

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

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

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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.

13

## 14 **Introduction**

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



## 38 **Elevation shifts of mountain vegetation**

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

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

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

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

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

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

86

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

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

101

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

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

106 28, Table S1). Heating soils by 4°C at the alpine treeline and in montane forests increased soil  
107 CO<sub>2</sub> effluxes by 40-50%, resulting from both accelerated rhizosphere activity and enhanced  
108 soil C mineralization (24, 29). These responses are likely transient as microbial communities  
109 acclimate to warmer conditions, without significantly changing their community structure  
110 and soils deplete in readily available C until a new quasi-equilibrium is reached (29–31). The  
111 magnitude and duration of warming responses vary among studies, but longer-term  
112 experiments observed accelerated soil C mineralization for more than a decade (29, 30,  
113 Table S1). Higher C losses through soil C mineralization tend to be compensated by increased  
114 soil C inputs from plants, resulting in small net effects on the soil C balance as compared to  
115 the pronounced warming effects on soil C fluxes (25, 32). Despite considerable research  
116 efforts, there is no consensus on the magnitude of warming effects on soil C storage (25).  
117 Soils of cold climates such as at high latitude or elevation seem particularly vulnerable to  
118 warming because they contain inherently high C stocks and high amounts of labile C,  
119 potentially promoting strong and sustained soil C losses (24, 29, 33). However, warming  
120 effects are contingent on water availability, and in semi-arid mountains the soil C balance  
121 appears less dependent on projected temperature changes than on variation in the amount  
122 and timing of precipitation (34). Impacts of climatic warming is especially large in permafrost  
123 soils that only exist above the shrubline in the Alps, but reach down to the subalpine zone in  
124 continental mountain ranges at mid and northern latitudes. On the Tibetan plateau, for  
125 instance, permafrost collapse has resulted in a 32% decline in soil C stocks in surface soils  
126 (35), and an alpine tundra meadow with discontinuous permafrost in Colorado was found to  
127 represent a substantial net C source to the atmosphere by releasing C from ancient buried  
128 soil C (36).

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

145

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

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

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

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

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

193 Elevational patterns of vegetation and SOM are partly reflected in soil microbial  
194 communities. Microbial biomass and the contribution of fungi as compared to bacteria  
195 typically increase from the nival zone to treeline, but decreases in forest at lower elevations  
196 (26, 50, 52, Table S1). But at the species level, elevational patterns in soil microbial diversity  
197 are heterogeneous and only weakly related to plant diversity (53). Early successional alpine  
198 habitats are an exception. Here, a higher microbial dependence on plant organic inputs

199 provides for a tighter positive relationship between plant and microbial taxonomic richness  
200 (50, 52). Nonetheless, elevational turnover in microbial community composition can be  
201 pronounced and varies according to plant type (54), suggesting that there will be  
202 interdependencies among plant and soil microbial responses to climate warming.

203

204

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

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

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



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

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

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

242

## 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

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

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

286

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

295

296

## 297 **List of Figures**

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

302

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

309 (SOM) due to low plant inputs and slow weathering (49) and host highly specific microbial  
310 taxa (50, 52, 60). Alpine grasslands have typically high SOM contents in the topsoil as low  
311 temperatures impede the decomposition of annual inputs of fine roots and leaf litter (45).  
312 The herbaceous vegetation relies strongly on symbiotic associations with arbuscular  
313 mycorrhizae for nutrient supply (60). Soils below the shrubline are characterized by a thick  
314 organic layer, consisting of recalcitrant plant residues from dwarf shrubs and coniferous  
315 trees (46, 47), with abundant ericoid and ectomycorrhizae, and free-living saprotrophs (41,  
316 46, 54). The low abundance of soil fauna, especially of earthworms, impedes the physical  
317 incorporation of litter into mineral soils (48). In montane forests, the increasingly favourable  
318 climate accelerates the processing of SOM, leading to a thinner organic layer (33, 37, 44) and  
319 a higher diversity and abundance of ectomycorrhizal fungi. See Table S1 for more details on  
320 belowground elevational patterns.

321  
322 **Figure 3.** Above- and belowground linkages in a changing climate. Mountain plants transfer  
323 more than 50% of assimilated carbon (C) to roots, to associated mycorrhizal fungi in  
324 exchange for soil nutrients, and to free-living bacteria and fungi feeding on rhizodeposits.  
325 Within hours, photosynthetic products are allocated belowground, nourishing soil  
326 organisms, and are respired back to the atmosphere as CO<sub>2</sub> (14, 31). On an annual timescale,  
327 leaf and root residues enter the soils and are broken down and transformed by soil biota.  
328 Only a small fraction — microbial products — are stabilized by reactive minerals formed  
329 during weathering and persist in the soil for centuries to millennia (31). Consequently, soil  
330 organic matter (SOM) consists of a continuum of compounds from litter to particulate soil  
331 organic matter (POM) comprised of decomposing plant residues and more stable mineral-  
332 associated organic matter (MOM) (33, 43). Climate change affects above and belowground

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

338

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

342

## 343 **List of Supplementary Materials**

344 **Table S1.**

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

346 **References:**

- 347 1. A. von Humboldt, A. Bonpland, *Essai sur la géographie des plantes - accompagné d'un*  
348 *tableau physique des régions équinoxiales, fondé sur des mesures exécutées, depuis le*  
349 *dixième degré de latitude boréale jusqu'au dixième degré de latitude australe, pendant*  
350 *les années 1799, 1800, 1801*, (Schoell, Paris, 1805; [https://doi.org/10.3931/e-rara-](https://doi.org/10.3931/e-rara-24316)  
351 [24316](https://doi.org/10.3931/e-rara-24316)).
- 352 2. P. Moret, P. Muriel, R. Jaramillo, O. Dangles, Humboldt's Tableau Physique revisited.  
353 *Proc. Natl. Acad. Sci.*, 201904585 (2019).
- 354 3. M. J. Steinbauer *et al.*, Accelerated increase in plant species richness on mountain  
355 summits is linked to warming. *Nature*. **556**, 231–234 (2018).
- 356 4. C. Körner, *Alpine Plant Life* (Springer Berlin Heidelberg, Berlin, Heidelberg, 2003;  
357 <http://link.springer.com/10.1007/978-3-642-18970-8>).
- 358 5. N. Pepin *et al.*, Elevation-dependent warming in mountain regions of the world. *Nat.*  
359 *Clim. Chang.* **5**, 424–430 (2015).
- 360 6. T. C. Parker, J.-A. Subke, P. A. Wookey, Rapid carbon turnover beneath shrub and tree  
361 vegetation is associated with low soil carbon stocks at a subarctic treeline. *Glob.*  
362 *Chang. Biol.* **21**, 2070–2081 (2015).
- 363 7. P. Möhl *et al.*, Twelve years of low nutrient input stimulates growth of trees and dwarf  
364 shrubs in the treeline ecotone. *J. Ecol.* **107**, 768–780 (2019).
- 365 8. J. B. Fisher *et al.*, Nutrient limitation in rainforests and cloud forests along a 3,000-m  
366 elevation gradient in the Peruvian Andes. *Oecologia*. **172**, 889–902 (2013).
- 367 9. M. A. Dawes, P. Schleppei, S. Hättenschwiler, C. Rixen, F. Hagedorn, Soil warming opens  
368 the nitrogen cycle at the alpine treeline. *Glob. Chang. Biol.* **23**, 421–434 (2017).
- 369 10. J. Paulsen, C. Körner, A climate-based model to predict potential treeline position

- 370 around the globe. *Alp. Bot.* **124**, 1–12 (2014).
- 371 11. E. Liang *et al.*, Species interactions slow warming-induced upward shifts of treelines  
372 on the Tibetan Plateau. *Proc. Natl. Acad. Sci.* **113**, 4380–4385 (2016).
- 373 12. M. A. Harsch, P. E. Hulme, M. S. McGlone, R. P. Duncan, Are treelines advancing? A  
374 global meta-analysis of treeline response to climate warming. *Ecol. Lett.* **12**, 1040–  
375 1049 (2009).
- 376 13. J. Dolezal *et al.*, Vegetation dynamics at the upper elevational limit of vascular plants  
377 in Himalaya. *Sci. Rep.* **6**, 24881 (2016).
- 378 14. A. Ferrari, F. Hagedorn, P. A. Niklaus, Experimental soil warming and cooling alters the  
379 partitioning of recent assimilates: evidence from a <sup>14</sup>C-labelling study at the alpine  
380 treeline. *Oecologia.* **181**, 25–37 (2016).
- 381 15. S. B. Rumpf *et al.*, Range dynamics of mountain plants decrease with elevation. *Proc.*  
382 *Natl. Acad. Sci.* **115**, 1848–1853 (2018).
- 383 16. I. H. Myers-Smith, D. S. Hik, Climate warming as a driver of tundra shrubline advance.  
384 *J. Ecol.* **106**, 547–560 (2018).
- 385 17. J. M. Alexander *et al.*, Lags in the response of mountain plant communities to climate  
386 change. *Glob. Chang. Biol.* **24**, 563–579 (2018).
- 387 18. S. M. Crimmins, S. Z. Dobrowski, J. A. Greenberg, J. T. Abatzoglou, A. R. Mynsberge,  
388 Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum  
389 Elevations. *Science (80-. ).* **331**, 324–327 (2011).
- 390 19. L. Lyu *et al.*, Drought limitation on tree growth at the Northern Hemisphere's highest  
391 tree line. *Dendrochronologia.* **53**, 40–47 (2019).
- 392 20. P. D. Henne, C. M. Elkin, B. Reineking, H. Bugmann, W. Tinner, Did soil development  
393 limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a



- 394 palaeobotanical hypothesis with a dynamic landscape model. *J. Biogeogr.* **38**, 933–949  
395 (2011).
- 396 21. A. Kulonen, R. A. Imboden, C. Rixen, S. B. Maier, S. Wipf, Enough space in a warmer  
397 world? Microhabitat diversity and small-scale distribution of alpine plants on  
398 mountain summits. *Divers. Distrib.* **24**, 252–261 (2018).
- 399 22. J. HilleRisLambers, M. A. Harsch, A. K. Ettinger, K. R. Ford, E. J. Theobald, How will  
400 biotic interactions influence climate change-induced range shifts? *Ann. N. Y. Acad. Sci.*  
401 **1297** (2013), doi:10.1111/nyas.12182.
- 402 23. W. H. van der Putten, M. A. Bradford, E. Pernilla Brinkman, T. F. J. van de Voorde, G. F.  
403 Veen, Where, when and how plant-soil feedback matters in a changing world. *Funct.*  
404 *Ecol.* **30**, 1109–1121 (2016).
- 405 24. K. Streit *et al.*, Soil warming alters microbial substrate use in alpine soils. *Glob. Chang.*  
406 *Biol.* **20**, 1327–1338 (2014).
- 407 25. N. van Gestel *et al.*, Predicting soil carbon loss with warming. *Nature.* **554**, E4–E5  
408 (2018).
- 409 26. A. T. Nottingham *et al.*, Climate Warming and Soil Carbon in Tropical Forests: Insights  
410 from an Elevation Gradient in the Peruvian Andes. *Bioscience.* **65**, 906–921 (2015).
- 411 27. J. R. Mayor *et al.*, Elevation alters ecosystem properties across temperate treelines  
412 globally. *Nature.* **542**, 91–95 (2017).
- 413 28. L. M. Kueppers *et al.*, Warming and provenance limit tree recruitment across and  
414 beyond the elevation range of subalpine forest. *Glob. Chang. Biol.* **23**, 2383–2395  
415 (2017).
- 416 29. A. Schindlbacher, J. Schnecker, M. Takriti, W. Borken, W. Wanek, Microbial physiology  
417 and soil CO<sub>2</sub> efflux after 9 years of soil warming in a temperate forest - no indications

- 418 for thermal adaptations. *Glob. Chang. Biol.* **21**, 4265–4277 (2015).
- 419 30. T. W. N. Walker *et al.*, Microbial temperature sensitivity and biomass change explain  
420 soil carbon loss with warming. *Nat. Clim. Chang.* **8**, 885–889 (2018).
- 421 31. M. A. Bradford *et al.*, Managing uncertainty in soil carbon feedbacks to climate  
422 change. *Nat. Clim. Chang.* **6**, 751–758 (2016).
- 423 32. J. Harte, S. R. Saleska, C. Levy, Convergent ecosystem responses to 23-year ambient  
424 and manipulated warming link advancing snowmelt and shrub encroachment to  
425 transient and long-term climate-soil carbon feedback. *Glob. Chang. Biol.* **21**, 2349–  
426 2356 (2015).
- 427 33. M. Zimmermann, J. Leifeld, F. Conen, M. I. Bird, P. Meir, Can composition and physical  
428 protection of soil organic matter explain soil respiration temperature sensitivity?  
429 *Biogeochemistry.* **107**, 423–436 (2012).
- 430 34. A. B. Moyes, D. R. Bowling, Interannual variation in seasonal drivers of soil respiration  
431 in a semi-arid Rocky Mountain meadow. *Biogeochemistry.* **113**, 683–697 (2013).
- 432 35. F. Liu *et al.*, Reduced quantity and quality of SOM along a thaw sequence on the  
433 Tibetan Plateau. *Environ. Res. Lett.* **13**, 104017 (2018).
- 434 36. J. F. Knowles, P. D. Blanken, C. R. Lawrence, M. W. Williams, Evidence for non-steady-  
435 state carbon emissions from snow-scoured alpine tundra. *Nat. Commun.* **10**, 1–9  
436 (2019).
- 437 37. A. Kammer *et al.*, Treeline shifts in the Ural mountains affect soil organic matter  
438 dynamics. *Glob. Chang. Biol.* **15**, 1570–1583 (2009).
- 439 38. J. T. Weedon *et al.*, Summer warming accelerates sub-arctic peatland nitrogen cycling  
440 without changing enzyme pools or microbial community structure. *Glob. Chang. Biol.*  
441 **18**, 138–150 (2012).

- 442 39. S. E. Hobbie, Plant species effects on nutrient cycling: revisiting litter feedbacks.  
443 *Trends Ecol. Evol.* **30**, 357–363 (2015).
- 444 40. E. F. Solly *et al.*, Experimental soil warming shifts the fungal community composition  
445 at the alpine treeline. *New Phytol.* **215**, 766–778 (2017).
- 446 41. D. R. Zak *et al.*, Exploring the role of ectomycorrhizal fungi in soil carbon dynamics.  
447 *New Phytol.* (2019), doi:10.1111/nph.15679.
- 448 42. R. K. Monson *et al.*, Winter forest soil respiration controlled by climate and microbial  
449 community composition. *Nature.* **439**, 711–714 (2006).
- 450 43. S. Doetterl *et al.*, Soil carbon storage controlled by interactions between geochemistry  
451 and climate. *Nat. Geosci.* **8**, 780–783 (2015).
- 452 44. S. Gosheva *et al.*, Reconstruction of historic forest cover changes indicates minor  
453 effects on carbon stocks in Swiss forest soils. *Ecosystems.* **20**, 1512–1528 (2017).
- 454 45. K. Budge, J. Leifeld, E. Hiltbrunner, J. Fuhrer, Alpine grassland soils contain large  
455 proportion of labile carbon but indicate long turnover times. *Biogeosciences.* **8**, 1911–  
456 1923 (2011).
- 457 46. K. E. Clemmensen *et al.*, Roots and associated fungi drive long-term carbon  
458 sequestration in boreal forest. *Science.* **339**, 1615–1618 (2013).
- 459 47. B. Adamczyk, O.-M. Sietiö, C. Biasi, J. Heinonsalo, Interaction between tannins and  
460 fungal necromass stabilizes fungal residues in boreal forest soils. *New Phytol.* (2019),  
461 doi:10.1111/nph.15729.
- 462 48. A. A. Wackett, K. Yoo, J. Olofsson, J. Klaminder, Human-mediated introduction of  
463 geoengineering earthworms in the Fennoscandian arctic. *Biol. Invasions.* **20**, 1377–  
464 1386 (2018).
- 465 49. R. H. Smittenberg *et al.*, Climate-sensitive ecosystem carbon dynamics along the soil

- 466 chronosequence of the Damma glacier forefield, Switzerland. *Glob. Chang. Biol.* **18**,  
467 1941–1955 (2012).
- 468 50. D. L. Porazinska *et al.*, Plant diversity and density predict belowground diversity and  
469 function in an early successional alpine ecosystem. *Ecology*. **99**, 1942–1952 (2018).
- 470 51. G. Moser *et al.*, Elevation effects on the carbon budget of tropical mountain forests (S  
471 Ecuador): The role of the belowground compartment. *Glob. Chang. Biol.* **17**, 2211–  
472 2226 (2011).
- 473 52. M. Adamczyk *et al.*, The Soil Microbiome of GLORIA Mountain Summits in the Swiss  
474 Alps. *Front. Microbiol.* **10** (2019), doi:10.3389/fmicb.2019.01080.
- 475 53. J. A. Bryant *et al.*, Microbes on mountainsides: Contrasting elevational patterns of  
476 bacterial and plant diversity. *Proc. Natl. Acad. Sci.* **105**, 11505–11511 (2008).
- 477 54. S. N. Kivlin, J. S. Lynn, M. R. Kazenel, K. K. Beals, J. A. Rudgers, Biogeography of plant-  
478 associated fungal symbionts in mountain ecosystems: A meta-analysis. *Divers. Distrib.*  
479 **23**, 1067–1077 (2017).
- 480 55. C. Poeplau *et al.*, Temporal dynamics of soil organic carbon after land-use change in  
481 the temperate zone - carbon response functions as a model approach. *Glob. Chang.*  
482 *Biol.* **17**, 2415–2427 (2011).
- 483 56. L. A. Cavieres *et al.*, Facilitative plant interactions and climate simultaneously drive  
484 alpine plant diversity. *Ecol. Lett.* **17**, 193–202 (2014).
- 485 57. A. Cardinaux, S. P. Hart, J. M. Alexander, Do soil biota influence the outcome of novel  
486 interactions between plant competitors? *J. Ecol.* **106**, 1853–1863 (2018).
- 487 58. M. A. Nuñez, T. R. Horton, D. Simberloff, Lack of belowground mutualisms hinders  
488 Pinaceae invasions. *Ecology*. **90**, 2352–2359 (2009).
- 489 59. C. D. Brown, M. Vellend, Non-climatic constraints on upper elevational plant range

- 490 expansion under climate change. *Proc. R. Soc. B Biol. Sci.* **281**, 20141779–20141779  
491 (2014).
- 492 60. C. P. Bueno de Mesquita *et al.*, Patterns of root colonization by arbuscular mycorrhizal  
493 fungi and dark septate endophytes across a mostly-unvegetated, high-elevation  
494 landscape. *Fungal Ecol.* **36**, 63–74 (2018).
- 495 61. M. A. Dawes *et al.*, Soil warming and CO<sub>2</sub> enrichment induce biomass shifts in alpine  
496 tree line vegetation. *Glob. Chang. Biol.* **21**, 2005–2021 (2015).
- 497 62. A. Anadon-Rosell *et al.*, Xylem anatomical and growth responses of the dwarf shrub  
498 *Vaccinium myrtillus* to experimental CO<sub>2</sub> enrichment and soil warming at treeline. *Sci.*  
499 *Total Environ.* **642**, 1172–1183 (2018).
- 500 63. S. C. Elmendorf *et al.*, Experiment, monitoring, and gradient methods used to infer  
501 climate change effects on plant communities yield consistent patterns. *Proc. Natl.*  
502 *Acad. Sci.* **112**, 448–452 (2015).
- 503 64. E. Kaarlejärvi, A. Eskelinen, J. Olofsson, Herbivory prevents positive responses of  
504 lowland plants to warmer and more fertile conditions at high altitudes. *Funct. Ecol.* **27**,  
505 1244–1253 (2013).
- 506 65. J. M. Melillo *et al.*, Soil warming, carbon-nitrogen interactions, and forest carbon  
507 budgets. *Proc. Natl. Acad. Sci.* **108**, 9508–9512 (2011).
- 508 66. H. Majdi, J. Ohrvik, Interactive effects of soil warming and fertilization on root  
509 production, mortality, and longevity in a Norway spruce stand in Northern Sweden.  
510 *Glob. Chang. Biol.* **10**, 182–188 (2004).
- 511 67. E. F. Solly *et al.*, Unravelling the age of fine roots of temperate and boreal forests. *Nat.*  
512 *Commun.* **9**, 1–8 (2018).
- 513 68. E. F. Solly *et al.*, Treeline advances and associated shifts in the ground vegetation alter

- 514 fine root dynamics and mycelia production in the South and Polar Urals. *Oecologia*.  
515 **183**, 571–586 (2017).
- 516 69. J. M. Melillo *et al.*, Long-term pattern and magnitude of soil carbon feedback to the  
517 climate system in a warming world. *Science*. **358**, 101–105 (2017).
- 518 70. H. Lim *et al.*, Boreal forest biomass accumulation is not increased by two decades of  
519 soil warming. *Nat. Clim. Chang.* **9**, 49–52 (2019).
- 520 71. M. Väisänen *et al.*, Consequences of warming on tundra carbon balance determined  
521 by reindeer grazing history. *Nat. Clim. Chang.* **4**, 384–388 (2014).
- 522 72. S. B. Devi, S. S. S. S. Sherpa, Soil carbon and nitrogen stocks along the altitudinal  
523 gradient of the Darjeeling Himalayas, India. *Environ. Monit. Assess.* **191**, 361 (2019).
- 524 73. M. G. Kramer, O. A. Chadwick, Controls on carbon storage and weathering in volcanic  
525 soils across a high-elevation climate gradient on Mauna Kea, Hawaii. *Ecology*. **97**,  
526 2384–2395 (2016).
- 527 74. J. D. M. Speed *et al.*, Continuous and discontinuous variation in ecosystem carbon  
528 stocks with elevation across a treeline ecotone. *Biogeosciences*. **12**, 1615–1627  
529 (2015).
- 530 75. J. Leifeld, M. Zimmermann, J. Fuhrer, F. Conen, Storage and turnover of carbon in  
531 grassland soils along an elevation gradient in the Swiss Alps. *Glob. Chang. Biol.* **15**,  
532 668–679 (2009).
- 533 76. E. Kolb, M. Kohlpaintner, Tangel humus forms – genesis and co-evolution with  
534 vegetation. *Appl. Soil Ecol.* **123**, 622–626 (2018).
- 535 77. M. A. Dawes, P. Schleppei, F. Hagedorn, The fate of nitrogen inputs in a warmer alpine  
536 treeline ecosystem: a <sup>15</sup>N labelling study. *J. Ecol.* **105**, 1723–1737 (2017).
- 537 78. Z. Wu, P. Dijkstra, G. W. Koch, B. A. Hungate, Biogeochemical and ecological feedbacks

- 538 in grassland responses to warming. *Nat. Clim. Chang.* **2**, 458–461 (2012).
- 539 79. S. Zhang *et al.*, Impacts of altitude and position on the rates of soil nitrogen  
540 mineralization and nitrification in alpine meadows on the eastern Qinghai–Tibetan  
541 Plateau, China. *Biol. Fertil. Soils.* **48**, 393–400 (2012).
- 542 80. L. Wang, D. L. Godbold, Soil N mineralization profiles of co-existing woody vegetation  
543 islands at the alpine tree line. *Eur. J. For. Res.* **136**, 881–892 (2017).
- 544 81. A. P. Baldos, M. D. Corre, E. Veldkamp, Response of N cycling to nutrient inputs in  
545 forest soils across a 1000–3000 m elevation gradient in the Ecuadorian Andes.  
546 *Ecology.* **96**, 749–761 (2015).
- 547 82. A. Fajardo, F. I. Piper, An assessment of carbon and nutrient limitations in the  
548 formation of the southern Andes tree line. *J. Ecol.* **105**, 517–527 (2017).
- 549 83. A. Thébault *et al.*, Nitrogen limitation and microbial diversity at the treeline. *Oikos.*  
550 **123**, 729–740 (2014).
- 551 84. K. Gavazov, F. Hagedorn, A. Buttler, R. Siegwolf, L. Bragazza, Environmental drivers of  
552 carbon and nitrogen isotopic signatures in peatland vascular plants along an altitude  
553 gradient. *Oecologia.* **180**, 257–264 (2016).
- 554 85. R. Amundson *et al.*, Global patterns of the isotopic composition of soil and plant  
555 nitrogen. *Global Biogeochem. Cycles.* **17** (2003), doi:10.1029/2002GB001903.
- 556 86. C. Körner, S. Leuzinger, S. Riedl, R. T. Siegwolf, L. Streule, Carbon and nitrogen stable  
557 isotope signals for an entire alpine flora, based on herbarium samples. *Alp. Bot.* **126**,  
558 153–166 (2016).
- 559 87. Y. Yang, R. T. W. Siegwolf, C. Körner, Species specific and environment induced  
560 variation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in alpine plants. *Front. Plant Sci.* **6**, 423 (2015).
- 561 88. C. Heer, C. Körner, High elevation pioneer plants are sensitive to mineral nutrient

- 562 addition. *Basic Appl. Ecol.* **3**, 39–47 (2002).
- 563 89. K. Klanderud, Species-specific responses of an alpine plant community under  
564 simulated environmental change. *J. Veg. Sci.* **19**, 363–372 (2008).
- 565 90. B. Sveinbjornsson, O. Nordell, H. Kauhanen, Nutrient Relations of Mountain Birch  
566 Growth at and Below the Elevational Tree-Line in Swedish Lapland. *Funct. Ecol.* **6**, 213  
567 (1992).
- 568 91. S. Bassin, M. Volk, J. Fuhrer, Species Composition of Subalpine Grassland is Sensitive  
569 to Nitrogen Deposition, but Not to Ozone, After Seven Years of Treatment.  
570 *Ecosystems.* **16**, 1105–1117 (2013).
- 571 92. K. E. Clemmensen, A. Michelsen, S. Jonasson, G. R. Shaver, Increased ectomycorrhizal  
572 fungal abundance after long-term fertilization and warming of two arctic tundra  
573 ecosystems. *New Phytol.* **171**, 391–404 (2006).
- 574 93. N. Fierer *et al.*, Microbes do not follow the elevational diversity patterns of plants and  
575 animals. *Ecology.* **92**, 797–804 (2011).
- 576 94. J. N. Hendershot, Q. D. Read, J. A. Henning, N. J. Sanders, A. T. Classen, Consistently  
577 inconsistent drivers of microbial diversity and abundance at macroecological scales.  
578 *Ecology.* **98**, 1757–1763 (2017).
- 579 95. I. Djukic, F. Zehetner, A. Mentler, M. H. Gerzabek, Microbial community composition  
580 and activity in different Alpine vegetation zones. *Soil Biol. Biochem.* **42**, 155–161  
581 (2010).
- 582 96. J. Donhauser, B. Frey, Alpine soil microbial ecology in a changing world. *FEMS*  
583 *Microbiol. Ecol.* **94**, 1–31 (2018).
- 584 97. R. D. Bardgett *et al.*, Heterotrophic microbial communities use ancient carbon  
585 following glacial retreat. *Biol. Lett.* **3**, 487–490 (2007).



- 586 98. M. Bahram *et al.*, Structure and function of the global topsoil microbiome. *Nature*.  
587 **560**, 233–237 (2018).
- 588 99. C. Shen *et al.*, Dramatic increases of soil microbial functional gene diversity at the  
589 treeline ecotone of Changbai mountain. *Front. Microbiol.* **7**, 1–12 (2016).

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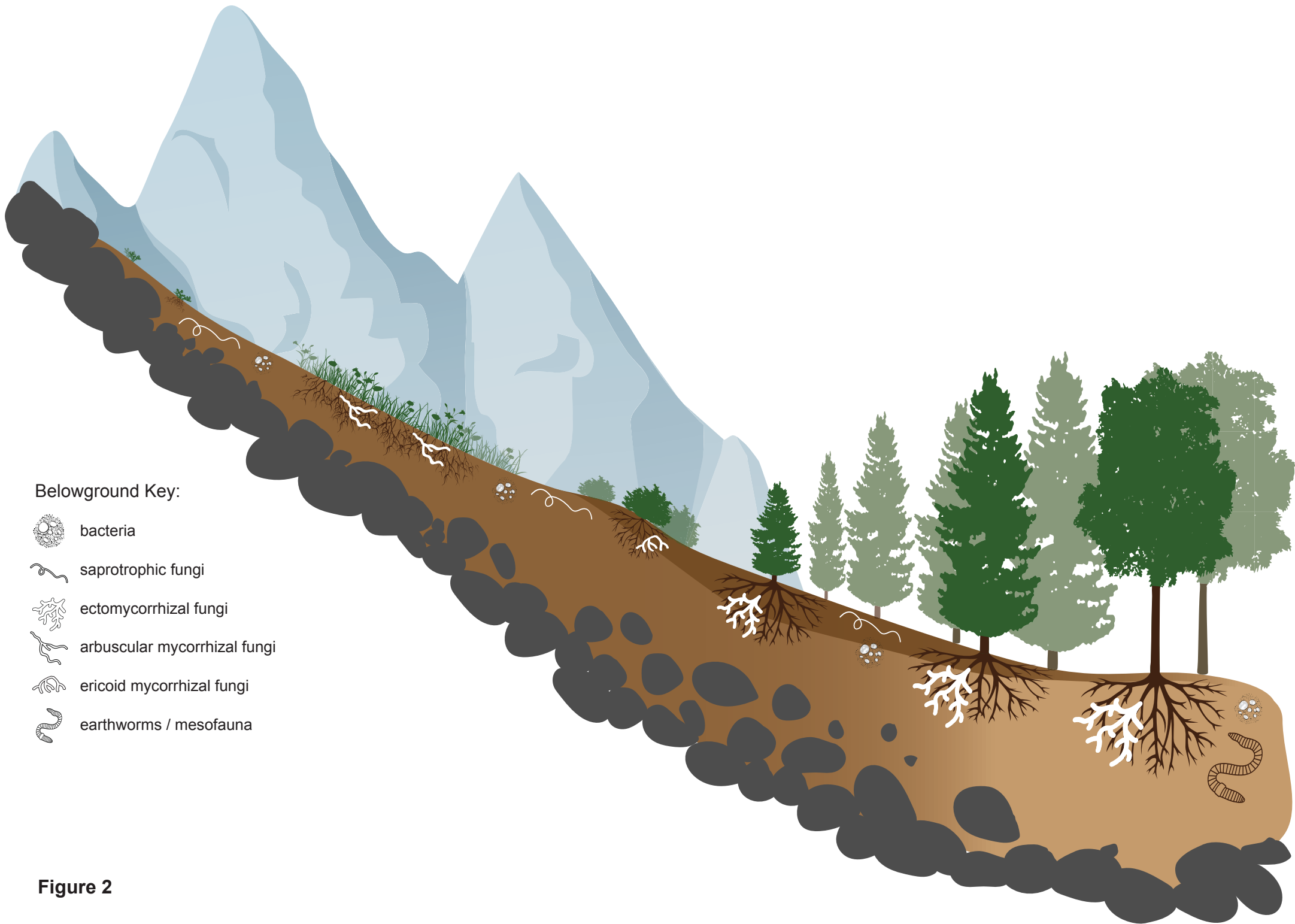
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604



**Figure 1**



Belowground Key:







-  bacteria
-  saprotrophic fungi
-  ectomycorrhizal fungi
-  arbuscular mycorrhizal fungi
-  ericoid mycorrhizal fungi
-  earthworms / mesofauna

Figure 2

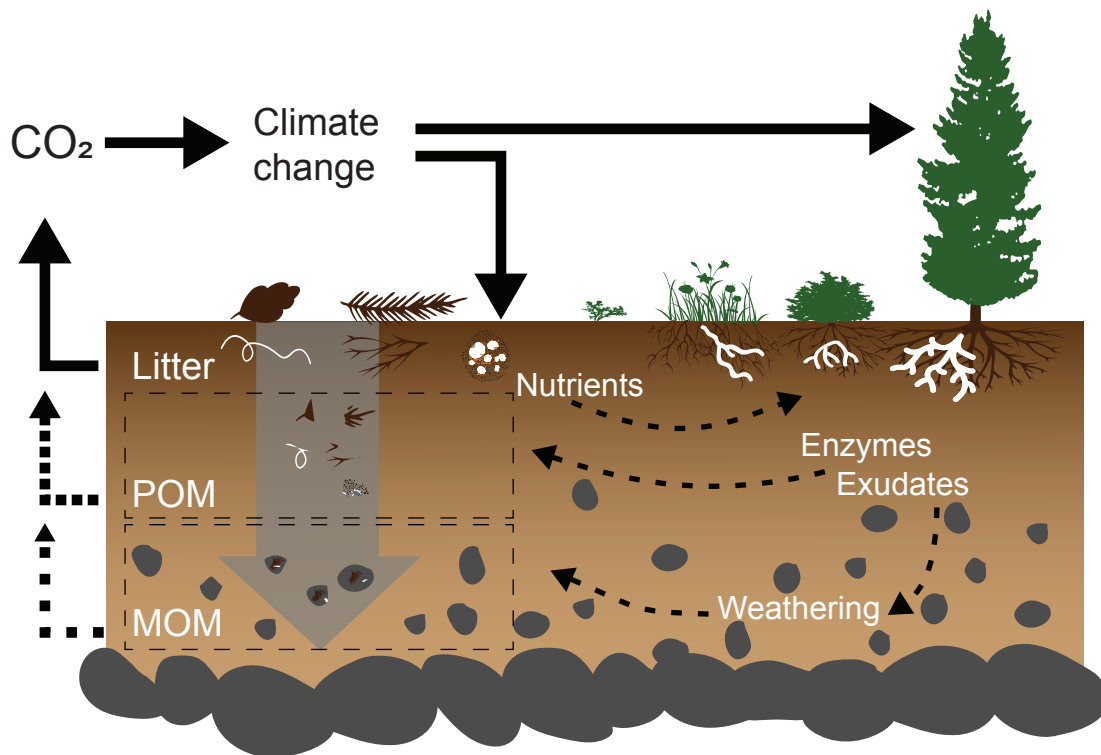
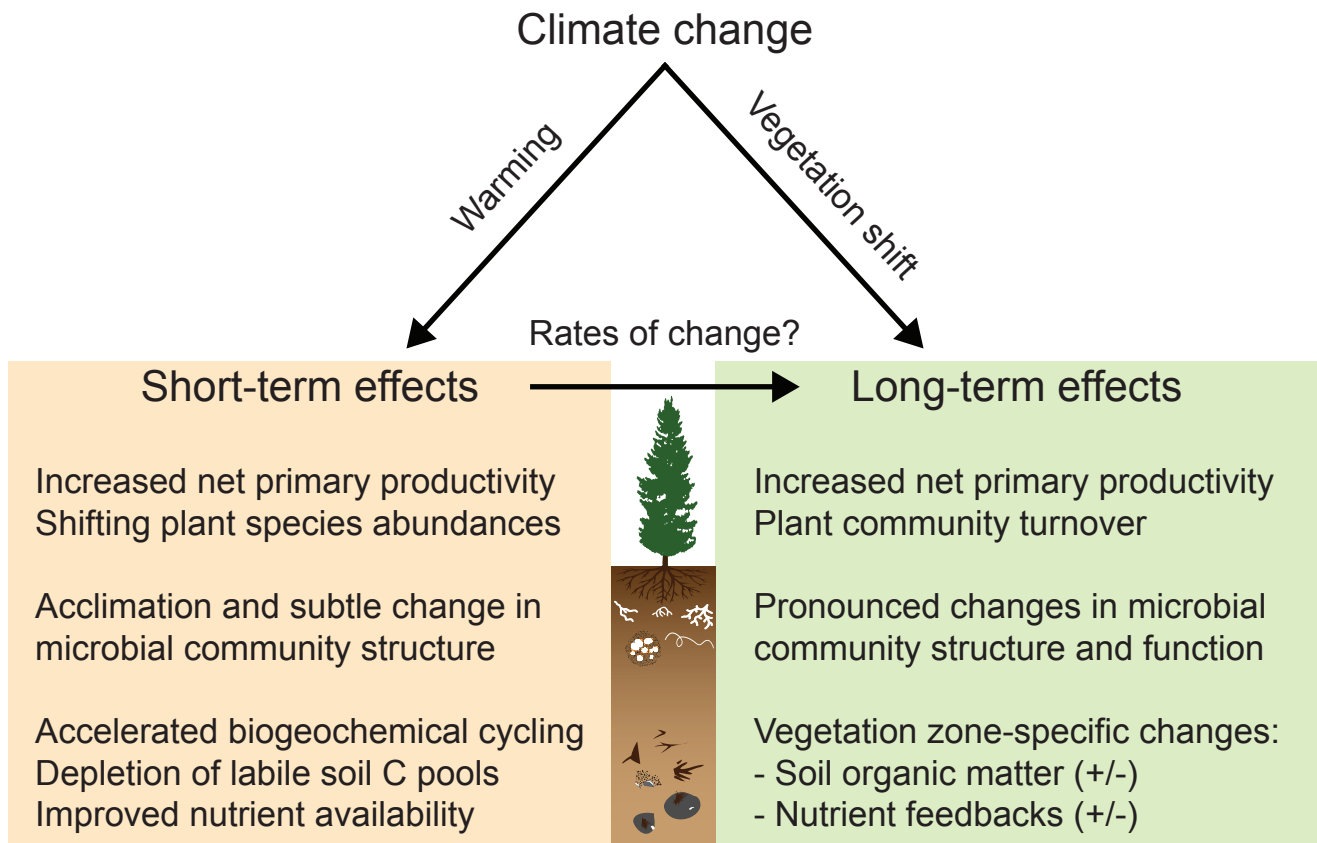


Figure 3



**Figure 4**



## Supplementary Materials for

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

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#### **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)
----	----	<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).	----- " -----	----- " -----
----	----	<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, montane forests</b> 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, peatlands:</b> 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.
---- " ----	---- " ----	<b>Dryas heath, Norway:</b> Nutrient addition combined with warming increased the abundance of high stature species, such as grasses and forbs, while low stature forbs and most bryophytes and lichens decreased in abundance (89).	Changes in microbial driven nutrient mineralization by an altered microclimate will strongly impact plant growth and diversity	Fertilization effect was greater than effect of open-top chambers with a small warming effect
---- " ----	---- " ----	<b>Treeline in Swiss Alps:</b> Growth enhancement of 2 tree species and understory vegetation to 12 years of N-P-K fertilization at low dose (15 kg N/ha/y) (7).	Increased N mineralization in warmer soils will promote forest growth and potentially forest expansion.	Effect of individual nutrients remains unknown.
---- " ----	---- " ----	<b>Treeline and subalpine forest in Sub-Arctic:</b> Greater responsiveness of treeline than valley forests to high dose fertilization (90).	----- " -----	----- " -----
---- " ----	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.