Preferential substrate use decreases priming effects in contrasting treeline soils

Jennifer Michel (jenny.michel@t-online.de)
Université de Liège Gembloux Agro-Bio Tech https://orcid.org/0000-0003-3705-4611
Iain P. Hartley
University of Exeter
Kate M. Buckeridge
Luxembourg Institute of Science and Technology
Carmen van Meegen
TU Dortmund University: Technische Universitat Dortmund
Rosanne Broyd
Lancaster Environment Centre
Laura Reinelt
Lancaster Environment Centre
Adan J. Ccahuana Quispe
Universidad Nacional de San Antonio Abdad del Cusco
Jeanette Whitaker
UK Centre for Ecology & Hydrology

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Jennifer Michel[1,2,3 *], Iain P. Hartley[2], Kate Buckeridge[4], Carmen van Meegen[5], Rosanne C. Broyd[6,7], Laura Reinelt[6], Adan J. Ccahuana Quispe[8] and Jeanette Whitaker[1]

[1] UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster, United Kingdom

[2] Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, United Kingdom

[3] Plant Sciences, TERRA research and training centre, University of Liège, Gembloux Agro Bio-Tech, Gembloux, Belgium

[4] Agro-environmental Systems, ERIN Department, Luxembourg Institute of Science & Technology (LIST), Belvaux, Luxemburg

[5] Mathematical Statistics with Applications in Biometrics, TU Dortmund University, Dortmund, Germany

[6] Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom

[7] The James Hutton Institute, Craigiebuckler, Aberdeen, United Kingdom

[8] School of Biology, Faculty of Science, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú

[*] **Correspondence:** jennifer.michel@uliege.be

Author ORCID IDs

Jennifer Michel 0000-0003-3705-4611

Iain P. Hartley 0000-0002-9183-6617

Kate Buckeridge 0000-0002-3267-4216

Carmen van Meegen 0000-0003-4125-5088

Rosanne C. Broyd 0000-0002-0532-0674

Laura Reinelt 0000-0003-2192-9938

Adan J. Ccahuana Quispe 0000-0003-0506-230X

Jeanette Whitaker 0000-0001-8824-471X

Author Contributions

JM, IPH and JW designed the experiment; JM, AJCQ and KB conducted fieldwork; JM, RCB and LR conducted the experiment; JM and CvM analysed the data; all authors contributed to and approved the final manuscript.

Competing interests

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Data availability

All data generated during the current study are presented in the manuscript and available from the authors.

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Abstract

In high altitudes and high latitudes climate change manifests in upward and northward shifting treelines. This entails changes to the carbon (C) and nitrogen (N) composition of organic inputs to soils and can increase or decrease microbial mineralisation of native soil organic matter (positive or negative priming effect). It is currently unknown whether the observed treeline shifts will lead to carbon loss or storage in the soils of these ecosystems.

We therefore investigated priming effects in treeline soils from high altitudes (Peruvian Andes) and high latitudes (subarctic Sweden). In a laboratory soil incubation, we added realistic amounts of organic carbon at a constant ratio of 30% substrate-C to each soils' microbial biomass C. Substrate additions were neutral in pH and covered different C:N ratios, representing naturally occurring substances of the studied ecosystems.

We observed a clear pattern linking the direction of priming (positive or negative) to land cover (boreal or tropical forest, tundra heath, Puna grassland) and soil horizon (organic or mineral). Mechanistically, no support was found for N-mining to induce positive priming, indeed half of all priming effects were negative. Whenever negative priming prevailed, the decrease in SOM-mineralisation was consistently linked to increased microbial substrate utilisation.

In line with other recent studies, our results suggest preferential substrate use is pervasive, linked to negative priming and a promising tool to increase soil carbon storage. Yet, the positive priming observed alerts climate change-induced upwards shifts in high altitudes and deeper rooting plants in high latitudes may cause C-loss via positive priming.

Keywords: treeline, soil carbon, priming effect, C:N, preferential substrate use

1. Introduction

Climate change can alter plant community composition and species distributions, which can change entire landscapes (Harsch et al., 2009; van der Putten et al., 2010; Körner & Paulsen, 2014; Feeley et al., 2020). It also changes the finely tuned interactions between plants, soils and microbes, and how nutrients, particularly carbon (C) and nitrogen (N), are distributed between the atmosphere and soils. Ecosystems in high altitudes and high latitudes share two features, which are of particular importance in the context of climate change: their soils have large carbon stocks (Zimmermann et al., 2010; Saatchi et al., 2011; Rolando et al. 2017; Yang et al., 2018) and these biomes are predicted to experience greater than average increases in temperature (Wookey et al. 2009; Classen et al. 2015; Wang et al. 2016), which has raised concerns about their function as global carbon sinks (Keuper, Wild et al., 2020; Nottingham et al., 2020). The direct abiotic impacts of climate change are increasingly well studied in these vulnerable ecosystems. However, the indirect biotic effects, like large-scale species shifts, and the related feedback on soil elemental cycling, remain widely uncertain.

Treeline shifts can have contrasting effects on the carbon cycle and terrestrial C stocks. Increasing amounts of above- and belowground biomass and greater recalcitrance of litter from different species can increase CO_2 uptake and the potential for new soil organic matter (SOM) formation (Lange et al., 2015; Rolando et al., 2017; Sullivan et al., 2020). Yet, greater C and nutrient inputs do not always result in greater C storage, as plant litter inputs and root exudation can counterintuitively enhance SOM mineralization by microbes. This phenomenon of altered SOM mineralisation in response to fresh organic inputs is known as ‘priming effect’ (PE) (Löhnis 1926; Bingemann et al. 1953; but see Kuzyakov et al., 2000). A positive priming effect refers to a situation where SOM mineralisation is enhanced following labile inputs. Accordingly, a negative priming effect describes reduced rates of SOM-mineralisation after substrate addition. Positive priming has the potential to outweigh the

carbon capture in biomass through mobilisation of the belowground carbon stocks, a major concern particularly for arctic ecosystems under climate change (Hartley et al.,2012; Parker et al. 2015, 2021; Keuper, Wild et al., 2020). Priming effects also concern ecosystem modellers, as they may undermine the suitability of applying first order kinetics to decomposition processes (Perveen et al., 2014).

It is agreed that priming effects result from the interplay of supply and demand of energy, usually carbon compounds, and nutrients that are exchanged between microbes and plants (Jones et al., 2009; Dijkstra et al., 2013; Murphy et al., 2015; Wang et al. 2016; Averill & Waring, 2017; Soong et al., 2018). The mechanistic basis of priming effects remains however controversial. The microbial N-mining hypothesis predicts that the addition of labile C to soils with low N availability (high C:N) increases the microbial demand for N, stimulating the mineralisation of SOM (positive priming), as microbes strive to meet their nutritional needs by releasing more N from soil (Schimel & Weintraub, 2003; Craine et al., 2007; Chen et al., 2014). On the other hand, preferential substrate use predicts that the addition of labile C in abundance of nutrients decreases the mineralisation of SOM (negative priming), as microbes shift from mineralizing SOM to using substrate-C as their primary nutrient source instead (Cheng et al., 1999; Blagodatskaya et al., 2011; Wang et al., 2015).

Compared to more temperate grasslands and forest, organic inputs in undisturbed high altitudinal and high latitudinal ecosystems are considerably lower, although changing with land cover type and season (Weintraub & Schimel, 2005; Kaiser et al., 2010; Girardin et al., 2016; Malik et al., 2018). In both Andean and subarctic ecosystems, N is considered a limiting factor and determinant for plant and microbial performance (Weintraub & Schimel, 2005; Buckeridge et al., 2010; Nottingham et al., 2012; Fisher et al., 2013). In this laboratory incubation study, we amended soils from above and below the treeline in high altitudes and high latitudes with low rates of substrates of varying C:N ratios to develop mechanistic understanding of how priming effects are controlled in these

123 contrasting N-limited ecosystems. This study particularly investigates the divergence of predicted
124 priming effects according to either N-mining (positive priming) or preferential substrate use
125 (negative priming), considering how the C:N ratio of organic inputs interacts with the inherent C and
126 N differences in soil and microbial biomass of the studied ecosystems.

127 We hypothesised that (H1) the respective upland soils (Puna grasslands in the Andes and tundra
128 heath in the Arctic) would be more suspectable to positive priming than their forest counterparts, due
129 to stronger microbial N-demand. This would lead to N-mining, which should be more pronounced
130 when carbon-rich, nitrogen-poor substrates are added and decrease with increasing substrate-N
131 content. On the other hand (H2), we hypothesised that when microbes switch their energy (carbon)
132 and nutrient (nitrogen) acquisition from soil to substrate, this preferential substrate use causes
133 negative priming. We expected this particularly in cases where the C:N ratio of the added substrate
134 was close to the C:N ratio of the microbial biomass of the receiving soil, as processes of microbial
135 anabolism would have the least stochiometric constraints.

136

137 ## 2. Material and methods

138 ### 2.1 Study sites

139 Soils were collected in 2016 in the high altitudes of the Peruvian Andes in Manú National Park in the
140 department of Cusco at an average elevation of 3300 m (13°07'S 71°36'W), and in the high latitudes
141 of the boreal subarctic near the Abisko Scientific Research Station, 250 km north of the Arctic Circle
142 in Northern Sweden (68º21'N 18º49'E) (Fig. 1).

143 The study area in the Peruvian Andes is situated at the high end of the Kosñipata transect on the
144 Eastern side of the Andes, but on the Western facing hill side of the Paucartambo river valley (Fig. 1

145 A2). The study area comprises a montane tropical forest with a short transition zone leading into
146 Puna grassland (Fig. 1 A3). The forest is a high Andean tropical mountain forest dominated by
147 *Weinmannia microphylla* (Kunth), *Polylepis pauta* (Hieron.) and *Gynoxys induta* (Cuatrec.). The
148 adjacent Puna grasslands are mainly composed of the genera *Festuca, Hypericum* and *Carex*. The
149 climate is characterised by a rainy season from October to April, but in the forest and at the treeline
150 cloud cover can be dense and humidity high throughout the year. The mean temperature is around
151 13°C at the treeline, but can reach up to 25°C in October and cool down to 3 - 6°C in the Puna
152 (UNEP World Conservation Monitoring Centre). The soils referred to as "Andean soils" in this study
153 are derived from volcanic material with mostly low base status (Fig. 1 A4). Because of the
154 mountains' diverse topography, slope and exposition, and varying history of erosion and landslides,
155 they represent a variety of soil types. The forest soils are mostly Cambisols with a large fraction of
156 organic matter in the upper soil horizon. The Puna grassland soils are shallower and mostly
157 Andosols, where the mineral sub soil contains notable quantities of amorphous clay (FAO Soil map
158 of the world 1971; Wilcox et al., 1988; FAO World reference base for soil resources, 2015).

159 The study region in the Swedish subarctic is located near Abisko, south of the lake Torneträsk. The
160 treeline transition along the elevational gradient has a Northeast – Southwest orientation (Fig. 1 B2).
161 The studied treeline forms the upper end of a fragmented birch forest, which fades into alpine tundra
162 (Fig. 1 B3). The dominant canopy-forming species of the studied mountain birch forests is *Betula*
163 *pubescens* (Ehrh.), while at some sites *Betula nana* (L.), *Salix glauca* (L.) and *Juniper sp*. were also
164 present. The forest understorey is mostly composed of ericaceous plants such as *Empetrum nigrum*
165 (L.), and several species of *Vaccinium.* The plant species composition of the upland heath lands is
166 similar to the forest understorey, mainly composed of dwarf shrubs and cryptogams. In contrast to
167 the Andean uplands, true grasses are widely absent, but species of the genera *Lycopodium* and
168 *Equisetum* were commonly present at low abundance. There is regularly snow on the ground until

late May and while average temperatures may be a little over 10 ºC in July, by mid-August the average temperature is already declining rapidly with frosts likely by early September. In winter, temperatures can drop down to – 34 ºC. Precipitation averages 15 mm per month during the year, with July and August being wetter (60 mm / month) (Abisko Scientific Research Station). Bedrock is formed by salic igneous rocks and quartic and phyllitic hard schists (Sundqvist et al., 2011). The subarctic soils referred to as "Boreal soils" in this study (Fig.1 B4) are permafrost-free and mostly Podsols and Cambisols with thin organic rich topsoils and sandy mineral soils from the B-horizon (FAO World reference base for soil resources, 2015).

2.2 Soil sampling

In both countries, the sampling area covered approximately 450 km^2, in which six individual sampling locations were identified with two to eight km between them. At each sampling location, a 30 m transect was marked orthogonally to the treeline, positioning the transition zone between the timberline and the tree species line at its middle (Berdanier, 2010). Hence, for each transect, one end point was inside the forest below the treeline and the other one in the corresponding upland above the treeline (Puna grassland or tundra heath). At each end point of each transect, a plot of 15 x 15 m (225 m^2) was established, 24 plots in total (6 Andean mountain forest, 6 Andean Puna grassland, 6 boreal birch forest, 6 boreal tundra heath).

Within each plot, soils were collected at five sampling points in a dice layout. At each of these, approximately five liters of soil were sampled separately from organic and mineral soil horizons. For the organic soils, the litter layer in the forests was removed before sampling. In the Puna grasslands and tundra heath, dense root mats were not included in the samples and mineral soils were sampled without large rocks. The five samples of each plot were combined into one composite sample, which

192 was homogenized by hand and approximately 20 liters were then sealed in plastic bags and stored at
193 4°C until the experiment was run in spring 2017. The total number of samples was 48 (4 land cover
194 types x 2 horizons x 6 field replicates). Within each plot, additional intact soil cores (h = 15 cm, d = 5
195 cm) were taken, one each from the organic and mineral soil horizons, to determine bulk density.

196 For this experiment, we classified eight soil types representing the treeline ecotone based on the soil
197 origin in terms of geographic region (Andean, Boreal), native land cover (tropical mountain Forest or
198 boreal Forest, Puna grassland, Tundra heath) and soil horizon (Organic, Mineral). We follow the
199 same labelling throughout the manuscript defining the soils by these three characteristics as: Andean
200 Forest Organic (AFO), Andean Forest Mineral (AFM), Andean Puna organic (APO), Andean Puna
201 Mineral (APM), Boreal Forest Organic (BFO), Boreal Forest Mineral (BFM), Boreal Tundra Organic
202 (BTO) and Boreal Tundra Mineral (BTM).

203

204 2.3 Pre-incubation analysis

205 For each composite sample, soil pH, maximum water holding capacity (max WHC), bulk density
206 (BD), soil texture, total carbon and nitrogen contents and extractable nitrogen were determined
207 (Table 1). Soil texture was first assessed in the field following standard protocols (VD LUFA I, D
208 2.1, 1997) and then detailed in the lab on three sub-samples of each soil type by analysis of
209 stratification in suds solution ("jar test" as in Sitton & Story (2006)). Dry matter and water content
210 were determined by drying soil samples at 105 °C until constant weight (Schlichting and Blume,
211 1967). Maximum water holding capacity was calculated as the difference in weight of soil at field
212 capacity (saturated soil after draining) and dry soil. To calculate field bulk density (BD), the mass
213 and volume of rocks and roots was determined and subtracted from the soil mass and volume from
214 15 cm soil cores (d = 5 cm), which were taken in each landcover type and for each soil horizon

215 individually. Soils were then sieved to 2mm. Soil pH was measured using a Hanna HI-111 pH/ORP
216 Metre according to Emmett et al. (2008). For each sample, 10 g of field moist soil was mixed with
217 25 ml deionised water, stirred and allowed to settle overnight, before the pH was recorded. Total soil
218 C and N concentrations were analysed on 5 g oven-dried (105 °C) sub-samples, which were ground
219 and analysed via combustion and thermal conductivity detection (Elemental analyser Vario EL). Sub-
220 samples of 5 g soil each were extracted with 0.5 M K_2SO_4 for analysis of mineral nitrogen
221 (extractable ammonium (NH_4^+) and nitrate (NO_3^-)). Extracts were colorimetrically analysed on an
222 autoAnalyser (Bran and Luebbe, Northampton, UK).

223 Microbial biomass C and N were analysed using the direct extraction method (Tate et al., 1988;
224 Gregorich et al., 1990; Fierer and Schimel, 2003): A K2SO4-salt solution was used as extractant and
225 liquid EtOH-free chloroform ($CHCl_3$ stabilised with amylene)) directly added to release C and N
226 from microbial cells. All soils were analysed in duplicates, where one sample was extracted with salt
227 solution only (5 g fwt soil + 25 ml 0.5 M K_2SO_4 (pH adjusted to 6.8-7 /w NaOH)) and the twin
228 sample was additionally treated with liquid $CHCl_3$ (5 g fwt soil + 25 ml 0.5 M K2SO4 (pH 6.8-7 /w
229 NaOH) + 0.5 ml $CHCl_3$). Extractable microbial C and N of all samples was analysed using a
230 TOC/TN analyser (5000A, Shimadzu, Milton Keynes, UK) and biomass C and N were calculated by
231 subtracting the C and N contents of the salt-extracted samples from the element contents of the
232 chloroformed samples. Given the heterogeneity of soil types studied, we present the microbial
233 biomass carbon and nitrogen data as the actual values that were measured, without applying general
234 correction factors as recommended in Halbritter et al. (2020), protocol 2.2.1 (Schmidt, I.K., Reinsch,
235 S., Christiansen, C.T.).

236

237 2.4 Preparing the substrate solutions

All substrate additions included 10% isotopically enriched glucose (Cambridge Isotope Laboratories) as a carbon source. To avoid substantial increases in microbial biomass and changes in microbial community composition, as well as an "apparent priming" effect, all substrate-C additions were proportional to 30% of each soils' microbial biomass carbon content (Blagodatskaya & Kuzyakov, 2008; Blagodatsky et al., 2010; Blagodatskaya et al., 2011). Substrate-C additions were calculated based on the average microbial biomass carbon of organic and mineral soil horizons separately. In both regions, values from forest and upland soils were comparable (Table 1) and therefore combined for calculating the substrate C-additions (Table 2). In addition to the water control, four substrate treatments were prepared: One treatment was glucose only ("glc") and three additional substrate treatments were made with combined C and N additions. Therefore, for each soil type the same amount of glucose was dissolved in different concentrations of Hoagland's No.2 solution (H2395, Sigma Aldrich, supplementary material 1) to obtain the final C:N ratios 71:1 ("glu +N"), 17:1 ("glu+NN"), 7:1 ("glu+NNN"). Hence, within each soil type, the carbon content of all substrate treatments was the same (30% of microbial biomass C), while the N-contents changed. The final C:N ratios of the substrates mimicked natural resources, such as microbial biomass, SOM and leaf litter (Mooshammer et al., 2014a), to represent the variety of substrates which microbes encounter in their natural environments. We used the buffered Hoagland's nutrient solution to avoid pH shifts (supplementary material 2) isolating the microbial response to substrate C:N from the effect of pH (Rousk et al., 2010) and eradicating potential micronutrient co-limitation (Liebig, 1841).

2.5 Running the experiment

Soils were adjusted to 75 % of maximum WHC using deionised water and equilibrated at 13 °C for five days prior to the experiment. Five aliquots of 5 g fresh weight of each of the six field replicates

261 of each of the eight soil types were then weighed into 250 ml Kilner jars. Aliquots were amended
262 with either one of the four substrate treatments (glc only, glc +N, glc +NN, glc +NNN) or water as
263 control and incubated for 21 days (n = 240 incubations). All substrate additions and deionised water
264 controls were pipetted as 1 ml liquid solution per replicate onto the relevant soil samples, then jars
265 were flushed with compressed air for 40 seconds, sealed and over-pressurised by injecting 40 ml
266 compressed air and incubated in the dark for 21 days at 13 °C, which corresponds to the field sites'
267 ambient mean summer temperature (Whitaker et al., 2014; Parker et al., 2015).

268 Gas sampling for total CO_2 analysis was conducted at t0 = 0 hours, t1 = 24 hours, t2 = 48 hours, t3 =
269 7 days, t4= 8 days, t5 = 14 days, t6 = 21 days) after starting the experiment and samples for ^{13}C
270 analysis were taken at t1, t3, t4 and t5. To keep CO_2 headspace concentrations in the jars below
271 10000 ppm to avoid related feedbacks on soil respiration, the jars were opened after sampling at t3,
272 then flushed, over-pressurised and sampled again as at the beginning of the experiment (t4). For
273 analysis of total CO_2 on the GC (Perkin Elmer Autosystem Gas Chromatograph, Speck & Burke,
274 UK), we took 5 ml sample air and transferred it to 3 ml evacuated exetainers (Labco, UK), which
275 were hence over-pressurised with sample-air. For ^{13}C analysis, we took 20 ml sample air and
276 transferred it to 12 ml exetainers before analysing them by cavity ring-down spectroscopy (CRDS)
277 using a Picarro G2201i with a multiplexor (Picarro Inc., USA). CO_2-accumulation was assumed to be
278 linear between the chosen time points for sampling as described above, so fluxes were expressed per
279 hour and then corrected for CO_2-C respired relative to each soils' C content, as this is also the unit
280 chosen to express priming effects (Fig. 2). Due to the loss of some samples, priming could not be
281 calculated for all replicates of all soil types at all time points, with the final number of observations
282 totaling n = 91 for Andean mountains and n = 88 for boreal subarctic.

283

2.5 Isotopic and source partitioning

The isotopic ^{13}C labelling of the added substrate solutions allowed the separation and quantification of CO_2-C originating from native soil organic matter and added glucose. In the following mass balance, RS represents the CO_2 respired from soil, R_G represents the CO_2 originating from glucose and R_T represents the total CO_2 respired (Eq. 1). These can be separated into their respective sources (Eq. 2) with the known isotopic abundance of ^{13}C of soil organic matter ($^{13}C_S$), glucose ($^{13}C_G$) and the total CO_2-C respired ($^{13}C_T$). The priming effect, i.e. the substrate-induced change in the amount of C respired from soil (RPE), is quantified (Eq.3) as the difference between soil organic matter-derived CO_2-C respired from soils amended with glucose (R_G) relative to the total amount of CO_2-C respired from soil organic matter in the untreated control soils (R_C):

$$R_S + R_G = R_T \quad \text{(Eq.1)}$$

$$R_S \times {}^{13}C_S + R_G \times {}^{13}C_G = R_T \times {}^{13}C_T \quad \text{(Eq.2)}$$

$$RPE = R_G - R_C \quad \text{(Eq.3)}$$

The amount of primed C was then expressed as μg CO_2-C g^{-1} soil C, in order to normalise for the differences in soil types and their C contents and increase comparability amongst the soils and their vulnerability to priming. The magnitude of priming (%) expresses the amount of primed carbon relative to the amount of carbon respired from untreated control soils. Substrate use (%) was calculated as the amount of added substrate-C detected in soil respiration, divided by the initial amount of substrate-C added to the soil and multiplied by 100.

2.6 Statistical analysis

Statistical analysis was carried out using R 4.0.5 (R Core Team, 2021) with the additional packages multcompView (Graves et al., 2015), PerformanceAnalytics (Peterson & Carl, 2020) and betareg (Cribari-Neto & Zeileis, 2010). To identify whether the observed priming effects were significantly different ($\alpha = 0.05$) in the high altitudes of the Andean mountains and the high latitudes of the boreal subarctic we used Welch Two Sample t-tests, and Wilcoxon tests to compare microbial substrate use in the two regions. For each data set, three-way analysis of variance (ANOVA) was conducted to identify differences between each of the observed variables (priming effect or substrate use) and the variables land cover type, soil horizon and substrate treatment. Data was transformed in order to meet assumptions of linear regression where necessary.

To unravel the role of nitrogen, we tested how soil, substrate and microbial biomass C:N ratios affected priming applying three-way ANCOVA with substrate C:N as categorical independent variable with four levels (each treatment) and microbial and soil C:N as covariates. To further identify potential drivers of priming effects, a multiple linear model was built for each ecosystems' data set (Peruvian high altitudes and Swedish high latitudes) using the explanatory variables of soil, substrate and microbial C and N contents. Models were simplified using backward stepwise selection according to the Akaike Information criterion (Akaike, 1974). Linear regression and the Spearman's rank correlation coefficient were used to describe the relationship between substrate use and priming and beta regression via maximum likelihood (Cribari-Neto & Zeileis, 2010) was applied to statistically determine potential drivers of substrate use.

3. Results

3.1 Soil and microbial characteristics

The studied soils represent a range of contrasting edaphic and microbial parameters (Table 1). Soil and microbial C:N ratios were lowest in Peruvian mineral forest soils (soil C:N = 15.3, microbial biomass C:N = 2.9) and highest in Swedish organic tundra soils (soil C:N = 34.7, microbial biomass C:N = 16). For each land cover type, soil and microbial C and N contents were higher in organic soils compared to their mineral counterparts. Mineral nitrogen was lower in Peruvian than in Swedish soils, and highest in Swedish organic soils. Water holding capacity (WHC: 50.3 (BFM) to 463.2 (BFO)), bulk density (BD: 0.1 (AFO) to 0.93 (BTM)) and soil texture also differed across a considerable range. All soils were slightly acidic and pH ranged from 4.2 (AFO) to 5.7 (BFM). Substrate-induced pH shifts were low and comparable for all soil and substrate combinations (on average - 0.16 ± 0.11), with the greatest shifts in mineral forest soils from both regions (supplementary material 2).

3.2 Soil respiration

All soils responded to substrate additions with an initial peak in respiration (Fig. 2). This occurred 24 hours after substrate addition in all Andean and the mineral tundra soils and 48 hours after substrate addition in the organic soils from, the subarctic. The greatest peak was observed in soil respiration of organic Tundra soils (BTO), where substrate addition approximately tripled the flux rates at 48 hours after substrate addition, compared to basal control soil respiration.The boreal mineral forest soils had unspecific peak times. In all cases, respiration rates stabilised thereafter at the level of the respective control soils. The control soils also showed moderate peaks in basal CO_2-respiration within the first 48 hours of incubation, as they were amended with 1 ml water at the beginning of the experiment in the same manner as substrate solutions were applied.

On average, respiration rates from subarctic soils were 4 – 20 times higher than respiration from the Andean soils. In both regions, mineral soils from above the treeline (APM, BTM) had the lowest respiration rates, followed by on average two-fold higher respiration from corresponding organic soils (APO, BTO). Similarly, mineral forest soil respiration (AFM, BFM) was half as high as respiration measured from corresponding organic forest soils (AFO, BFO).

3.3 Soil carbon priming and substrate use

Direction and magnitude of priming varied amongst the different treeline soils with equal observations of positive and negative priming (Fig. 3 left panels). Priming effects were significantly different in the Andean soils and the boreal subarctic soils ($p = 0.03$), with the absolute amounts of primed C (μg C (g soil C) -1) ten times higher in the subarctic soils, notably the forest soils (Fig. 3a,e). The magnitude of priming was however similar in both regions ($p = 0.6$), with most values between 10% and 35% (Fig. 3c,g). In the Andean mountain soils, primed C was statistically different between land cover types ($p = 0.007$), with predominantly negative priming in forest soils (AFO, AFM) and more positive priming in Puna grassland soils (APO, APM) (Fig. 3a,c). For the subarctic soils, significant differences in priming effects were observed between soil horizons ($p < 0.001$), with mostly positive priming in mineral soils (BFM, BTM) and predominantly negative priming in organic soils of both forest (BFO) and tundra (BTO) (Fig. 3e,g). The magnitude of priming was significantly higher in forest soils (BFO, BFM) compared to tundra soils (BTO, BTM). Within each land cover type, priming was higher in mineral soils compared to their organic counterparts.

Substrate use (Fig. 3 right panels) was significantly higher in the Andean soils compared to the boreal subarctic soils ($p < 0.001$). In the Andean soils, substrate use was significantly higher ($p < 0.001$) in organic (AFO, APO) compared to mineral (AFM, APM) soils (Fig.3b,d), with a significant

372 interaction with substrate treatment regarding the relative amounts of substrate used ($p = 0.02$). In the
373 organic soils, relative substrate use was highest for the C-only addition, while in mineral soils it was
374 highest for substrate additions with a C:N ratio of 17:1 (Fig. 3d). In the subarctic soils, substrate use
375 was significantly higher ($p < 0.001$) in the organic (BFO, BTO) than in the mineral soils (BFM,
376 BTM) (Fig. 3f, h), with larger quantities used in the forest compared to the tundra soils ($p < 0.001$)
377 (Fig. 3f).

378 Microbial substrate use was inversely correlated with the magnitude of priming in most of the soils
379 (Fig. 4), notably in the Andean forest soils (AFO, AFM) and the organic soils from the subarctic
380 (BFO, BTO). Consistent amongst these soils, increased substrate use decreased priming effects, a
381 relationship which was supported in the linear models (Fig. 5).

382

383 3.4 Effect of N-availability on priming

384 We conducted an ANCOVA to investigate the interactive effects of soil, substrate and microbial
385 biomass C:N ratios on priming and found that soil C:N was a significant covariate determining the
386 magnitude of priming effects in 7 of the 8 soils studied (Table 3). This is in line with the significant
387 differences observed in priming effects and microbial substrate use between land cover types and
388 organic and mineral soil horizons (Fig. 3, Fig. 4), which are inherently linked to the different soil
389 C:N ratios (Fig.1). Soil C:N does however not indicate N-availability (Table 1), which in this study
390 was manipulated solely via the added substrate C:N.

391 Substrate C:N, and therewith N-availability, was mostly not linked to the observed priming effects
392 (Table 3), but had a significant effect in the organic boreal soils (BFO), where priming decreased
393 with increasing added N content (Fig. 3e). In the mineral forest soils of both geographic regions

(AFM, BFM), the interaction between soil and substrate C:N also had a significant effect on priming, as well as the interaction between soil and microbial biomass C:N (Table 3). The tree-way interaction and the interaction between microbial biomass C:N and substrate C:N was not significant in any soil.

In the Andean soils, soil mineral N was significant in determining substrate use, which in turn determined priming effects (Fig. 5A). In the subarctic soils, microbial biomass N contributed to microbial substrate use, which was also related to microbial biomass, soil and substrate C (Fig. 5B).

4. Discussion

4.1 Land cover type

In a direct comparison using standardised methodology for soils from both high altitudinal and high latitudinal ecosystems both positive and negative priming effects occurred, with magnitude and direction strongly linked to land cover type and soil horizon. The direction of priming was consistent with our hypothesis in the Andes, with more positive priming above the treeline and more negative below (H1). This was not observed in the subarctic soils, where soil horizon determined the direction of priming under both land cover types (forest and tundra). In this study, half of the observed priming effects were negative, with the strongest negative priming in organic boreal forest soils. Our findings contrast with some previous studies, particularly those concerning subarctic and arctic soils, which typically report positive priming, though usually at high rates of substrate addition (> 30% microbial biomass) (Wild et al., 2014; Parker et al. 2015, 2016; Hicks et al., 2020).

Our results align with other studies from the same area in the Abisko region (Hartley et al., 2012; Rousk et al. 2016) and the Kosñipata transect in the Andes (Whitaker et al., 2014; Hicks et al., 2019), which report both positive and negative priming effects. This observation of both positive and

416 negative priming following the addition of labile substrates aligns with many studies on a global
417 scale (Qiao et al., 2014, 2016; Wang et al., 2015; Heitkötter et al., 2017; Bastida et al., 2019).
418 Concerning the treeline ecotone, species range shifts have been reported for various montane and
419 alpine ecosystems around the world, though the tropical treeline has so far remained relatively stable
420 (Kramer et al., 2009; Harsch et al., 2009; Rehm & Feeley, 2015). In the Andean soils studied here,
421 we found positive priming in Puna grasslands above the treeline and negative priming in the soils of
422 the Andean mountain forest (Fig.3a, 3c). If climate change causes large scale range shifts of plant
423 communities on mountain systems like the Andes, and this triggers consistently positive priming
424 effects as observed in the Puna soils of this study, the disproportionally increased rates of soil C-
425 mineralisation have the potential to disturb the C balance of these ecosystems with unknown
426 consequences for atmospheric carbon dioxide concentrations.

427

428 4.2 Soil horizon

429 Several studies indicate that the mechanisms of carbon cycling are different in organic and mineral
430 soils (Fontaine et al., 2007; Keiluveit et al., 2015; Heitkötter et al., 2017; Yang et al., 2018), which
431 our results support particularly for the subarctic ecosystem. The mineral soils from the subarctic were
432 more prone to carbon losses through positive priming than the organic soils (Fig. 3). A similar pattern
433 was observed in a previous study in subarctic birch forest soils, which found positive priming in
434 mineral soils, but no priming in the organic soils (Hartley et al. 2010). And a study by Heitkötter et
435 al. (2017) reports a similar situation in a German forest, where the organic top soils showed negative
436 priming under nutrient additions, while positive priming was observed for deeper mineral soils. Thus,
437 negative priming might be a consistent feature in the upper soil layers of forest ecosystems, when
438 microbes preferably utilise recently fixed C (Briones et al.,2021). The distribution of plant-fixed C

through the soil profile could therefore be an important factor in regulating an ecosystems' C balance. The treeline at the Abisko study site has shifted northwards in recent years (Wookey et al. 2009). Several studies indicate that this might accelerate carbon turnover and thus link to the lower soil C stocks in the soils of the mountain birch forests (Hartley et al., 2010; Parker et al. 2015; Keuper, Wild et al., 2020). Our results also indicate that increasing inputs through changes in land cover and plant community might disproportionally stimulate microbes in the deeper soil horizons, causing additional carbon losses from these soils through positive priming effects. This might become more evident if warming soils facilitate deeper rooting of plant species above the treeline and labile inputs to soils increase due to higher plant productivity in a greening Arctic.

4.3 Soil C:N

The studied treeline ecotones exhibit contrasting gradients of soil C:N ratios: In the Peruvian Andes, soils have higher C:N ratios in the forests below the treeline compared to the Puna grasslands. In Sweden, the opposite is the case with higher C:N ratios in tundra soils above the treeline and lower soil C:N in the boreal forests below the treeline. In addition to these reversed gradients across respective treelines, taken together the two ecosystems form a continuous C:N spectrum from the mineral Puna grassland soils (C:N = 12.3) to the organic tundra soils (C:N = 34.7) (Table 1). Soil C:N and land cover type are closely linked, however the observed priming effects did not linearly follow the soil C:N gradient. In the Andes, priming was positive where soil C:N was lower, that is in the Puna grasslands (Fig. 3a,c). In the subarctic soils, priming effects were better described by the interaction of land cover and soil horizon (Fig. 3e,g). This may be, because the bulk soil C:N ratio does not necessarily indicate soil N availability, as demonstrated by the measurements of soil mineral N (Table 1). N-availability is also affected by soil clay content (Keiluveit et al., 2015; Kyker-

462 Snowman, et al., 2019) which may have reinforced the C:N effect in the Andean soils, as particularly
463 the studied Puna soils have considerable contents of amorphous clay.

464

465 4.4 Preferential substrate use

466 Negative priming prevailed in half of the studied soils in both ecosystems (Fig. 3). Inverse
467 correlations between the magnitude of priming and microbial substrate use (Fig. 4) support our
468 hypothesis that preferential use of the added substrate decreased rates of SOM-mineralisation,
469 contributing to the negative priming effects observed (H2). In recent literature, negative priming
470 received less attention than positive priming, but it is an important process across ecosystems
471 (Guenet et al., 2010; Blagodatskaya et al., 2011; Bastida et al., 2019). It has been shown that
472 preferential substrate use can be a beneficial microbial strategy of resource acquisition, reducing the
473 investment into SOM-degrading enzymes (Sinsabaugh et al., 2016; Merino et al., 2016; Amenabar et
474 al., 2017). Our results indicate that preferential substrate use is also one of the key drivers of negative
475 priming effects (Cheng & Kuzyakov, 2005; Blagodatskaya et al., 2007; Wang et al., 2015).
476 Preferential substrate use and negative priming are likely constantly occurring, particularly in
477 immediate plant-soil-microbe interactions in the rhizosphere where exudates provide a range of
478 substances with variable C:N ratios (Jones et al., 2009; Gunina & Kuzyakov, 2015; Canarini et al.,
479 2019). Preferential substrate use could therefore also shape C cycling at the ecosystem scale. For
480 example, in a large-scale warming experiment in a forest in the UK, Briones et al. (2021) found no
481 evidence for positive priming, while enhanced turnover of recently fixed carbon suggests that
482 preferential substrate use can take place at forest scale. We did however not observe that substrate
483 use was highest when the C:N composition matched that of the receiving microbial community, and
484 the interaction term between substrate C:N and microbial biomass C:N was not a significant predictor

485 of priming (Table 3). Microbes are hence not generally more likely to utilize substances when they
486 match their biomass C:N ratios, however there may be stochiometric linkages, as for example in the
487 Andean mineral soils, microbes had a higher substrate use for substrate with a C:N ratios of 17:1 and
488 in organic soils substrate use was highest when only C was supplied (Fig. 3d). This could indicate
489 different functional capacities of different microbial communities (Kaiser et al., 2010; Krause et al.,
490 2014). While substrate use was mostly independent from substrate C:N, it was characteristic of land
491 cover type and soil horizon (Fig. 2 bottom panels), similar to the priming effects observed (Fig. 2 top
492 panels). Microbial substrate use explained particularly the negative priming effects observed (Fig. 3,
493 Fig. 4, Fig. 5), thus supporting the central role of microbes in the soil C cycle (Cortufo et al., 2013;
494 Classen et al., 2015; Kyker-Snowman et al., 2019; Buckeridge et al., 2020).

495

496 4.5 Microbial N-mining

497 Priming effects were related to soil C:N, which in turn is directly related to land cover type and soil
498 horozion (Fig. 1), but not directly to the availability of mineral nitrogen (Table 1). Priming effects
499 were indirectly determined by soil mineral nitrogen availability in the Andes (Fig. 5A), and microbial
500 N in the subarctic (Fig. 5B). However, there was not more positive priming in the soils of lowest N-
501 availability, nor decreased positive priming when more N was added. These results thus do not
502 support the N-mining hypothesis, in line with other studies (Mason-Jones et al., 2018; Wild et al.,
503 2019). The microbial N-mining hypothesis however remains an intriguing principle (Schimel &
504 Weintraub, 2003; Craine et al., 2007; Chen et al., 2014). It implies that the energy supplied to
505 microbes is used to liberate N from the bulk soil (Craine et al., 2007), however this is only the case
506 when the N obtainable from bioavailable sources (e.g. exogenous organic substrates, microbial
507 necromass) is insufficient to meet an increased microbial nutrient demand and when adjustment of

508 microbial C and N use efficiencies cannot compensate for temporal C or N shortages (Cotrufo et al.,
509 2013; Mooshammer et al. 2012; Mooshammer et al. 2014b; Spohn, 2016; Averill & Waring, 2017). It
510 is therewith not surprising to find no support for N-mining at the low rates of substrate added in this
511 study. N-mining is more likely to occur when the active microbial community grows or its
512 composition changes (Mondini et al., 2006; Li et al., 2018; Salazar et al., 2019). N-mining, in terms
513 of more N released from the soil matrix, can also occur as the result of purely physio-chemical
514 interactions between soil particles and root exudates (e.g. oxalic acid) or pH shifts in the rhizosphere
515 (Rousk et al. 2010; Keiluveit et al, 2015).

516

517 4.5 Microbial stoichiometric flexibility at low levels of substrate addition

518 A novelty of this study is that we show preferential substrate use at low levels of substrate additions
519 (30% of microbial biomass C), while it was previously assumed to occur when substrate additions
520 equal or exceed the C content of microbial biomass in soil by 50% - 1200% (Blagodatskaya &
521 Kuzyakov, 2008). For the addition rates used here, no correlation with the direction of priming has
522 been previously established. We suggest that it is the ecological threshold within which microbial
523 plasticity can buffer against the stoichiometric variability of the exogenously supplied substrates
524 (Spohn, 2016; Buckeridge & McLaren, 2020; Camenzind et al., 2020). Thus, the C:N of the added
525 substrate as such is less deterministic for soil C cycling rates, which might be better accessed through
526 microbial carbon and nitrogen use efficiencies (Manzoni et al., 2012; Mooshammer et al., 2014a, b;
527 Kyker-Snowman et al., 2019; Soares & Rousk, 2019). This is in accordance with a study on
528 grassland soils, which showed that priming effects can be disentangled from even larger gradients of
529 N-additions through plasticity of microbial carbon use efficiency (Zhang et al., 2020) and with a
530 study demonstrating highly flexible C:N:P ratios in fungal hyphae (Camenzind et al., 2020). This

may also explain why we found no support for the hypothesis that substrate use would be highest, and priming lowest, when the C:N ratio of inputs matched that of microbial biomass (Table 3). Establishing a direct link between the stoichiometry of added substrate and microbial soil C and N mineralisation rates can be further impeded when microbes selectively target soil resources of a higher nutritional value, for example high N-content and C:N ratio (Murphy et al., 2015; Rousk et al., 2016). In this case, microbial nutrient uptake can be enhanced while the cost - and loss - of C is reduced. This mechanism of selective N-targeting, which is effectively a form of carbon neutral N-mining, can explain reduced rates of SOM-mineralisation and CO_2-respiration, despite increased microbial N demand and uptake.

4.6 Scale dependency

To obtain realistic estimates of the impact of priming effects on the study system, it is important to also account for the amount of exogenous C which was added, but not metabolised by microbes at all. When the amount of experimentally added C exceeds the amount of additional C respired from SOM, C losses caused by positive priming can be cancelled out or even reversed (Liang et al., 2018; Perveen et al., 2019). This is also the case for the positive priming reported in this study, meaning that the C inputs to soils exceed the C outputs in all cases despite positive priming being reported. The true impact of priming effects on the C-balance of ecosystems remains therefore contingent between negligible (Cardinael et al., 2015) or severe (Keuper, Wild et al., 2020). Priming effects are seldom measured in situ and across geographic and temporal scales. It will be an important step to test the mechanistic insights gained in this and other laboratory studies at scales that account for the diurnal and seasonal variability of organic inputs in natural ecosystems and that take the activity of live plants into account, which act as a major sink of nutrients as well! To bridge the gap between

554 reductionist laboratory approaches and modelling the huge complexity of carbon cycling in natural
555 ecosystems, it could be helpful to further conceptualise the resource acquisition strategies of different
556 soil microbial communities and quantify the carbon inputs and nutrient uptakes of different plant
557 species and communities (Kuzyakov & Domanski, 2000; Kaiser et al., 2011; Krause et al., 2014;
558 Shahzad et al., 2015; Guyonnet et al., 2018). This would help to disentangle the link between land
559 cover type and soil C cycling and make informed decisions about land use (Jenny, 1980).

560

561 5. Conclusions

562 In Puna grassland soils of the Andean mountains and in mineral soils from the subarctic, rates of
563 SOM-mineralisation increased after substrate additions (positive priming). If we expect largescale
564 upwards shifts of treelines in the Andes and deeper rooting plants in a greening Arctic, this could
565 translate to disproportionate carbon losses from the carbon-rich soils in these regions. However, in
566 our experimental set-up, negative priming effects were also frequent and consitently correlated with
567 increased microbial substrate use. Preferential substrate use as a key driver of negative priming could
568 thus contribute to the accumulation of organic carbon in soils over time. A better understanding of
569 the mechanisms of priming effects *in situ* could help to quantify the impact of climate change
570 induced species shifts on soil C stocks with less uncertainty and improve process-based models of
571 ecosystem C cycling.

572

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Figure captions

Fig. 1 Location of the two sampling sites in A: the high altitudes of the Andean mountains in Manú National Park in Peru (3300 m above sea level) and B: the high latitudes of the Swedish subarctic in Abisko National Park 250 km north of the Arctic Circle World map is south-up centered on the Atlantic Ocean. Schematic figures show respective treelines with numbers of soil C:N ratios of organic (ORG) and mineral (MIN) soil horizons given within each figure for the soils above and below the treeline. Smaller pictures show A1: sunrise in the Peruvian Andes, A2: topographic map indicating the sampling region with a white triangle, A3: transition from high Andean tropical mountain forest into Puna grassland, A4: soils of tropical mountain forest (left) and Puna grassland (right), B1: sunset in the boreal subarctic, B2: topographic map indicating the sampling region with a white triangle, B3: transition from boreal birch forest into tundra heath,B4: soils of birch forest (left) and tundra (right)

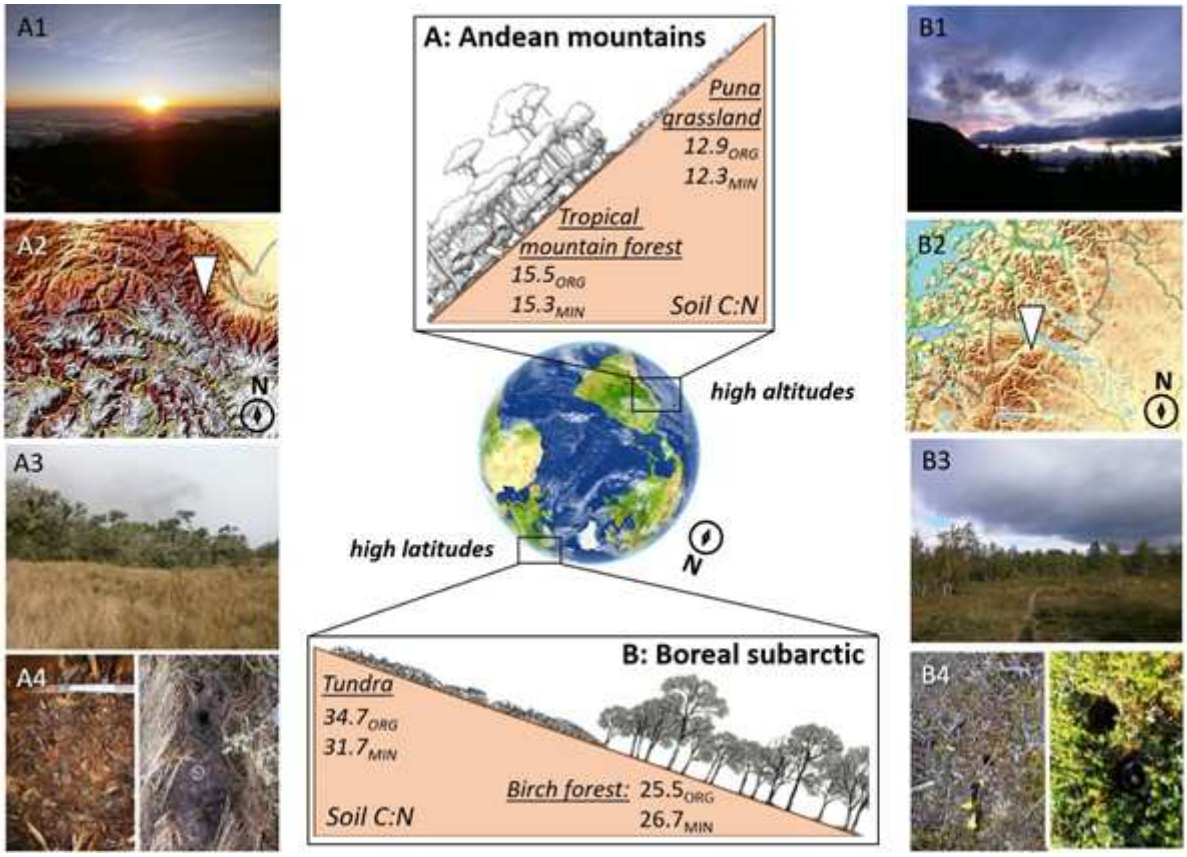
Fig. 2 Soil respiration (µg CO_2-C per unit of g soil C per hour) from the eight treeline soils studied Each soil was amended with four substrate treatments, all of which contained glucose (glu) as C source, and three contained also nitrogen (N) at different concentrations (C:N 7:1, 17:1 and 71:1), as indicated in the legend in the upper right figure. Respiration was measured during 504 hours (21 days) in controlled laboratory soil incubations. Please note different scale of y-axis scales. One panel per soil type: Andean Forest Organic (AFO), Andean Forest Mineral (AFM), Andean Puna Organic (APO), Andean Puna Mineral (APM), Boreal Forest Organic (BFO), Boreal Forest Mineral (BFM), Boreal Tundra Organic (BTO), Boreal Tundra Mineral (BTM)

Fig. 3 Priming effects and substrate use in Andean (a-d) and boreal (e-h) treeline soils. Left panels show absolute priming effects ([µg C] [g soil C]$^{-1}$) and magnitude of priming (%) and right panels show absolute ([µg C] [g soil C]$^{-1}$) and relative (%) substrate use. Each soil was amended with four substrate treatments, all of which contained glucose (glu) as C source, and three contained also nitrogen (N) at different concentrations (C:N 7:1, 17:1 and 71:1), as indicated in the upper right panels for each region. Boxes show median lines and interquartile ranges. Statistically significant results of three-way ANOVA testing for correlation between each of the observed variables (priming effect or substrate use) and the explanatory variables (land cover, soil horizon and treatment) are provided in each plot with asterisk indicating the significance level at < 0.001 '***' ≤ 0.01 '**' ≤ 0.05 '*'. The soil types are Andean Forest Organic (AFO), Andean Forest Mineral (AFM), Andean Puna Organic (APO), Andean Puna Mineral (APM), Boreal Forest Organic (BFO), Boreal Forest Mineral (BFM), Boreal Tundra Organic (BTO), Boreal Tundra Mineral (BTM)

Fig. 4 Relationship between substrate-use (%) and magnitude of priming (%) in the eight soil types studied Plots show individual data points, the resistant line in black, the least square line in red and p and *r* values. Strongest correlation ($p < 0.1 \wedge r > 0.45$) in organic soils from the subarctic (BFO and BTO) and forest soils of the Andes (AFO and AFM)

Fig. 5 Main drivers of the observed priming effects and substrate use for treeline soils in A) the Andes and B) the boreal subarctic Priming was modelled using linear regression (results in black) and substrate use was modelled using beta regression (results in red). Numbers displayed next to the arrows are the coefficients of the respective variable and asterisk indicate the significance levels at < 0.001 '***' ≤ 0.01 '**' ≤ 0.05 '*'

Figures



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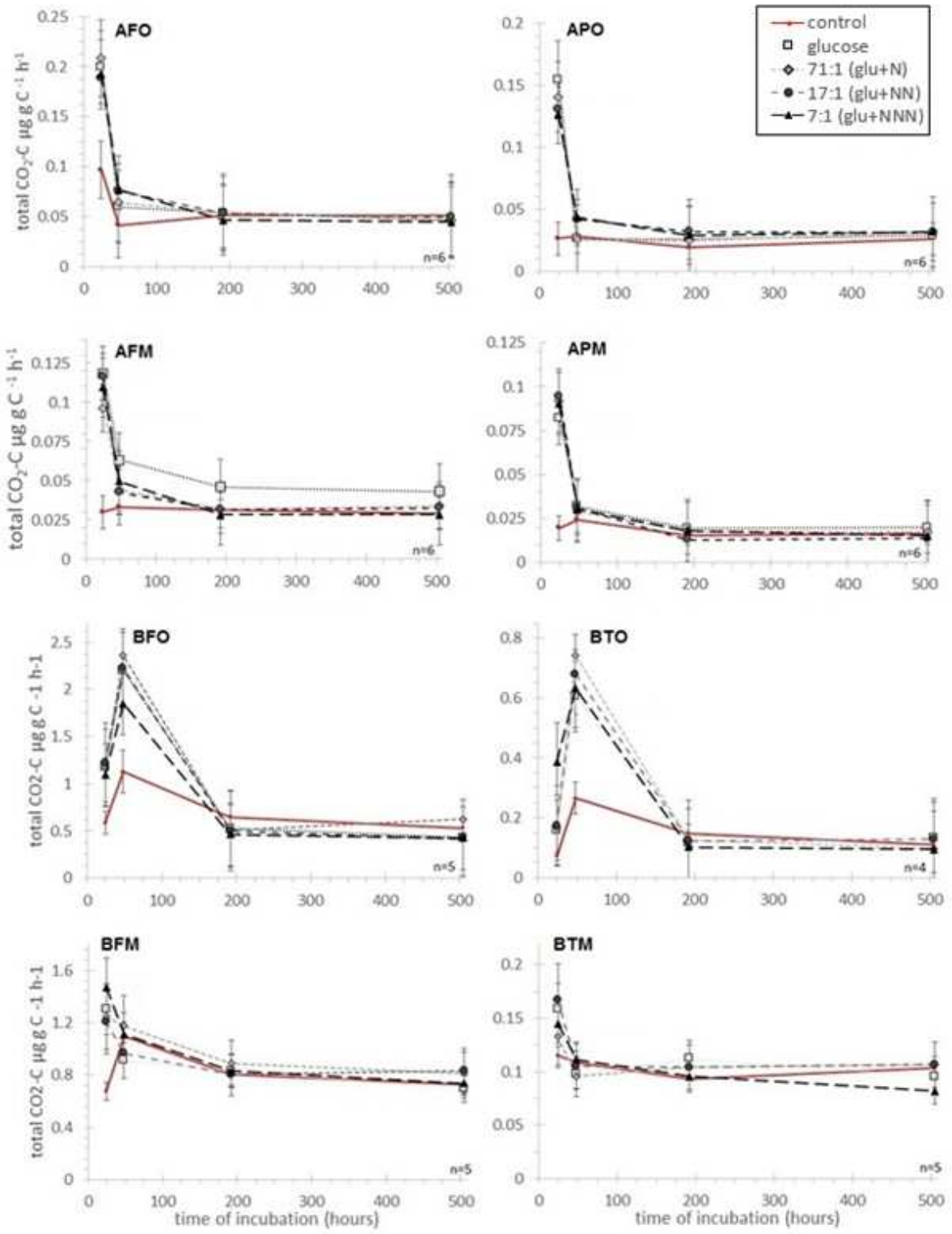
Location of the two sampling sites in A: the high altitudes of the Andean mountains in Manú National Park in Peru (3300 m above sea level) and B: the high latitudes of the Swedish subarctic in Abisko National Park 250 km north of the Arctic Circle World map is south-up centered on the Atlantic Ocean. Schematic figures show respective treelines with numbers of soil C:N ratios of organic (ORG) and mineral (MIN) soil horizons given within each figure for the soils above and below the treeline. Smaller pictures show A1: sunrise in the Peruvian Andes, A2: topographic map indicating the sampling region with a white triangle, A3: transition from high Andean tropical mountain forest into Puna grassland, A4: soils of tropical mountain forest (left) and Puna grassland (right), B1: sunset in the boreal subarctic, B2: topographic map indicating the sampling region with a white triangle, B3: transition from boreal birch forest into tundra heath,B4: soils of birch forest (left) and tundra (right)



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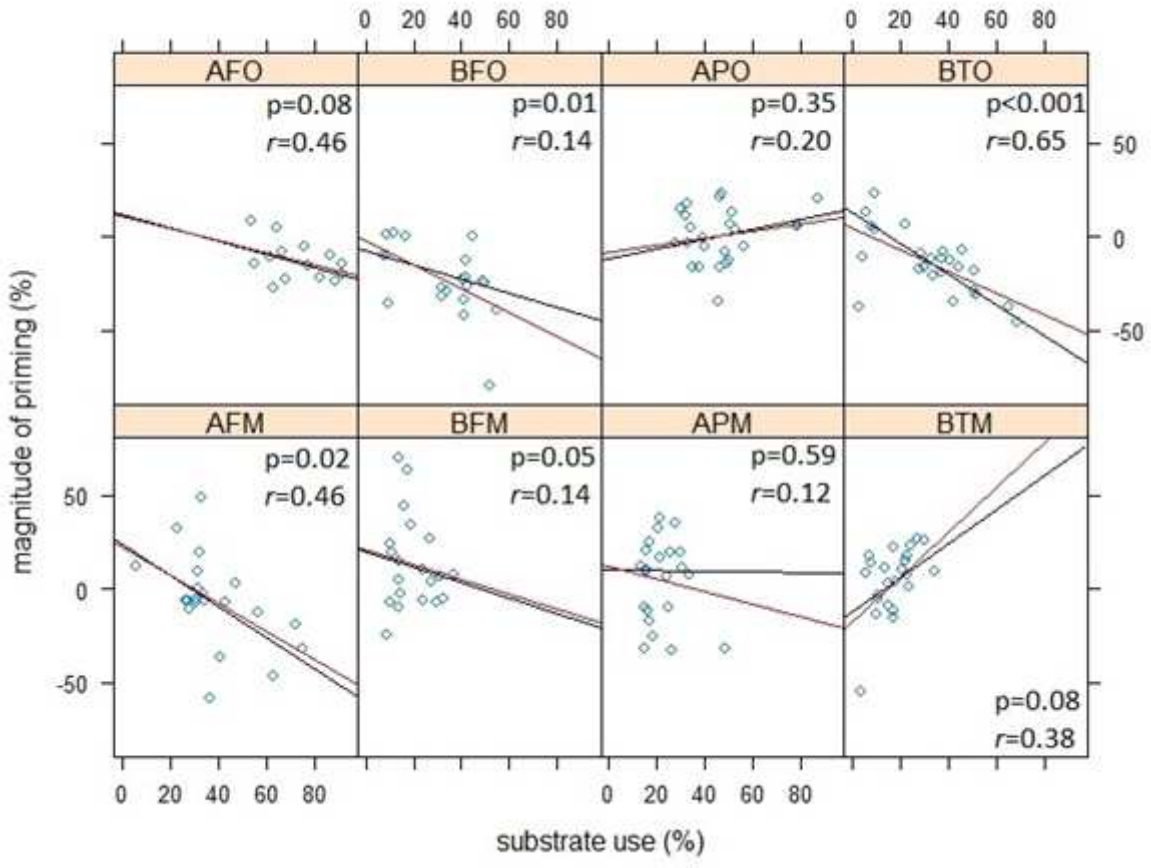

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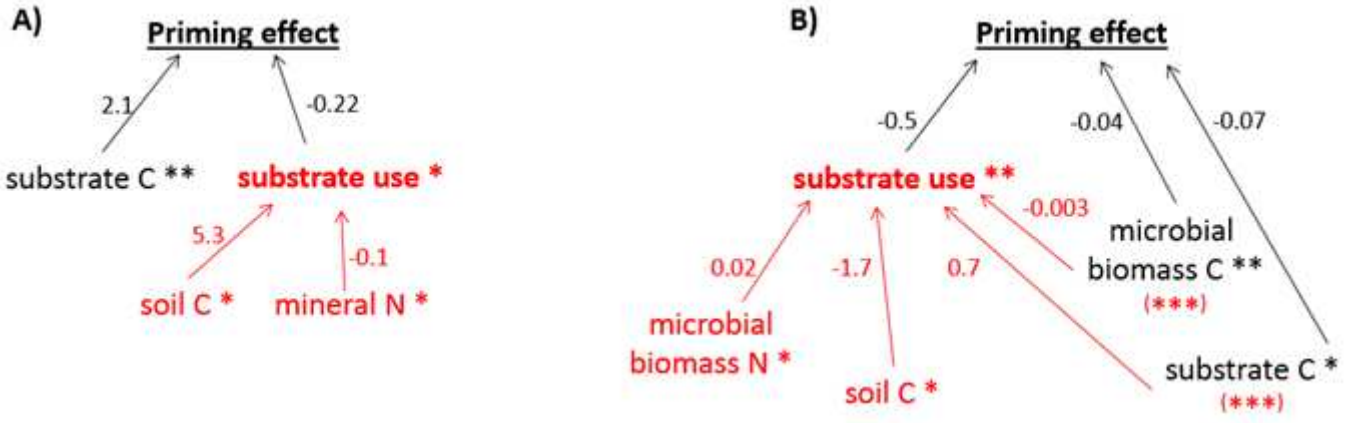

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Main drivers of the observed priming effects and substrate use for treeline soils in A) the Andes and B) the boreal subarctic Priming was modelled using linear regression (results in black) and substrate use was modelled using beta regression (results in red). Numbers displayed next to the arrows are the coefficients of the respective variable and asterisk indicate the significance levels at < 0.001 '***' ≤ 0.01 '**' ≤ 0.05 '*'

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