

# **Above- and belowground linkages shape responses of mountain vegetation to climate change**

Frank Hagedorn<sup>1\*</sup>, Konstantin Gavazov<sup>1†</sup>, Jake M. Alexander<sup>2†</sup>

<sup>1</sup>Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

<sup>2</sup>Institute of Integrative Biology, ETH Zurich, Universitätstrasse 16, 8092 Zürich, Switzerland

\* corresponding author: [frank.hagedorn@wsl.ch](mailto:frank.hagedorn@wsl.ch)

† Equal contribution to authorship

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## 1   **Abstract**

2   Upwards shifts of mountain vegetation lag behind rates of climate warming, partly related to  
3   interconnected changes belowground. Here, we unravel above and belowground linkages by  
4   drawing insights from short-term experimental manipulations and elevation gradient  
5   studies. Soils will likely gain carbon in early successional ecosystems, while losing carbon as  
6   forest expands upwards, and the slow high-elevation soil development will constrain  
7   warming-induced vegetation shifts. Current approaches fail to predict the pace of these  
8   changes, and how far they will be modified by interactions among plants and soil biota.  
9   Integrating mountain soils and their biota into monitoring programs, combined with  
10   innovative comparative and experimental approaches, will be crucial to overcome the  
11   paucity of belowground data and to better understand mountain ecosystem dynamics and  
12   their feedbacks to climate.

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## Introduction

The distinct zonation of mountain vegetation has inspired generations of biologists interested in how environmental – and especially climatic – variation shapes ecosystem structure and function (1, 2), and mountain plants have served as bioindicators for the impacts of climate changes over the last century (3). Despite comprising only 12% of the terrestrial surface, mountains host high levels of biodiversity and provide crucial ecosystem services (e.g. carbon storage, raw material provisioning, natural hazard protection, water reservoirs) with far reaching effects on lowland ecosystems and global climate (4). Mountain ecosystems are experiencing especially strong climate warming (5). The expected warming of 2-4°C this century (5) could extend vegetation zones and the thermal limits of plant life upwards by as much 300-600 m in elevation, with profound consequences for ecosystem functioning (Figure 1). But while responses of mountain vegetation have been widely studied aboveground, there are parallel changes occurring in the “dark” side of ecosystems belowground, where plant roots and their associated microbial communities form a complex but largely unknown world in the soil. Alpine soils above treeline store more than 90% of ecosystem carbon (4), and thus even small changes in soil carbon storage will have a large effect on the overall climate balance of mountain ecosystems (6). Soils also provide nutrients to sustain plant growth, which is strongly nutrient-limited in mountain plants (7, 8), and so changes in nutrient availability and in soil microbial community composition could represent a strong modifier of vegetation shifts in a warming climate (9). In our review, we show how plant communities, soils and their associated microorganisms are interlinked in mountain ecosystems, identify how belowground ecosystems might respond to vegetation shifts in a changing climate and, finally, indicate how short- and long-term changes in carbon and nutrient cycling may feedback to climate and modify vegetation shifts.

## Elevation shifts of mountain vegetation

Mountains have characteristic vegetation belts transitioning from forest, heathland and alpine grassland up to the nival zone with a permanent snow cover (Figure 2). While vegetation forms a mosaic controlled by parent materials, soil development and topography at the local scale, climate conditions are of primary importance for the formation of distinct vegetation belts along mountain slopes, such as at treeline (10–12) and at the upper limit of vascular plant life (13). Temperatures belowground are more buffered than aboveground and remain lower for the duration of the short vegetative season, critically limiting plant growth below  $\sim 5^{\circ}\text{C}$  (4, 14). Due to their climate sensitivity, shifts in the distributions of individual plant species and vegetation types to higher elevations therefore provide evidence for the impact of climate warming on natural ecosystems worldwide (3, 15). Revisiting Humboldt's plant surveys documents an upward migration of c. 250 m over 215 years (2). The colonization of new species has accelerated this century on European mountains (3), and even the upper limit of continuous plant life has advanced at high elevations, such as in the NW Himalaya (13), in striking synchrony with increased rates of climate warming (3). Treelines are expanding at 52% of 166 sites around the world (Figure 1, 12), and available evidence also suggests that shrublines are advancing upwards in the northern hemisphere, consistent with increasing shrub encroachment in tundra vegetation at high latitudes (16).

Although upward elevational shifts provide strong evidence for the impact of climate change on mountain vegetation, they are also remarkably heterogeneous. On average, rates of range expansion lag significantly behind advances in isotherms on mountains (2, 15), and average values conceal huge variation in the rates, and even directions, of range changes. This variation can be explained by a complex suite of interacting drivers of species'

distributions and abundances, including variation in species' demography and physiological responses to changing climate, interactions among species, and the physical environment (17). Notably, climate warming effects on vegetation are frequently superimposed by land-use changes in Eurasian mountains and downward range shifts can occur as climate change alters water availability, especially in more arid (18) and subtropical (19) mountain regions.

Interactions at the vegetation-soil interface can play a key role in shaping variation in species' responses to warming. For example increasing canopy cover with shrub and treeline advances shades and cools the soil during the growing season, which is likely to slow further vegetation shifts (4, 10, 16). Range expansions can also be constrained by insufficient water retention and low nutrient availability due to low organic matter content in poorly-developed high-elevation soils (20), while plants that successfully establish at higher elevations tend to be those that can colonize open scree (21). Soil development will therefore be a key factor limiting the expansion of species to higher elevations with climate warming (22), and could explain why diffuse timberlines are more likely to advance, while abrupt ones, that are more constrained by soil development, drought and wind, do not (12).

In addition to physical and chemical properties of the soil, rates of plant range expansion can be influenced by biotic interactions in the soil. Warmer temperatures towards the soil surface might provide shallow-rooted herbs with a competitive advantage over woody plants (14), potentially contributing to negative effects of alpine grassland and shrubby vegetation on tree recruitment (11) and slowing forest expansion. Plants also engage in a multitude of positive and negative, direct and indirect interactions with soil organisms (23). Although evidence from mountain systems is so far limited, changes to plant-soil biota

interactions are likely to influence plant responses to changing climate (17), similar to their influence on the dynamics of biological invasions.

## **Belowground impacts of climate change in mountains**

Vegetation shifts are paralleled belowground, where plants and soils interact at time scales ranging from hours to millennia (Figure 3), spanning the extremely rapid transfer of photosynthetic products to roots, mycorrhizal fungi and other root-associated microorganisms, to the formation of soil organic matter (SOM) over thousands of years. Climate change will therefore have short-term effects on ecosystems by modifying above and belowground linkages in current species assemblages, as well as longer-term impacts that unfold as species shift their distributions in response to climate warming. Inference about future climate change impacts therefore requires complementary approaches to study these processes, that have included (i) manipulative experiments identifying short-term effects of climate on the interaction between plants and soils (24, 25), and (ii) “space-for-time” substitutions along elevational gradients, which assume that the spatial changes in ecosystem structure and function moving from high to low elevation are analogous to longer-term temporal trajectories of mountain ecosystems under climatic warming (26, 27).

## **Short-term and direct effects of climate warming**

Higher temperatures accelerate the metabolic activity of organisms both above and belowground, which strongly impacts carbon (C) and nutrient cycling. In mountain ecosystems, experimental warming stimulates plant productivity unless water is limiting (9,

28, Table S1). Heating soils by 4°C at the alpine treeline and in montane forests increased soil CO<sub>2</sub> effluxes by 40-50%, resulting from both accelerated rhizosphere activity and enhanced soil C mineralization (24, 29). These responses are likely transient as microbial communities acclimate to warmer conditions, without significantly changing their community structure and soils deplete in readily available C until a new quasi-equilibrium is reached (29–31). The magnitude and duration of warming responses vary among studies, but longer-term experiments observed accelerated soil C mineralization for more than a decade (29, 30, Table S1). Higher C losses through soil C mineralization tend to be compensated by increased soil C inputs from plants, resulting in small net effects on the soil C balance as compared to the pronounced warming effects on soil C fluxes (25, 32). Despite considerable research efforts, there is no consensus on the magnitude of warming effects on soil C storage (25). Soils of cold climates such as at high latitude or elevation seem particularly vulnerable to warming because they contain inherently high C stocks and high amounts of labile C, potentially promoting strong and sustained soil C losses (24, 29, 33). However, warming effects are contingent on water availability, and in semi-arid mountains the soil C balance appears less dependent on projected temperature changes than on variation in the amount and timing of precipitation (34). Impacts of climatic warming is especially large in permafrost soils that only exist above the shrubline in the Alps, but reach down to the subalpine zone in continental mountain ranges at mid and northern latitudes. On the Tibetan plateau, for instance, permafrost collapse has resulted in a 32% decline in soil C stocks in surface soils (35), and an alpine tundra meadow with discontinuous permafrost in Colorado was found to represent a substantial net C source to the atmosphere by releasing C from ancient buried soil C (36).

Plant growth in mountain ecosystems is strongly limited by soil nutrients (7), and in particular by nitrogen (N) (8), of which more than 90% is bound to organic matter. N availability for plants is therefore predominantly driven by microbial mineralization, at rates that are naturally constrained by low temperatures in mountain ecosystems to less than 2% of total soil N per year (37). More rapid processing of soil organic matter (SOM) due to warming therefore enhances N cycling, approximately doubling the release of plant available N and thereby stimulating the growth of some plant species (9, 27, 38, Table S1). Increased N contents in foliage, either resulting from higher N availability or a higher abundance of nitrophilous plants, can promote litter decomposition, further stimulating the release of N and generating a positive feedback to soil N availability (39). Conversely, in some cases enhanced plant productivity can bind N in living biomass, decreasing available N (9). Warming-induced changes in N availability are also reflected in soil microbial communities. Soil warming at treeline led to the proliferation of ectomycorrhizal fungi (ECM) adapted to high N availability (40), which may have further longer lasting consequences in these ecosystems, due to the importance of mycorrhizal fungi for soil C cycling and plant nutrient supply (41).

### **Longer-term above and belowground linkages**

Over longer time scales, the upward migration of mountain vegetation impacts the entire soil system. While increasing canopy height caused by shrub and treeline advances cools the soil during the growing period (4), it warms it during winter by promoting the accumulation of an insulating snow cover (16). Higher winter soil temperatures stimulate soil processes driven by microbial communities (36, 42), and enhances N mineralization that stimulates

shrub and tree growth in high elevation and latitude systems (37). On decadal, centennial or even longer time scales, vegetation primarily affects the soil system by its influence on SOM. SOM is of central importance for climate feedbacks, represents a key reservoir for water and nutrients, and serves as a substrate for microbial communities. However, the impact of vegetation has to be disentangled from other key factors affecting SOM – climate and geochemistry – that can be of similar importance (31, 43). To better understand how these processes might play out in response to future climate change, we can gain insight from studies of vegetation-soil interactions across elevation gradients, under the assumption that these represent plant-soil systems in quasi-equilibrium with current climate (27).

The large reservoir of SOM encompasses a continuum of compounds which can be separated into old mineral-associated organic matter (MOM) that is stabilized through its interaction with mineral surfaces and labile young particulate organic matter (POM), primarily consisting of decomposing plant residues (Figure 3, 31). In temperate soils, POM contributes only 10% of total SOM stocks, but high elevation soils typically have POM fractions as high as 30-60%, including organic layers on top of mineral soils (26, 33, 44, 45). On poorly weathered bedrock, SOM can even be entirely comprised of POM. High POM accumulation reflects slow litter decomposition due to low temperatures, the recalcitrant nature of plant residues with high contents of polyphenols (45–47), and the low abundance of soil fauna, especially earthworms, which limits the incorporation of litter into mineral soils (48). Particulate organic matter represents a soil C pool that is highly vulnerable to loss when plant inputs are altered through plant community shifts (e.g. by expansion of broadleaf forests) or when temperature constraints on microbial and faunal decomposition are alleviated by climatic warming.

Along elevation gradients, soil C stocks are very small in early successional alpine ecosystems where low C inputs from plants and slow weathering retard SOM accumulation (Figures 2 and 3, 49, 50). Soil C stocks typically peak in high-elevation forests, at treeline or in the shrub zone above, reaching up to 20-30 kg C m<sup>-2</sup> in the Swiss Alps, Andes, and Himalaya, and then decline in low-elevation forests, which have 5-20 kg C m<sup>-2</sup> smaller soil C stocks (26, 44, Table S1). This decrease partially offsets C gains with increasing biomass (averaging 12 kg C m<sup>-2</sup> in Swiss forests), and can be explained by faster litter decomposition, higher litter quality, and a decreasing input of below as compared to aboveground litter (e.g. 51). Moreover, forest trees may release labile root exudates, fuelling microbial metabolism that in turn induces C losses from older SOM in a process known as priming (6). Shifts in the fungal community from ericoid mycorrhiza and arbuscular mycorrhiza under shrubs and grasses to ECM in forests (Figure 2) may cause further soil C losses through mining for nutrients. In their quest for SOM-bound nutrients, ECM secrete powerful oxidative enzymes to outcompete free-living saprotrophic fungi and bacteria, which further promotes SOM decomposition (e.g. 41). At the subarctic treeline, soil C stocks were found to decrease by 70% along transects from ericaceous shrubs to deciduous shrubs and forests (6). The decline was associated with an increasing C turnover and was closely correlated with ECM productivity, consistent with nutrient mining (6).

Elevational patterns of vegetation and SOM are partly reflected in soil microbial communities. Microbial biomass and the contribution of fungi as compared to bacteria typically increase from the nival zone to treeline, but decreases in forest at lower elevations (26, 50, 52, Table S1). But at the species level, elevational patterns in soil microbial diversity are heterogeneous and only weakly related to plant diversity (53). Early successional alpine habitats are an exception. Here, a higher microbial dependence on plant organic inputs

provides for a tighter positive relationship between plant and microbial taxonomic richness (50, 52). Nonetheless, elevational turnover in microbial community composition can be pronounced and varies according to plant type (54), suggesting that there will be interdependencies among plant and soil microbial responses to climate warming.

## **Implications of above and belowground linkages in mountains**

Collectively, the patterns of above and belowground linkages in mountain ecosystems that have been observed from short-term experimental manipulations and across elevation gradients lead to several insights into how mountain vegetation and soil ecosystems might respond to changing climate, which we outline below.

1. Shifts in vegetation and the associated belowground system will feedback to climate warming through their impact on soil C, but this effect will differ between vegetation zones on mountains. Because of the peak in soil C storage and labile POM around treeline, soils are expected to gain C with advances of alpine grass and heathlands, but are highly vulnerable to C loss when forests shift upwards. The latter might at least partly outweigh the increased C storage in tree biomass. Gradient studies provide no information about how fast these changes could occur, but soil C dynamic is known to follow a “slow in, fast out” principle, with a disparity between the rates of soil C gains and losses, as observed following land-use change (55). Overall, this pattern suggests that soil carbon will be lost with vegetation shifts in a warming climate, but the rates remain unknown. Studies along glacier forefields lend

support for a slow SOM build-up ( $\sim 2 \text{ kg C m}^{-2}$  in 100 years), due to slow vegetation succession and low weathering impeding SOM stabilization (49).

2. Plant migration and soil development operate at different timescales, such that chemical and physical processes belowground will constrain the rate of vegetation changes in mountains. The slow SOM accumulation and low nutrient availability in early-successional soils will restrict warming-induced shifts for a number of species, especially for those whose thermal tolerance would allow them to advance to high elevations but which require SOM and nutrient rich soils (21). Paleobotanical studies show that time lags between suitable temperatures and upward migration of subalpine forests during the Holocene were as long as 3000-6000 years, possibly due to slow soil development following deglaciation (20). Nonetheless, feedbacks between plants and soil conditions will influence the rate of vegetation change, potentially facilitating plant establishment and growth. For example, SOM accumulation by cushion-forming plants facilitates the establishment of new plants in high alpine ecosystems (56), while snow accumulating around taller plants prevents soils from freezing, which improves N availability and promotes plant growth (16, 37).

3. Rhizosphere microbial communities are central to many soil processes and microbial community composition is likely to modulate the responses of mountain vegetation to climate change in both the short and long term. Asynchrony in the rates at which plants and their associated soil biota establish at higher elevations could impact plant population and community dynamics in the longer term (57). For instance, the absence of key mycorrhizal fungi (58) or presence of soil pathogens (59) can limit the range expansions of trees, although the quantitative importance of such effects is poorly understood.

## 243    **Conclusions and future prospects**

244    Above and belowground linkages play a central role in the responses of ecosystem processes  
245    in mountains to climate warming, but in contrast to well documented shifts in plant  
246    assemblages (2, 3), changes in belowground systems remain largely unknown. Historically,  
247    high-elevation soils have not been analysed quantitatively nor archived, and we still lack  
248    basic data on belowground plant productivity, the diversity and functional role of soil  
249    microbial communities, nutrient mineralization rates and SOM stocks. To improve our  
250    limited understanding of plant-soil interactions in mountains, we need to address the  
251    following key questions:

252    1. How quickly will vegetation and belowground systems shift in response to changing  
253    climate, and how big will be the corresponding feedbacks to climate?

254    2. What is the role of parent material and its weathering on soil development and SOM  
255    accumulation in mountain ecosystems and how is it linked to vegetation change?

256    3. To what extent can warming-induced increases in nutrient availability keep pace with the  
257    increasing nutrient demands of upward shifting plant communities?

258    4. What are the key drivers of soil biota across elevation gradients, how are they linked to  
259    vegetation, and what is the functional role of microbial communities in range shifts?

260    Elevational gradients document fundamental changes in the belowground system along  
261    mountain slopes, while soil warming experiments frequently reveal that soil processes such  
262    as increased C and N mineralization are transient, counteracted by feedbacks and difficult to  
263    detect in the large soil reservoir. Reconciling these sometimes conflicting observations is  
264    challenging; experiments rarely capture longer-term changes to ecosystems caused by

turnover in species composition as range shifts occur, while gradient studies provide no information about the timescales of range shifts and ecosystems changes. Yet impacts of climate change on ecosystem functioning and climate feedbacks on timescales of decades to centuries will be governed by the non-equilibrium dynamics occurring during range shifts. There is therefore a need to bridge this gap and to better understand the rate and impacts of shifts in vegetation and belowground ecosystems, using a suite of approaches.

Firstly and most urgently, soils and their biota should be integrated into existing monitoring programs of vegetation change (e.g. GLORIA (3, 52)) and national soil inventories, setting a baseline for assessing belowground changes over the coming decades. Secondly, temporal changes in soil ecosystems and their interactions with vegetation might be extrapolated by sampling current soils across chronosequences of vegetation changes that have been documented from historical photographs, maps or satellite images, similar to studies conducted on glacial forefields (37, 49). Thirdly, comparative studies of plant-soil interactions across replicated elevation gradients within and between regions remain scarce (27), yet can exploit variation in the elevational covariance between climate, soil, land-use and biological communities to gain insight into drivers of ecosystem structure and function, while filling data gaps in remote and understudied mountain regions. Finally, experiments might be conducted that approximate non-equilibrium conditions by manipulating climate and assembling the novel combinations of plants, soils and soil organisms that are expected following range shifts (57), and studying their impacts on ecosystem processes, ideally in combination with elevational gradient studies.

In many respects, the belowground still represents the “*Terra incognita*” of mountain ecosystems, and despite its importance for ecosystem functioning and global climate, the linkage between below- and aboveground ecosystems is one of the least understood research frontiers. Recent advances in molecular tools make it increasingly possible to open the “black box” of soil ecosystems, hopefully motivating renewed efforts to collect basic data on belowground process. Such information will be essential to accurately predict how current and future vegetation will interact with soil biota, soil chemistry and physics, and how these interactions will feedback to climate change.

## List of Figures

**Figure 1.** Mountain landscapes in transition. Comparisons of present and historic photographs give evidence for the upward migration of trees to higher elevations in remote areas of the Ural mountains in response to the climatic warming in the 20<sup>th</sup> century (from 37). The forest expansion is paralleled by changes in the belowground ecosystem.

**Figure 2.** Mountain ecosystems above and below the ground. Vegetation forms distinct belts across climatic gradients in elevation, spanning the nival zone with cryptogams and cushion plants, alpine grassland and heathlands, and subalpine forests (1, 2, 4). These vegetation zones are paralleled belowground. The contribution of roots to total plant biomass typically increases with elevation (51), as perennial plants relocate resources belowground to survive harsh alpine winters. Early successional ecosystems store very little soil organic matter

(SOM) due to low plant inputs and slow weathering (49) and host highly specific microbial taxa (50, 52, 60). Alpine grasslands have typically high SOM contents in the topsoil as low temperatures impede the decomposition of annual inputs of fine roots and leaf litter (45). The herbaceous vegetation relies strongly on symbiotic associations with arbuscular mycorrhizae for nutrient supply (60). Soils below the shrubline are characterized by a thick organic layer, consisting of recalcitrant plant residues from dwarf shrubs and coniferous trees (46, 47), with abundant ericoid and ectomycorrhizae, and free-living saprotrophs (41, 46, 54). The low abundance of soil fauna, especially of earthworms, impedes the physical incorporation of litter into mineral soils (48). In montane forests, the increasingly favourable climate accelerates the processing of SOM, leading to a thinner organic layer (33, 37, 44) and a higher diversity and abundance of ectomycorrhizal fungi. See Table S1 for more details on belowground elevational patterns.

**Figure 3.** Above- and belowground linkages in a changing climate. Mountain plants transfer more than 50% of assimilated carbon (C) to roots, to associated mycorrhizal fungi in exchange for soil nutrients, and to free-living bacteria and fungi feeding on rhizodeposits. Within hours, photosynthetic products are allocated belowground, nourishing soil organisms, and are respired back to the atmosphere as CO<sub>2</sub> (14, 31). On an annual timescale, leaf and root residues enter the soils and are broken down and transformed by soil biota. Only a small fraction — microbial products — are stabilized by reactive minerals formed during weathering and persist in the soil for centuries to millennia (31). Consequently, soil organic matter (SOM) consists of a continuum of compounds from litter to particulate soil organic matter (POM) comprised of decomposing plant residues and more stable mineral-associated organic matter (MOM) (33, 43). Climate change affects above and belowground

linkages either directly through higher temperatures accelerating C and nutrient cycling, or indirectly as vegetation changes alter the quantity and quality of litter inputs into soils and modify the microclimate. Because SOM represents the key reservoir for water and nutrients and hosts soil microbial communities, changes in SOM will feedback to mountain vegetation shifts in a warming climate.

**Figure 4.** Climate warming impacts on mountain vegetation, soils and their biota either directly or indirectly through elevational shifts of plant communities. See Table S1 for pertinent examples from the literature.

## **List of Supplementary Materials**

### **Table S1.**

References listed from 61 to 99 appear only in the Supplementary Materials

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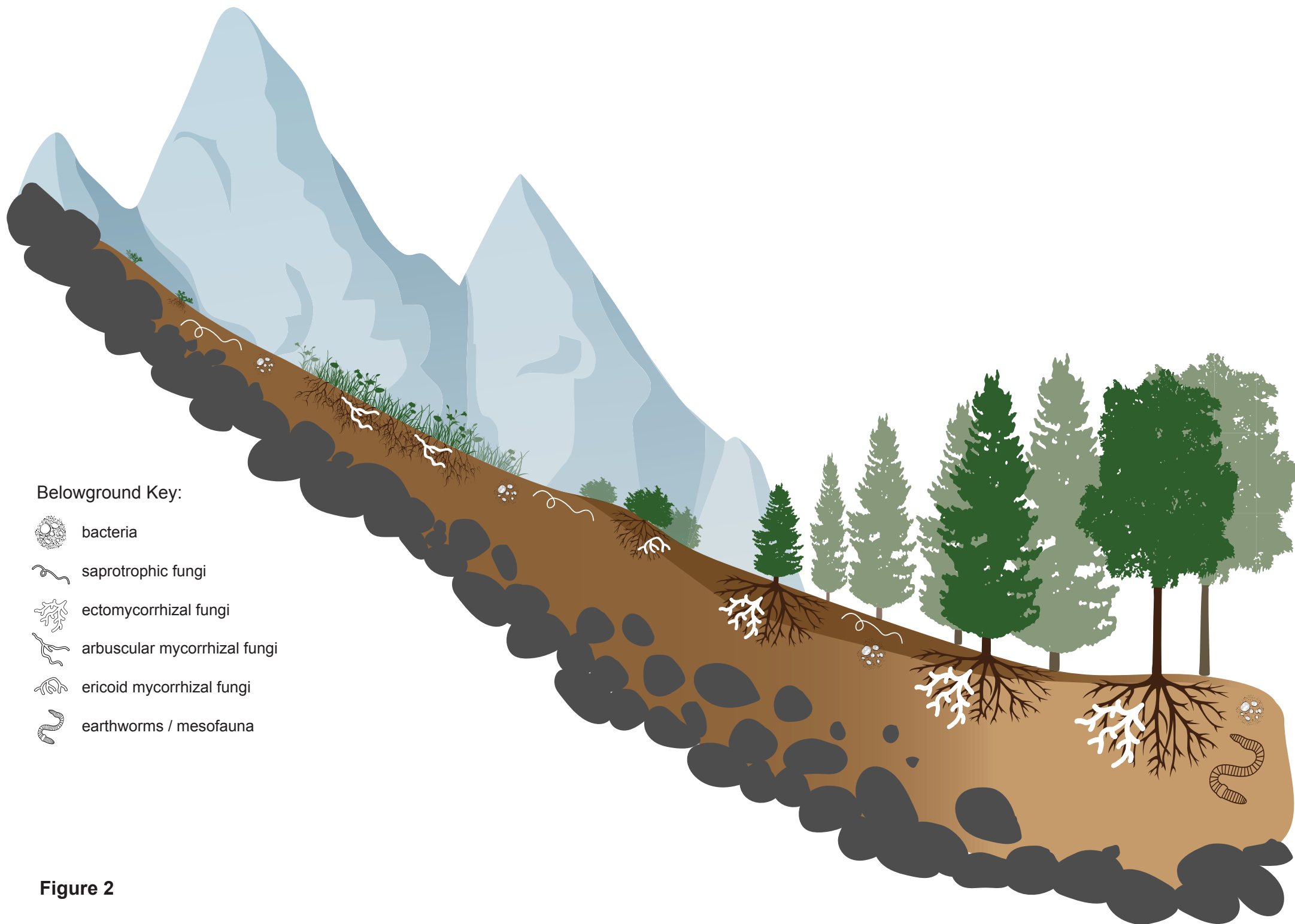
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**Figure 1**



**Figure 2**

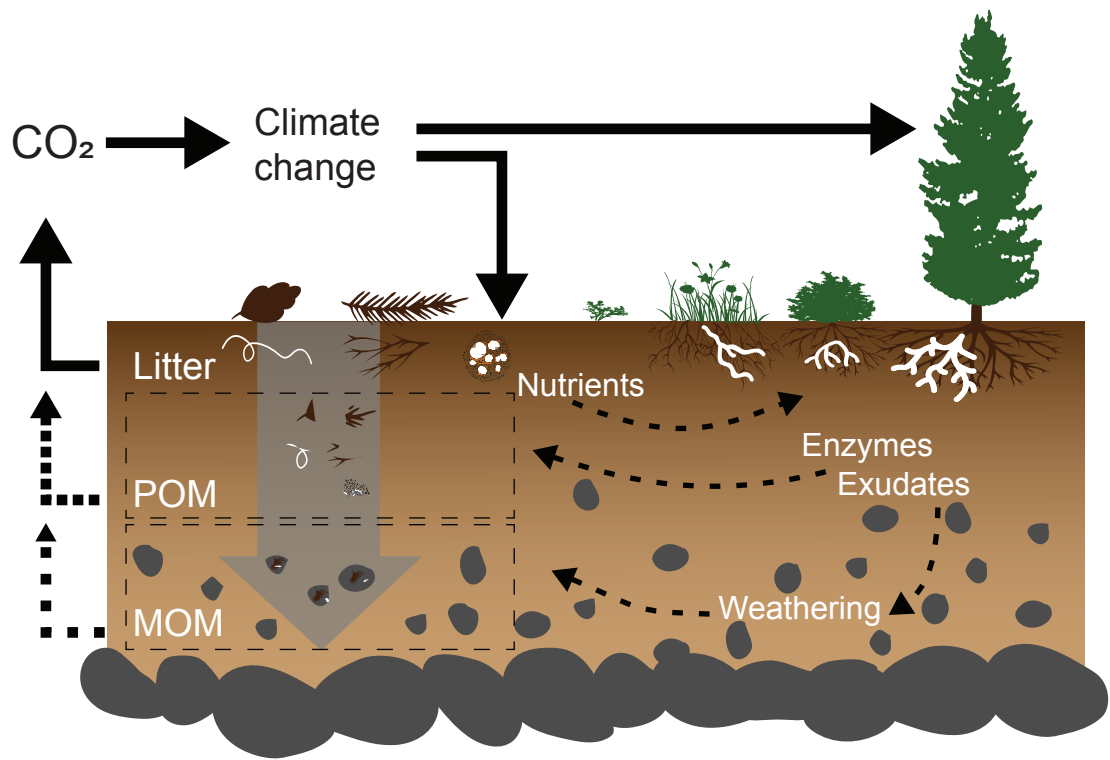
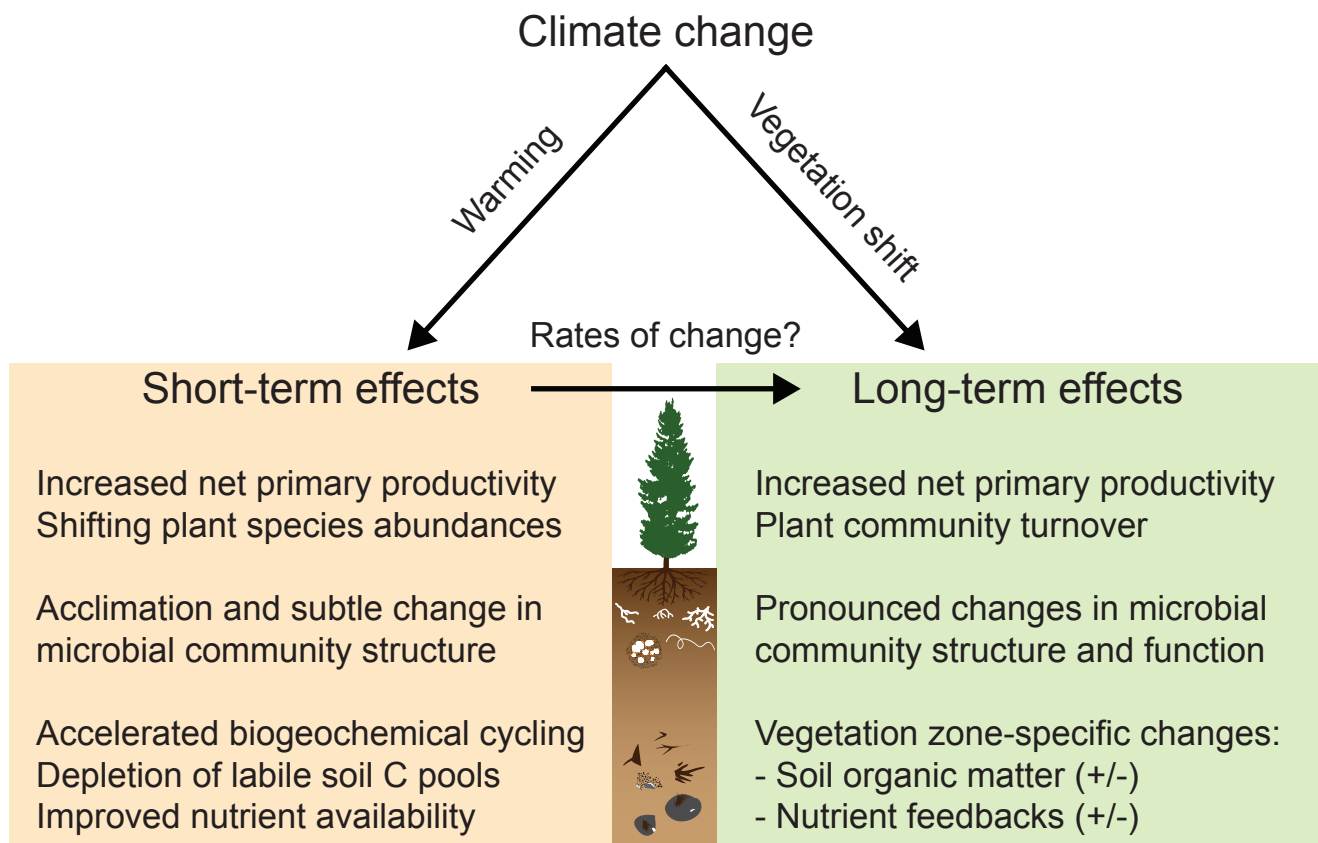


Figure 3



**Figure 4**



## Supplementary Materials for

### **Above- and belowground linkages shape responses of mountain vegetation to climate change**

Frank Hagedorn, Konstantin Gavazov, Jake M. Alexander

correspondence to: [frank.hagedorn@wsl.ch](mailto:frank.hagedorn@wsl.ch)

#### **This PDF file includes:**

Tables S1

**Table S1.**

Supporting examples of belowground responses to experimental manipulations and along natural gradients in mountain ecosystems or in relevant similar ecosystems. ECM, ectomycorrhizal fungi; POM, particulate organic matter; SOC, soil organic carbon; SOM, soil organic matter.

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
Plant productivity and community composition	Experimental warming; various approaches	<b>Alpine meadow, Colorado; Treeline (Switzerland, Colorado):</b> Thermophilization of plant communities with decreased growth of forbs but increased growth of shrubs and an increased productivity (32, 61, 62) unless water is limiting such as in dry mountain ranges (28).	Warming experiments are in accordance with vegetation monitoring, but effect sizes are smaller than along natural temperature gradients (63).	Results are mostly short to mid-term and site specific. Warming by open-top chambers is small in the soil (approx. 1°C). Warming for whole ecosystems by electric power is experimentally difficult and thus mostly confined to surface soil whilst plant canopy remains non-warmed. Reduced soil water content can have a confounding effect.
---- " ----	Transplant experiment; warming; N-P-K fertilization; grazing exclosure	<b>Alpine meadow, Finnish Lapland:</b> Disproportional growth of lowland plants within the alpine community favoured by warming and fertilization, but cancelled out by grazing (64).	Grazing limits plant range expansion in elevation, but if kept low, the colonised alpine communities become more responsive to warmer temperatures and intensified nutrient cycling.	Site specific results for a set of forb species only.
Root biomass	Soil warming by heating cables	<b>Alpine treeline:</b> 38%-decrease of fine root biomass after 6 years of warming (61); <b>Hardwood forest:</b> 60% decline in fine roots after 7 years of warming (65); <b>Boreal forest:</b> warming reduced root longevity (66).	Reduced belowground plant allocation and thus smaller soil C inputs. Faster root turnover may partly compensate for the smaller root biomass	Results are mostly short to mid-term and site specific. Warming by open-top chambers is small in the soil (approx. 1°C). Warming for whole ecosystems by electric power is experimentally difficult and thus mostly confined to surface soil whilst plant canopy remains non-warmed. Reduced soil water content can have a confounding effect.

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
Root biomass	Elevation gradient across 2000 m	<b>Andes, mountain forests:</b> Increase root-to-shoot ratio with elevation from 1050 to 3060 m a.s.l., fine root productivity remains constant, while aboveground productivity decreases. (51).	In relative terms C inputs into soils from roots decrease with decreasing elevation as compared to aboveground organs. These shifting C sources impact microbial communities and soil C stocks because root-derived C is more strongly stabilized in the mineral soil than aboveground litter.	Fine root production depends on root longevity which is rarely assessed but typically increases towards colder climates (67)
---- " ----	Elevation gradient across treeline	<b>South and Polar Urals:</b> elevational increase in fine root biomass of trees and ground vegetation, but decline in aboveground biomass across treeline (68).	----- " -----	----- " -----
---- " ----	Elevation gradient across 2000 m	<b>Alps:</b> in herbaceous plants, greater relative dry matter allocation to fine roots than to leaves with increasing elevation (4).	----- " -----	----- " -----
Soil carbon cycling	Soil warming by heating cables	<b>Montane forest, Austria:</b> 4°C soil warming: increased soil CO <sub>2</sub> efflux (+50%) for at least 9 years without thermal adaptation of microbial communities. Stimulation of both root respiration and SOM mineralization (29).	Warming accelerates SOC cycling for several years, but effects on soil C stocks remain unclear. Soils with high SOC stocks seem particularly vulnerable.	Uneven warming, reduced water contents can have confounding effects.
---- " ----	---- " ----	<b>Alpine treeline (Switzerland):</b> 4°C soil warming: enhanced soil CO <sub>2</sub> efflux by 30-50% for 6 years. Stronger acceleration of SOM mineralization than root respiration (9, 24).	----- " -----	----- " -----
---- " ----	---- " ----	<b>Hardwood forest:</b> 5°C soil warming: increased soil CO <sub>2</sub> efflux for at least 26 years. SOC loss amounted 1.5 kg C/m <sup>2</sup> (69).	Long-term, self-reinforcing carbon feedback in forests.	----- " -----
---- " ----	---- " ----	<b>Boreal forest, Sweden,</b> 5°C soil warming: increase in soil CO <sub>2</sub> efflux was only transient for about 10 years (70).	Limited and short-lived effect of soil warming on soil C cycling	----- " -----

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
Soil carbon cycling	Ecosystem warming by infra-red heaters	<b>High elevation dry mountain meadow (Colorado):</b> Transient decline in SOC contents for 12 years, followed by a recovery due to increased shrub abundance (32).	Vegetation shift from forbs to shrubs with recalcitrant litter may lead to recovery of declined SOM stocks following warming.	Potentially confounding warming effect by an earlier snowmelt.
---- " ----	Ecosystem warming by OTCs; N-fertilization; grazing exclosure	<b>Alpine meadow, Finnish Lapland:</b> warming decreases ecosystem C sink strength in lightly grazed alpine heath, but has no effect in heavily grazed alpine grassland, which is a weaker sink than heath (71).	Grazing-induced vegetation shifts can overarch warming impacts on C-cycling, but the direction of the response is the same.	Seasonal CO <sub>2</sub> fluxes do not reflect above and belowground stocks and their long-term responses.
Soil organic matter stocks	Elevation gradient across > 1500 m, natural ecosystems	Total SOC stocks increase from low elevation forests to shrubline, in particular in organic layer. <b>Andes:</b> SOC stocks increase across 100 m in elevation by 1 kg C/m <sup>2</sup> (26); <b>Himalaya:</b> increase along 100 m in elevation by 0.9 kg C/m <sup>2</sup> (72); <b>Swiss Alps</b> , 1000 forest soil profiles: SOC increase towards treeline by 0.45 kg/m <sup>2</sup> per 100 m in elevation (44). <b>Colorado, Alps, Hawaii:</b> Above treeline, SOC stocks decline towards nival zone, where SOC is negligible on rocky terrain (50, 52, 73).	Soil C is likely lost from soils with upward shifts of forested zones as opposed to C gains with ecosystem development below nival zone.	Rates of change and underlying mechanisms remain uncertain. Drivers are difficult to disentangle, temperature gradient with elevation is frequently confounded with precipitation, and outcome could be biased by changing conditions other than climate (parent material, slope, erosion, land-use). Site selection is also critical. SOM pool sizes considering soil density and stone contents have hardly been quantified above treeline.
Soil organic matter stocks	Elevation gradient across treeline; grazing exclosure	<b>South Norway treeline:</b> Higher organic horizon SOC stocks above treeline, but no difference in mineral horizon across elevations. No effect of 12 year intensified grazing pressure (74).	Forest expansion in elevation would lead to SOC losses from labile organic horizons. Neither above-, nor belowground C stocks along the gradient are affected by grazing.	Uncertain relative importance of browsing versus grazing mammalian herbivory for shaping treeline ecotones.

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
Soil organic matter composition	Elevation gradient across > 1500 m, grassland, forests	<b>Andes</b> , tropical montane forests: POM increases from 5% at 1000 m a.s.l. to 40% at 3000 m a.s.l. (26, 33). <b>Swiss Alps</b> : Contribution of POM in grassland soils (0-20 cm) and in forest soils (0-100 cm) increase from 10% at 400 m a.s.l. to 50% at 2400 m a.s.l. (44, 45, 75). The mean residence time of POM (based on <sup>14</sup> C) also increases with elevation (45). On non-weathered bedrock, there are up to 100 cm thick organic horizons in the Alps (classified as 'Tangel') (76).	As POM represents labile SOM, high POM contents in mountain soils imply a high vulnerability. The decline in POM towards lower elevation/warmer climate reflects a loss in POM, resulting in smaller SOM stocks that are less decomposable. POM potentially represents SOM pool that becomes depleted in soil warming experiments.	Rates of change and underlying mechanisms remain uncertain. Drivers are difficult to disentangle
Nitrogen cycling	Experimental warming by open-top chambers	<b>Sub-arctic mountain peatland</b> , 9 year warming: doubling of extractable organic and mineral N (38).	Accelerated N-cycling in warmer soils improves N availability and plant growth	Potential interaction with water status; mid-term nature
----- " -----	Soil warming by heating cables	<b>Alpine treeline</b> , 6 year soil warming: transient increase in mineral N (+100%), declining response resulted from enhanced plant N uptake. <sup>15</sup> N tracer experiment showed sustained increase in N mineralization by warming (9, 77).	Improved N-availability in warmer soils	----- " -----
Nitrogen cycling, Plant communities	Transplant experiment	<b>Arizona, 4 grassland communities</b> from dessert to high montane: Warming caused encroachment by species typical of warmer environments. Ephemeral stimulation of plant productivity by enhanced N availability which declined with time (78).	Improved N-availability in warmer soils likely contributing to enhanced plant growth	Vegetation shift influenced by adjacent plant communities. Transplant disturbs plant and soil system.
Nitrogen mineralization	Elevation gradient across 1000 m, grassland	<b>Alpine grasslands, Tibet</b> : Doubling of <i>in situ</i> N mineralization along an elevational decrease of 1000 m (79).	Nitrogen supply for plant communities improves in a warming climate.	Short-term experiment. Inference to annual scale uncertain.

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
Nitrogen mineralization	Elevation gradient across treeline	<b>South Urals:</b> Potential N mineralization more than doubles from tundra to closed forest (37).	Potential N mineralization increases when forests expand into alpine shrubland.	Short-term laboratory experiment. Inference to annual scale difficult.
---- " ----	At treeline	<b>Austrian treeline:</b> greater in situ mineralization under coniferous treeline trees than under <i>Rhododendron</i> shrubs (80).	N mineralization is species-dependent.	Short term in situ study.
---- " ----	Elevation gradient across 2000 m	<b>Andes, montane forest:</b> Strong increase in N mineralization and transformation with decreasing elevation (81).	Faster N cycling and potentially greater N plant supply in warmer climate.	Short-term <sup>15</sup> N-based assays within longer term fertilization experiments.
Mineral, plant available N	Elevation gradient across treeline	<b>Treeline, temperate zone:</b> Mineral (=plant available) N pool increases across treeline from the alpine to forest in 5 out 7 regions (27). N binding in biomass also increases strongly <b>South and Polar Urals:</b> Doubling of mineral N contents from tundra to closed forest (68). <b>Patagonia:</b> increase of mineral N by 60% along 4 elevational gradients (300-500 m in elevation) from treeline towards subalpine forests (82) and from subalpine forests to the alpine zone (83).	Nitrogen availability for plant communities increases when forests are expanding to alpine shrubs.	Instantaneous measurement, net effect from N mineralization and plant N uptake
<sup>15</sup> N natural abundance as an indicator of N availability	Elevation gradient at various scales and global patterns	<b>Andes,</b> montane forests 1000 to 3000 m a.s.l.: Broader scale decrease in $\delta^{15}\text{N}$ values with increasing elevation (81); <b>South and Polar Urals:</b> increase in $\delta^{15}\text{N}$ values in fine roots from tundra to forest (68); <b>Swiss Alps,</b> peatlands: increase in $\delta^{15}\text{N}$ values in foliage of ericoid shrubs (84);	<sup>15</sup> N natural abundance in plants is a measure of N availability and plant nitrogen uptake via mycorrhizal associations. Elevational patterns in $\delta^{15}\text{N}$ values shows improving N availability for plants toward lower elevation ecosystems.	$\delta^{15}\text{N}$ value is only an indicator for nitrogen uptake via mycorrhizal associations.

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
<sup>15</sup> N natural abundance	Global patterns	<b>Global latitudinal pattern</b> corresponds with elevation gradients that show decreasing $\delta^{15}\text{N}$ values towards colder climates (85).	Improving N availability for plants in a warming climate	
---- " ----	Alpine vegetation, site differences	<b>Alpine vegetation:</b> $\delta^{15}\text{N}$ value in alpine plants show large differences among plant species and plant functional groups reflecting different pathways of nitrogen uptake from soils (e.g. via symbiotic fungi). Differences among sites (heath, meadow, snow beds) (86, 87).	Intimate linkage of site and soil properties, N availability and plant communities.	----- " -----
Nutrient limitation of plant communities	N-P-K fertilization experiments to test for nutrient limitation	<b>High elevation pioneer vegetation in Swiss Alps:</b> Fertilization more than doubled biomass production in early and late successional system, responses were species specific (88).	Changes in microbial driven nutrient mineralization by an altered microclimate will strongly impact plant growth and diversity	Effect of individual nutrients remains unknown.
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---- " ----	N fertilization experiment with various doses	<b>Subalpine grassland in Swiss Alps:</b> Above-ground productivity and altered species composition at doses >5 kg N/ha/y (91).	Small warming-induced changes in N availability will affect alpine plant communities.	Indirect effects of warming via nutrient mineralization availability cannot be quantified.

Parameter	Study design	Key information	Inference on impacts of vegetation shifts	Limitations and Shortcomings
Plant nutrient limitation	N and P fertilization experiment	<b>Cloud and rain forest, Andes:</b> N and P fertilization shows increasing N limitation with increasing elevation (8).	High elevation system is primarily N limited.	----- " -----
Soil microbial communities	Experimental warming various approaches	Decreases in microbial biomass (24, 29, 30), but limited effect on microbial community structure (29, 30). DNA-based analysis show shifts in fungal communities towards nitrophilous species (40); greater abundance of N-favoring ECM (92), but warming effects are small compared to difference between soil horizons and among plant species in the plots.	Species shift in fungal communities affect C and N cycling	Potentially confounding warming effect by an earlier snowmelt.
Soil microbial communities	Global pattern and elevation gradient across more than 2000 m in elevation	Global elevational and latitudinal patterns in microbial and plant diversity do not run in parallel (93, 94). <b>Andes:</b> Microbial diversity increases with elevation from lowlands to shrubline (93); <b>Swiss Alps:</b> decrease in microbial diversity towards nival zone (52). The contribution of fungi to microbial biomass increases with elevation in forests (Andes (26)), but decrease towards the shrubzone and alpine grasslands (Austria (95)). Soils from early successional ecosystems already contain high diversity (50), and show an initial dominance of soil bacteria (96) and an increasing contribution of fungi with ecosystem development (97).	Microbial communities are linked to vegetation zones either directly or indirectly by SOM. Changes in microbial community structure feedback on plant growth.	Estimates are potentially biased by considering surface soils only and not quantifying pool sizes per surface area. Only a small part of microbial species is known, their functions remain uncertain and are frequently redundant among species.
---- " ----	Global patterns	Microbial biomass correlates with soil organic carbon content (52, 95), while diversity is primarily linked to soil C:N (fungi) and soil pH (bacteria) (98, 99).	Accumulation of soil organic matter and parent material exert dominant influence on soil microbial community structure	Direct linkage of microbial and plant communities remains hidden and is difficult to identify.