base of the tent, which was covered with a 5 m long chain weighing 5 kg, and four fans mixed the air inside the chamber for 30 s prior to and during each measurement. The CO_2 concentration was recorded every second throughout a 120 s light measurement followed by a 120 s dark measurement, so that in total the chamber remained on each plot for 240 s. From the light measurement net ecosystem exchange (NEE) was determined, and from the dark measurements ER was determined.

We corrected the CO_2 concentration for water content (C′) and then used linear regression to find the CO_2 flux (Jasoni, Smith, and Arnone 2005).

$$C' = \frac{[CO_2](\mu mol\, mol^{-1})}{[H_2O](mmol\, mol^{-1})}$$

$$CO_2 flux = \frac{VP}{RT_{air}S}\frac{d'C}{dt}$$

Where V = volume chamber (m^2), P = air pressure (kPa; estimated to be 90 kPa at our sites at 1,100 m elevation), R = the ideal gas constant (8.314 J mol −1 K^{-1}), T_{air} = average air temperature (°C) during the measurement, S = surface area (m^2), $d'C/dt$ = the slope of linear regression of C' on time. Gross ecosystem photosynthesis was calculated by subtracting ER from NEE. We performed light-curve measurements one time on all plots. One light-curve measurement consisted of one measurement in full light, measurements at three increasing levels of shading, and one measurement in full darkness (Williams et al. 2006; Street et al. 2007). There was a gap of at least 30 s between each measurement period. The shading was done with three layers of black tulle. For dark measurements, we used an opaque hood to block out the light (Street et al. 2007). In the period from July 16 to August 20, we measured NEE and ER from one to two times per plot on fourteen different days, and light-curve measurements were done once per plot on eight different days. We found no statistical difference between normal GEP and GEP standardized to 600 μmol m^2 s^{-1} based on the light-curve measurements (Sørensen et al. 2017), and we used the standardized estimates based on the light-curve measurements in the final data set.

For more details on the flux measurement methods see Sørensen et al. (2017).

During all flux measurements, we measured light (PAR, μmol m^2 s^{-1}) with a LI-190S quantum sensor (LI-COR Inc., Lincoln, NE, USA), air temperature with PT100 sensors inside (at 40 cm height) and outside the chamber (at 60 cm), soil temperature at 8 cm depth (digital dial thermometer, Traceable® Ultra™, VWR International), and soil moisture at 5 cm depth with a TRIME-PICO32 sensor (IMKO, Germany). Additionally, soil moisture was measured in early, mid-, and late-growing season. Surface temperature (at 1 cm depth) was recorded every four hours with temperature sensors (iButtons, Maxim Integrated Products, Sunnyvale, CA, USA). The surface temperatures during the flux measurements were estimated by interpolation. Snow depth was measured four times per plot with an avalanche probe in March 2015 and April 2016; if marking sticks were not visible, plots were located by a handheld GPS receiver (3 m precision).

Above- and belowground respiration

To separate ER into above- and belowground respiration, we identified the specific fractions of above- and belowground respiration with CO_2 flux measurements before and after harvest of biomass in harvest plots as described in Strimbeck et al. (2019). The measurements were performed on six plots in each community during nine different days between July 17 and August 13. To minimize flux because of additional root decomposition, we tried to complete the harvest in four or six hours, and measured soil respiration immediately after removing the last layer. On five plots, however, measurements were interrupted by one or two days because of unpredictable weather conditions. The same measurement equipment as described earlier was used, except that a smaller plexiglas chamber (0.25 m × 0.25 m × 0.3 m) was used in the heath and meadow communities. A rubber skirt was attached to the base of the chamber and it was sealed by the chain. A sampling tube, a return tube, and a PT100 sensor to measure air were placed 0.2 m above the soil surface. After initial measurements, the vegetation was harvested sequentially by functional group with a knife or scissor. Bryophytes and lichens were cut at the soil surface and the litter was removed last, leaving the bare soil surface. The CO_2 fluxes were measured after the removal of each layer. There was little difference in ER or NEE before and after removal of the litter layer (or in light and dark), so a mean of the four measurements was used as a robust estimate of belowground

respiration. The aboveground respiration was found by subtracting belowground respiration from ecosystem respiration before harvest. Because of differences in temperature during the day, respiration was standardized to temperature following the same method as described further on. The specific ratios of above- and belowground respiration were then identified based on means across community. For more details see Strimbeck et al. (2019).

Aboveground plant traits

Leaf traits

Samples for SLA and leaf dry matter content (LDMC) of the dominant vascular species were collected in each block outside of the experimental plots in each plant community during the peak growing seasons of 2013, 2014, and 2016. Dominant species were those that collectively made up 80 percent of cumulative relative abundance in each plant community (Pérez-Harguindeguy et al. 2013), based on vegetation analysis performed in 2013. Between three and twenty leaves per species from two individuals per block were sampled. Leaves (on twigs when possible) were placed in plastic bags with moist paper towels and stored at 4° C (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Fresh leaves, including petioles, were weighed to ±0.1 mg, scanned at 600 dpi, and the area was measured with Image J software (National Institutes of Health, Bethesda, MD, USA). The leaves were then oven dried at 70°C for 72 h and weighed again (Cornelissen et al. 2003).

Community weighted means were calculated (Garnier et al. 2004; Violle et al. 2007) for SLA (SLA_{CWM}) and LDMC ($LDMC_{CWM}$) for each plot in each community, based on the mean trait value per species per block in each community and the relative abundance in the plots. The relative abundances of species were recorded with the point intercept method (Goodall 1952) in July 2015 during mid-growing season with a 25 × 25 cm quadrat and twenty-five pins.

Aboveground biomass harvest

Aboveground biomass ($Biomass_{above}$) was destructively sampled from harvest plots during the mid-growing season in July 2015. All plant material was oven dried at 70°C for 72 h before weighing to ±0.001 g. Leaves were separated from the woody stem for deciduous and evergreen shrubs. Aboveground plant and litter C and N pools (g C m^{-2}) were estimated by multiplying the oven-dry weight (g) by the average C and N concentration (mg^{-1} g) per functional group. The C concentration per functional group was determined from plant material harvested in an earlier study in 2013 from the same sites (see appendix 2 in Sørensen et al. 2017).

Belowground properties

Each soil pit was dug to bedrock or the BC horizon. The mean total depth of the soil pits was 56 ± 8 cm and ranged from 42 cm to 70 cm. Duplicate soil samples were extracted from each horizon, identified by color and texture. Each sample was extracted for a defined volume (5 × 5 × 5 cm) using a knife. The duplicate samples were analyzed in two different laboratory locations. One sample was used for measurements of microbial activity, root biomass, and soil pH and the other was used to determine soil and root C and N content. The samples were stored at 4°C for a maximum of five days before being processed.

Root biomass, carbon, and nitrogen

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

Soil properties

To determine total soil C and N content, soils were oven dried at 60°C for 48 h. Roots and stones (>2 mm) were removed by sieving the soil. 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 and N concentrations via elemental combustion (ECS 4100, Costech). Average LOI per horizon (FractionLOI (%)) was significantly correlated with bulked soil C concentration—C concentration (%): C concentration (%) = 0.44 × FractionLOI (%) – 0.26, $p < 0.0001$, $R^2 = 0.92$, $n = 74$). This relationship between FractionLOI (%) and C concentration (%) was used to calculate 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 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 on a threshold of 80 percent LOI for organic soils (Hodgson 1997). Soil pH was measured using 0.01 M $CaCl_2$ in a 1:3 soil-to-solution mixture for each soil horizon in each soil pit.

Microbial activity

We assessed the activity of the soil community 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 in all of the soil pits. Enzymes that are important in C degradation (a-gluc, b-gluc, cbh, and xylo) break down carbohydrates and polysaccharides and nag mineralizes nitrogen from chitin (Read and Perez-Moreno 2003; Bell et al. 2013).

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

Hyphal ingrowth

Mycorrhizal ingrowth bags (5 × 3.5 cm, 50 µm nylon to allow hyphal ingrowth but too fine for plant roots) were buried 2–11 cm below the soil surface between the organic and mineral soil horizon for thirteen weeks from mid-June to September in each block in the three communities. Each bag contained approximately 30 g autoclaved quartz sand (Moore et al. 2015). Hyphal biomass was measured by extracting hyphae from the ingrowth bags within two weeks after collection, using standard floating techniques (Wallander, Göransson, and Rosengren 2004). The extracted hyphae were freeze dried at −20°C prior to weighing (Moore et al. 2015) and the biomass was reported as mg of hyphal biomass per g sand (Wallander, Göransson, and Rosengren 2004). These data were insufficient for analysis because there was poor ingrowth in some plots, but the results are reported in Table 1 as background data.

Data analysis

Flux analysis

Ecosystem respiration was separated into aboveground (R_{above}) and belowground respiration (R_{below}) based on the sequential harvest measurements decribed earlier. Because we know from earlier studies that shrub expansion has an effect on canopy and soil temperature (Sturm et al. 2005; Myers-Smith and Hik 2013; Sørensen et al. 2017) and to limit the number of factors in statistical models (a result of the few data points), we standardized ER to a specific temperature (ER_{temp}) using Q10 = 2 (Tjoelker, Oleksyn, and Reich 2001). Aboveground respiration was standardized to 20°C (R_{above}), corresponding to mean air temperature inside the chamber during flux measurements (T_{air}), whereas belowground respiration was standardized to 10°C (R_{below}), corresponding to mean soil temperature at 8 cm depth during the measurements (T_{soil}).

$$ER_{temp} = R_{above} + R_{below}$$

$$R_{above20} = fabove_{community} ERQ10^{\left(\frac{20-Tair}{10}\right)}$$

$$R_{below10} = fbelow_{community} ERQ10^{\left(\frac{10-T_{soil}}{10}\right)}$$

The above- and belowground components of ER were estimated using the mean ratio of above- and belowground respiration for each community ($fabove_{community}$ and $fbelow_{community}$; Strimbeck et al. 2019). To standardize GEP to a photosynthetically active radiation (PAR) of 600 (µmol $m^{-2}s^{-1}$; GEP_{600}), we used light-response curves for each plot, derived using the nls functions in R (R Core Team 2017):

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

Where GEP = ER_{temp} − NEE, I = incident PAR (µmol $m^{-2}s^{-1}$), 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}. We tried with different values of P_{max}, and chose the one with the best fit according to the observed data and to the p value for P_{max}. Even though GEP_{600} was not significantly different from nonstandardized GEP measurements (Sørensen et al. 2017), we chose to use GEP_{600} to reduce the variance between the plots.

Hypothesis testing

To test the hypothesized framework of ecosystem controls of C fluxes, we used multiple linear models with *z*-standardized variables (x – mean (x))/sd (x). Variables included in the final full models followed the a priori models described in Hypotheses 1–3: SLA_{CWM}, $Biomass_{above}$, soil moisture, $Biomass_{roots}$, and $Microbes_{sum}$. Variables excluded because of collinearity (following Alain et al. 2010) were $LDMC_{CWM}$ and Community type. The flux data were ln-transformed to meet model assumptions. We used backward model selection (drop1 function in R) to identify the significance of each predictor variable. Additionally, we used exhaustive model selection on the a priori models (Burnham and Anderson 2002), with AICc as the selection criterion (glmulti package and MuMIn package; Grueber et al. 2011). We visualized the different ecosystem controls across and within the three communities by keeping two variables constant by their means and plotting the third variable against the C fluxes.

Because of limited degrees of freedom, we did not test interaction effects in the model selection.

To test if microbial activity beneath woody vegetation differed from that in non-woody vegetation (the meadow) we summed up the activity of enzymes degrading recalcitrant litter (b-gluc, cbh, xylo). The activity of those C-degrading enzymes was tested for correlation with C:N ratios of total ecosystem, aboveground vegetation, soil, and roots and SLA_{CWM}, respectively. We used one-way ANOVAs to test for community differences in microbial activity, and tested significance using multiple comparisons with a Tukey's honest significant difference test ($p < 0.05$).

The enzyme activities were estimated per m^2, but to test if any were driven by the content of C in the soil, we also converted the enzyme activity to per g soil C per m^2 (Stone, DeForest, and Plante 2014). There were some outliers in the enzyme data, which we decided to keep because of the small sample size, except for one, agluc H4_P1B1 (Figure S4).

All analyses were performed in the R programing environment (R Core Team 2017).

Results

Soil moisture had the greatest effect on gross ecosystem photosynthesis

Soil moisture had the greatest effect and was the only significant predictor of GEP across community (Table 2 and Figure 2C). $Biomass_{above}$ and SLA_{CWM} had less effect on GEP but made strong contributions to the explanation of variance (Table 3). The model with the lowest AICc contained only soil moisture and $Biomass_{above}$ and explained 52 percent of the variance, whereas the full model containing all three variables SLA_{CWM}, moisture, and $Biomass_{above}$ explained slightly more variation (R^2 = 0.55; Table 3).

Within communities, models were overall very poor, with high uncertainty because of the few data points. Soil moisture and SLA_{CWM} were significant predictors in the shrub community only (Figure 2A–C, Table S1).

Table 2. Effects (μmol m^{-2} s^{-1}) $SD^{-1}$of each variable in full models across community. Explanatory variables were *z*-standardized (x – mean(x))/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 (μmol m^{-2} 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

Aboveground biomass was the best predictor of aboveground respiration

Aboveground respiration (R_{above}) was highest in the shrub community, intermediate in the heath community, and lowest in the meadow community (Figure 2D–E). $Biomass_{above}$ had the greatest effect on R_{above}, but was nonsignificant in backwards model selection (Table 2). $Biomass_{above}$ alone constituted the best model with lowest AICc, explaining 32 percent of the variance. The full model with both $Biomass_{above}$ and SLA_{CWM} was second best and explained slightly more (R^2 = 0.36; Table 4). The effect of SLA_{cwm} on R_{above} across the community was nonsignificant (Table 2 and Figure 2D).

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

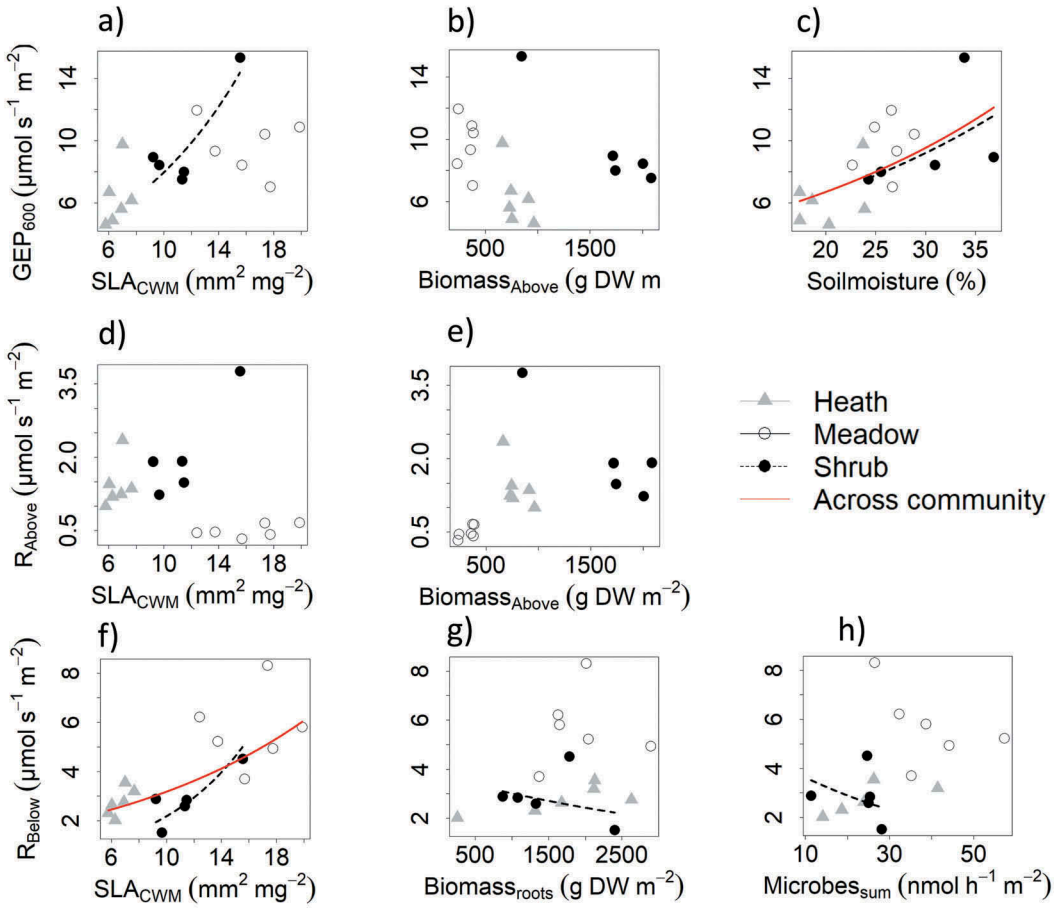

Figure 2. Full model variable relationships when plotting one variable and keeping the others constant. Relationships are across community and within community, based on growing-season measurements in alpine *Empetrum*-heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, central Norway (n = 17). Lines drawn are for significant variables across (red) and within community (black dashed line), tested with a likelihood-ratio test (Chi-square test) performed on backward model selection (drop1 function in R). Top (A–C): Gross ecosystem photosynthesis standardized to 600 PAR (GEP_{600}; µmol m^{-2} s^{-1}) and the variables community-weighted means of specific leaf area (SLA_{CWM}; mm^{-2} mg^{-1}), total aboveground biomass ($Biomas_{above}$; g DW m^{-2}), and soil moisture (%). Middle (D,E): Estimated aboveground respiration standardized to 20°C (R_{above}; µmol m^{-2} s^{-1}) and the variables SLA_{CWM} and $Biomass_{above}$ (g DW m^{-2}). Bottom (F–H): Estimated belowground respiration standardized to 10°C (R_{below}) and the variables SLA_{CWM}, root biomass ($Biomass_{roots}$; g DW m^{-2}), sum of all measured microbial activity ($Microbes_{sum}$; nmol h^{-1} m^{-2}). Biomass $_{roots}$ and $Microbes_{sum}$ was summed across the total soil pit with mean depth 56 ± 8 cm.

Table 3. Gross ecosystem photosynthesis model selection based on AICc on multiple linear models, testing Hypothesis 1. GEP was standardized to 600 PAR (GEP_{600}) and log-transformed. Soil moisture (%), specific leaf area (SLA_{CWM}; mm^{-2} mg^{-1}), and aboveground 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. R^2 adjusted was 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	$ln(GEP_{600}) \sim 1 + zBiomass_{above} + zMoisture$	2.24	NA	−0.12	0.42	4	3.19	4.95	0	0.68	0.52
m2	$ln(GEP_{600}) \sim 1 + zSLA_{CWM} + zBiomass_{above} + zMoisture$	2.21	0.09	−0.07	0.32	5	4.36	6.73	1.79	0.28	0.55
m3	$ln(GEP_{600}) \sim 1 + zSLA_{CWM} + zBiomass_{above}$	2.1	0.2	0.03	NA	4	0.46	10.41	5.47	0.04	0.33
m4	$ln(GEP_{600}) \sim 1 + zBiomass_{above}$	2.09	NA	−0.05	NA	3	−3.92	15.69	10.74	0	−0.04
m5	$ln(GEP_{600}) \sim 1 + zMoisture$	2.12	NA	NA	0.14	3	−8.25	23.83	18.88	0	0.09
m6	$ln(GEP_{600}) \sim 1 + zSLA_{CWM} + zMoisture$	2.11	0.07	NA	0.12	4	−7.83	26	21.06	0	0.08
m7	$ln(GEP_{600}) \sim 1 + zSLA_{CWM}$	2.06	0.16	NA	NA	3	−10.88	28.95	24.01	0	0.1
m8	$ln(GEP_{600}) \sim 1$	2.06	NA	NA	NA	2	−12.67	29.92	24.97	0	0

Table 4. Aboveground 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}; mm^{-2} mg^{-1}) and aboveground 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. R^2 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	$ln(R_{above}) \sim 1 + zBiomass_{above}$	0.05	NA	0.41	3	−13.08	34.01	0	0.55	0.32
m2	$ln(R_{above}) \sim 1 + zSLA_{CWM} + zBiomass_{above}$	0.04	−0.19	0.33	4	−11.96	35.25	1.24	0.29	0.36
m3	$ln(R_{above}) \sim 1 + zSLA_{CWM}$	0.04	−0.31	NA	3	−14.68	37.21	3.21	0.11	0.18
m4	$ln(R_{above}) \sim 1$	0.05	NA	NA	2	−16.92	38.69	4.68	0.05	0

Specific leaf area predicts belowground respiration

Belowground soil respiration (R_{below}) was highest in the meadow and lowest in the heath and shrub communities. Specific leaf area (SLA_{CWM}) had the greatest effect and was the only significant predictor of R_{below} (Figure 2F and Table 2). The best model with the lowest AICc scores only contained SLA_{CWM} (R^2 = 0.45; Table 5). However, slightly more variation was explained when the model also contained microbial activity (R^2 = 0.51) or $Biomass_{roots}$ (R^2 = 0.50; Tables 2 and 5).

Within the shrub community, SLA_{CWM}, $Biomass_{roots}$, and $Microbes_{sum}$ were significant, but SLA_{CWM} had the greatest effect on R_{below} (Table S1). Unexpectedly, there was a negative relationship between R_{below} and $Biomass_{roots}$ and $Microbes_{sum}$ in the shrub community (Figure 2G–H).

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

Microbial activity was similar in the woody heath and shrub communities, and the carbon-degrading enzyme activity related to cellulose and lignin degradation (cbh and xylo) in the soils was lowest in the woody communities and highest in the meadow ($p < 0.05$, TukeyHSD; Figure 3A and Table 6). In the organic horizon, the activities of all enzymes except a-gluc were highest in the meadow community ($p < 0.001$, TukeyHSD; Table 6, Figure S2a). We tested if this could be because of the high carbon content in the meadow soil by controlling for amount of SOC. This evened out the differences, except for the potential enzyme activities of a-gluc and b-gluc, which were marginally higher in the heath than the other communities (a-gluc per gram C: mineral horizon: $p \leq 0.05$, total horizon: $p \leq 0.07$, TukeyHSDand b-gluc per gram C: mineral horizon: $p = 0.05$, Total horizon: $p = 0.06$, TukeyHSD; Figure 3B, Figure S2d, Table S2).

Vegetation woodiness, represented by the C:N ratio of aboveground vegetation, was negatively related to carbon-degrading microbial activity (R^2 = 0.28, $p < 0.05$). However, more variation was explained by SLA_{CWM} (R^2 = 0.34, $p < 0.01$), which was positively related to carbon-degrading microbial activity (Figure 4). The C:N ratios of soil, roots, and total ecosystem (aboveground vegetation, roots, and soil) were also negatively related to carbon-degrading microbial activity, although the relationships 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 $ratio_{total\ ecosystem}$: R^2 = 0.15, p = 0.07).

Discussion

This study demonstrates the varying importance of ecosystem controls of C cycling in three alpine plant communities when CO_2 flux estimates are controlled for temperature and light (Figure 5). Gross ecosystem photosynthesis was least driven by plant functional traits, whereas soil moisture and aboveground biomass were more important. Aboveground respiration was also driven by the amount of aboveground biomass, whereas belowground respiration was

Table 5. Belowground 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}; mm^{-2} mg^{-1}), the sum of microbial activity ($Microbes_{sum}$; nmol h^{-1} m^{-2}), and standing root biomass ($Biomass_{roots}$; 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	$zSLA_{CWM}$	$zBiomass_{roots}$	$zMicrobes_{sum}$	*df*	logLik	AICc	ΔAICc	w	R^2 Adjusted
m1	$ln(R_{below}) \sim 1 + zSLA_{CWM}$	1.24	0.28	NA	NA	3	−4.19	15.57	0	0.44	0.45
m2	$ln(R_{below}) \sim 1 + zSLA_{CWM} + zMicrobes_{sum}$	1.26	0.28	NA	0.07	4	−2.61	16.55	0.98	0.27	0.51
m3	$ln(R_{below}) \sim 1 + zSLA_{CWM} + zBiomass_{roots}$	1.26	0.3	0.05	NA	4	−2.77	16.88	1.3	0.23	0.5
m4	$ln(R_{below}) \sim 1 + zSLA_{CWM} + zMicrobes_{sum} + zBiomass_{roots}$	1.26	0.28	0.02	0.06	5	−2.59	20.63	5.05	0.04	0.48
m5	$ln(R_{below}) \sim 1 + zMicrobes_{sum}$	1.25	NA	NA	0.22	3	−7.44	22.72	7.15	0.01	0.2
m6	$ln(R_{below}) \sim 1 + zMicrobes_{sum} + zBiomass_{roots}$	1.25	NA	0	0.22	4	−7.44	26.21	10.64	0	0.14
m7	$ln(R_{below}) \sim 1 + zBiomass_{roots}$	1.25	NA	0.12	NA	3	−9.19	26.23	10.66	0	0.01
m8	$ln(R_{below}) \sim 1$	1.24	NA	NA	NA	2	−11.99	28.55	12.98	0	0

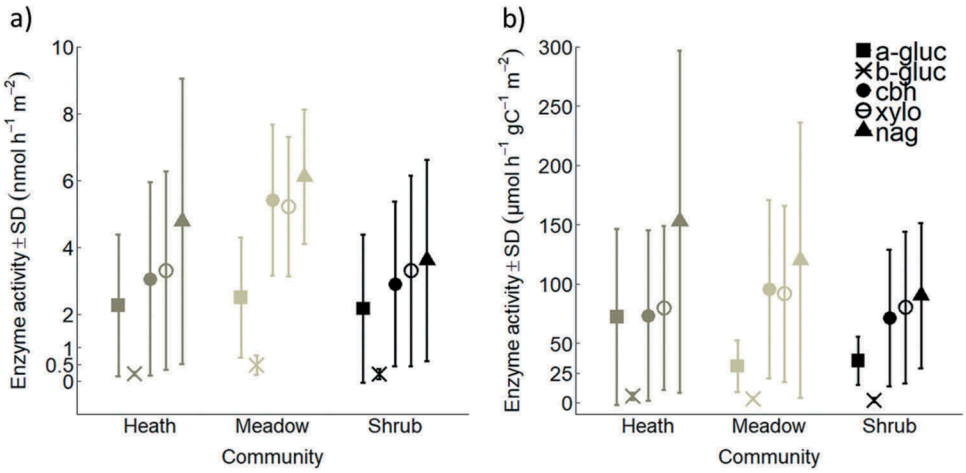

Figure 3. Mean enzyme activity ±SD of α-glucosidase (a-gluc), β-glucosidase (b-gluc), cellobiohydrolase (cbh), β-xylosidase (xylo), and N-acetylglucosaminidase (nag), (A) in nmol h^{-1} m^{-2} and (B) in µmol h^{-1} gC^{-1} m^{-2} for alpine *Empetrum*-dominated heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, central Norway. Activity for each enzyme is the sum across the total soil pit with mean depth 56 ± 8 cm (n = 17). See activities in organic and mineral horizons in Figure S2, and statistical differences in Table 6 and Table S2.

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

Horizon	Enzyme	*F* Value	df_{num}	df_{den}	*p* 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**

dependent on the community-weighted mean of SLA (SLA_{CWM}). Potential microbial activity was highest in the meadow, and carbon-degrading microbial activity decreased with vegetation woodiness and increased with SLA_{CWM}. The results suggest that changes in community composition associated with shrub expansion, acting via these control points, may cause significant changes in gas-exchange processes and carbon source-sink dynamics.

Soil moisture and aboveground biomass controls aboveground C fluxes

Soil moisture was the best predictor of GEP and the effect is probably related to the shift in vegetation composition along the moisture gradient with heath vegetation at the driest end and shrub community at the wettest. Soil moisture was even more important than the aboveground standing biomass ($Biomass_{above}$) of the system. Other studies also identified soil moisture as limiting GEP in arctic-alpine ecosystems (Sjögersten, van der Wal, and Woodin 2006; Dahl et al. 2017; Martin et al. 2017; Westergaard-Nielsen et al. 2017). Soil moisture may affect GEP via stomatal conductance. On exposed sites in alpine regions, the selective pressure for dealing with drought stress events is clearly seen in many plants that have low growth, small leaves, and high content of leaf dry matter (Körner 2003). Soil moisture may also affect GEP indirectly via nutrient mineralization and availability. Desiccation of soils limits the flow of nutrients to the roots and also microbial activity and nutrient mineralization (Körner 2003; Berdanier and Klein 2011).

Contrary to expectations and Hypothesis 1 (Lavorel and Garnier 2002; Klumpp and Soussana 2009), we can conclude that SLA_{CWM} was a less important predictor of GEP across communities. Community-weighted means of SLA for vascular plants do not capture the amount of leaf area in a community, and may therefore be inferior to LAI, which is often used to predict GEP (Chapin 2003; Street et al. 2007).

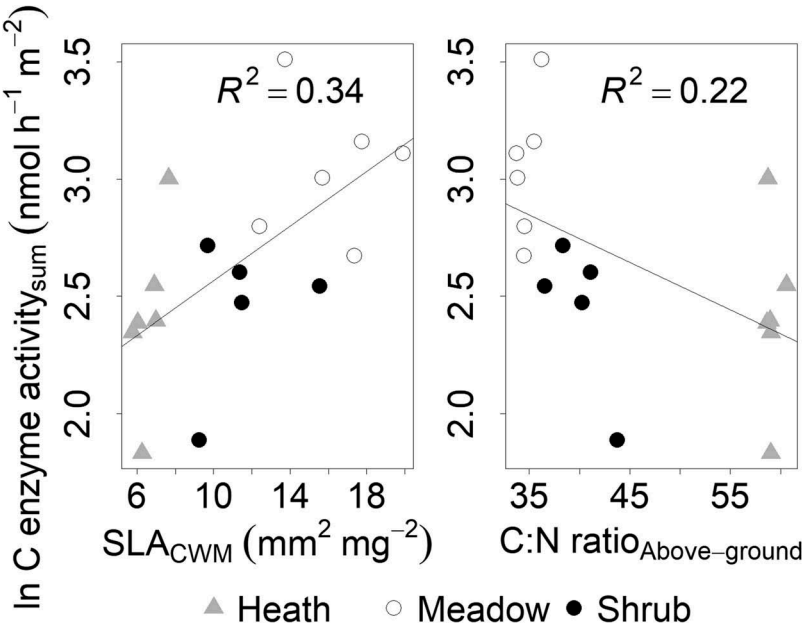

Figure 4. Total enzyme activity of β-glucosidase (b-gluc), cellobiohydrolase (cbh), β-xylosidase (xylo) (C enzyme activity$_{sum}$) (nmol h^{-1} m^{-2}) correlated with "vegetation woodiness" across alpine *Empetrum*-dominated heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, central Norway. Left, community-weighted mean of SLA (SLA$_{CWM}$; $p = 0.009$) and right, C:N ratio of aboveground vegetation (C:N ratio$_{Above-ground}$; $n = 17$).

The high fraction of bryophytes and lichens in the communities (Sørensen et al. 2017) may have played a role in the importance of soil moisture and the lack of importance of vascular leaf traits for the GEP. Cryptogams survive desiccation by their poikilohydric strategies, and the importance of soil moisture on GEP may have been related to the high abundance of cryptogams (Sancho et al. 2016; Chadburn et al. 2017). Some studies suggest that cryptogams may be important contributors to NEE in spring and autumn seasons (Douma et al. 2007; Sancho et al. 2016), but in our sites cryptogams contribute little to gas exchange during peak growing season (Strimbeck et al. 2019).

Consistent with Hypothesis 2a, R_{above} followed the same trend as Biomass$_{above}$, highest in the shrub community, intermediate in the heath, and lowest in the meadow, but the relationship was not a linear fit (Figure 2E). The nonsignificant influence of Biomass$_{above}$ could potentially be explained by the relatively large woody biomass component in the shrub community and heath communities (see more on fluxes and biomass in Strimbeck et al. 2019). In the shrub community, deciduous shrub leaves made up only 8–18 percent of the deciduous biomass, whereas evergreen leaves in the heath community made up 52–65 percent of total evergreen shrub biomass. Also, the high biomass and low productivity of cryptogams in some of our sites may contribute to the lack of correlation between Biomass$_{above}$ and R_{above}.

Specific leaf area drives soil respiration across the community

Community-weighted means of SLA had the greatest effect on belowground respiration (R_{below}). High SLA$_{CWM}$ indicates labile leaves that decompose fast and should therefore increase heterotrophic respiration (Garnier et al. 2004; Questad et al. 2007; De Deyn, Cornelissen, and Bardgett 2008; Bardgett 2017), but few studies have confirmed this effect. SLA is also strongly correlated with leaf nitrogen (Wright et al. 2004), and can be a surrogate for nitrogen availability (Hodgson et al. 2011), which may in turn relate to microbial activity and heterotrophic respiration.

SLA$_{CWM}$, Biomass$_{roots}$, and Microbes$_{sum}$ were significantly important for R_{below}, supporting Hypothesis 2b. Across communities there was a positive relationship between SLA$_{CWM}$ and R_{below} within the shrub community (Figure 2F), and this variable showed the strongest effect on R_{below}. Unexpectedly, there was a negative relationship between R_{below} and Microbes$_{sum}$ and Biomass$_{roots}$ in this community. We suspect, however, that the significance of these relationships could be because of type 1 error, caused by the very small sample

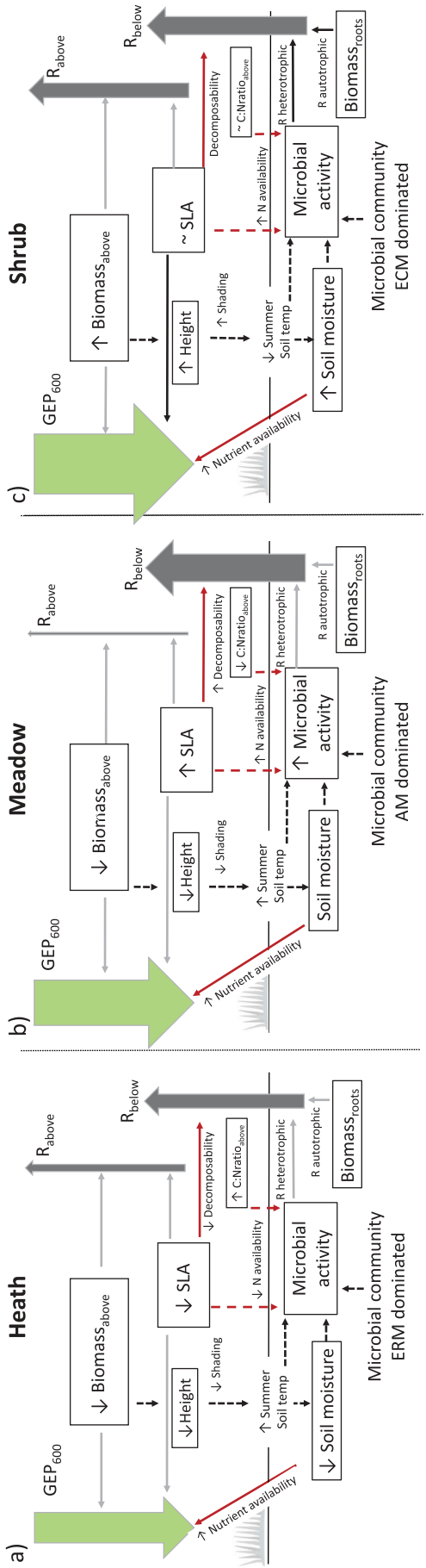

Figure 5. Summary of results with respect to hypothesized mechanisms based on actual measurements of growing-season summer C fluxes (GEP_{600}) and ecosystem respiration partitioned into estimated aboveground (R_{above}) and belowground respiration (R_{below}) in alpine *Empetrum*-heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, central Norway ($n = 17$). Up and down arrows indicate high or low values. Arrow style indicates a significant variable in the full model across community (red line), significant variable in simple correlation (red dashed line), significant variable within the community (black line), presumed relationship not tested in this study (black dashed line), nonsignificant variable across community (grey). The flux arrow width is proportional to its measured flux size transformed to gC m^{-2} h^{-1}.

size in this community. Given the high variability of the systems, and in the shrub community in particular, higher intensity sampling is needed for full delineation of these relationships. Ideally, sampling of fluxes and potential enzyme activity should also be measured concurrently (German, Chacon, and Allison 2011), but this was prevented by logistics in our study.

In this study, R_{below} was not separated into autotrophic and heterotrophic respiration. $Biomass_{roots}$ was not significantly different among the communities and SLA_{CWM} and not $Biomass_{roots}$ had the greatest effect on R_{below}. This could imply that the difference among communities consists primarily in the heterotrophic respiration compartment and not so much in the autotrophic respiration.

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

Mycorrhizal fungi should be common members of the microbial community in all the plant communities we studied, and we found hyphal growth in both the ERM heath and ECM shrub community, but not in the AM-dominated meadow community (Table 1). We predicted that microbial enzyme activity would be highest where plant root and fungal production were also the highest, because an increase in inputs should increase microbial activity overall (e.g., priming). We found that the C:N ratio in plant material, here an indication of woodiness, was negatively correlated with potential microbial enzyme activity (Figures 2 and 3A), supporting Hypothesis 3. Interestingly, we found that the function of the microbial community was more related to a key functional plant trait, as the C-degrading microbial activity was positively correlated with SLA_{CWM}. This finding is supported by the proposed Mycorrhizal Associated Nutrient Economy Framework that was suggested for AM- and ECM-dominated temperate forests, which states that AM-dominated vegetation has higher rates of decomposition and higher chemical quality litter, as compared to ECM-dominated vegetation with lower quality litter (Phillips, Brzostek, and Midgley 2013). Indeed, microbial activity was highest in the meadow ecosystem and likely reflects the more labile inputs and higher root production found in meadow ecosystems relative to the woody heath and shrub ecosystems (Stark and Väisänen 2014; German, Chacon, and Allison 2011; Iversen et al. 2015) together with higher nitrogen availability (Garnier et al. 2004; Hodgson et al. 2011). Additionally, the meadow had twice as much SOC and total soil nitrogen as well as higher minimum pH compared to in the heath and shrub communities (Table 1; Sørensen et al. 2017). An alternative source of N in both the meadow and the shrub communities could be provided by cryptogams (*Pleurozium schreberi, Hylocomium splendens*, and *Peltigera*) that are associated with N-fixing cyanobacteria (Knowles, Pastor, and Biesboer 2006; Jonsson et al. 2015). When we corrected our measured activities for SOC, the differences among the three communities were eliminated, suggesting that the enzyme activities were positively related to total soil carbon.

Proposed mechanisms for changes in C cycling under shrub expansion

Understanding the ecosystem processes of arctic-alpine plant communities is important for predicting the impacts of the ongoing deciduous shrub expansion. The results from this study are best estimates based on few data points. The shrub community is very heterogeneous not only because of the patchy nature of the shrubs both above- and belowground, but also because of a gradient in shrub cover throughout the blocks, with the result that one point appears to drive the patterns within this community (Figure 2). Further studies are needed to refine these results and to corroborate the findings. Figure 6 synthesizes the knowledge gained from our and others' studies (e.g., Wookey et al. 2009; Becklin, Pallo, and Galen 2012; Clemmensen et al. 2015; Parker, Subke, and Wookey 2015; Veen, Sundqvist, and Wardle 2015) on how shrub expansion may affect growing-season C cycling in alpine heath and meadow vegetation.

Shrub expansion in heath and meadow would increase mid-growing season C sequestration (GEP), in the heath most likely because of increased SLA, and in both communities because of increased soil moisture (Figure 6). In Norway, temperature, precipitation, and growing-season lengths are expected to increase during the next century (Hanssen-Bauer et al. 2015). We standardized respiration to a fixed temperature to limit the number of factors in our models. However, arctic-alpine summer soil temperatures decrease with shrub expansion (Table 1; Sturm et al. 2005; Myers-Smith and Hik 2013), and we would therefore expect slightly lower R_{below} in the shrub community than presented in this study if we had not standardized to a similar temperature. Some studies have found that shrub expansion conserves soil moisture (Mann et al. 2002; Naito and Cairns 2011; Myers-Smith et al. 2015), while others found that soil moisture decreased as evapotranspiration increased (Christiansen et al. 2018). This highlights the need for more species- and community-specific studies about the effects of shrub expansion on soil moisture.

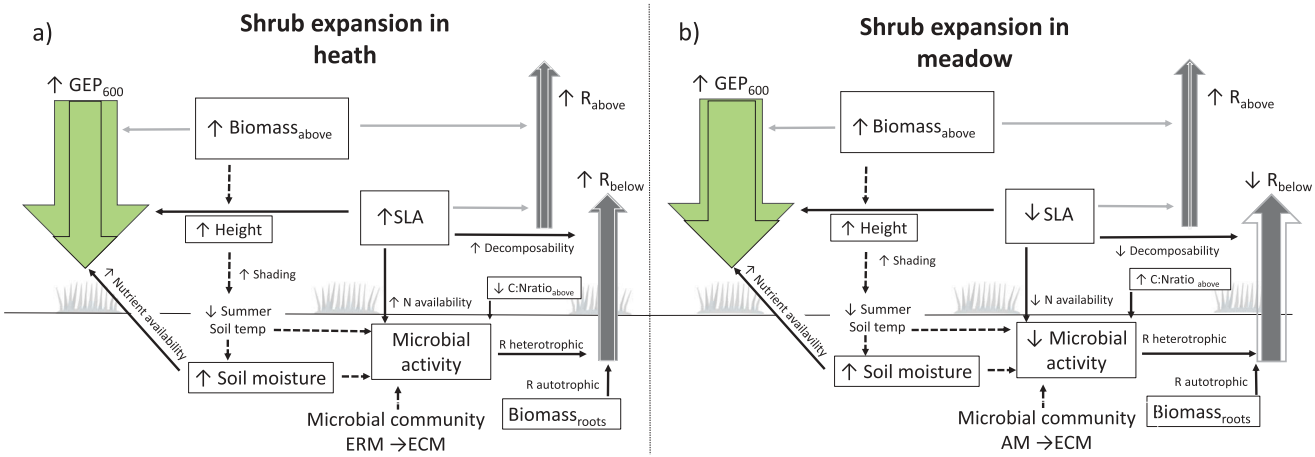

Figure 6. Summary of results with respect to suggested implications of shrub expansion based on actual measurements of growing-season summer C fluxes (GEP_{600} and ecosystem respiration partitioned into estimated aboveground (R_{above}) and belowground respiration (R_{below}) in alpine *Empetrum*-heath, meadow, and *Salix*-shrub plant communities in Dovre Mountains, central Norway ($n = 17$). Up and down arrows indicate an increase or decrease in variables because of shrub expansion in the respective community. Arrow style indicates a significant variable within the community (black line), presumed relationship not tested in this study (black dashed line), nonsignificant variable across community (grey). The flux arrow width is proportional to its measured flux size transformed to gC m^{-2} h^{-1}. The transparent arrows correspond to the flux in the community invaded by shrubs.

Shrub expansion into the heath could also decrease the local growing-season length or growing degree hours because of deeper and more persistent snow cover (Table 1).

Shrub expansion could have different effects on above- and belowground respiration in heath versus meadow ecosystems. As shrub cover expands, aboveground respiration might increase in both heath and meadow, because of increased aboveground biomass. However, in heath communities, belowground respiration may increase with shrub expansion (Figure 6A) because of increased decomposability of the litter (reflected by higher SLA), whereas in meadows belowground respiration may decrease (Figure 6B) because of lower root productivity and lower decomposability of leaf, woody stems, and roots (Cornelissen et al. 2007; Iversen et al. 2015; Veen, Sundqvist, and Wardle 2015; Christiansen et al. 2018). This might seem counterintuitive because we previously found greater soil C pools in the meadow than in the shrub community (Table 1; Sørensen et al. 2017), but shrubs could easily reduce these pools because of seasonal changes in belowground respiration (Bardgett et al. 2005; Grogan and Jonasson 2006). More knowledge is needed on how C cycling and stocks relate to mycorrhizal abundance of ECM, ERM, and AM in arctic-alpine ecosystems (Soudzilovskaia et al. 2015; Myers-Smith et al. 2015).

In this study, we offer a framework for understanding the role of ecosystem controls on C dynamics in a changing arctic. We recommend further studies to test the framework and corroborate the predicted C-budget consequences in specific plant communities.

We demonstrated that the use of plant traits related to the leaf economic spectrum is useful when analyzing C cycling, and we have demonstrated the importance of including both above- and belowground processes and pools when looking at ecosystem properties and processes related to carbon dynamics. Our results illustrate how shrub expansion into alpine tundra communities may influence summer C cycling (ecosystem respiration) differently depending on plant community, as belowground respiration might increase in the heath and decrease in the meadow communities.

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Authors' 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 article with input from all coauthors.

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