Lowland plant migrations into alpine ecosystems amplify soil carbon loss under climate warming

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Abstract

Climate warming is releasing carbon from soils around the world[1–3], constituting a positive climate feedback. Warming is also causing species to expand their ranges into new ecosystems[4–9]. Yet, in most ecosystems, whether range expanding species will amplify or buffer expected soil carbon loss is unknown[10]. Here we used alpine grasslands as a model system to determine whether the establishment of herbaceous lowland plants in alpine ecosystems influences short-term soil carbon storage under warming. We found that warming (< 1 year) led to negligible alpine soil carbon loss, but its effects became significant and 52% ± 31% (mean ± 95% CIs) larger after lowland plants were introduced at low density into the ecosystem. We present evidence that soil carbon loss likely occurred *via* lowland plants increasing rates of root exudation, soil microbial respiration and CO_2 release. Our findings suggest that warming-induced range expansions of herbaceous plants may yield a rapid positive climate feedback in this system, and that plant range expansions among herbaceous communities may be an overlooked mediator of warming effects on carbon dynamics.

Introduction

Climate warming is accelerating the release of soil carbon to the atmosphere[1–3], creating a positive climate feedback. At the same time, warming is driving uphill and poleward range expansions of native plant species around the globe[4–9]. Yet while warming and plant range expansions are now co-occurring in many terrestrial ecosystems, the impact of range expanding plants on soil carbon storage under warming remains poorly understood[10]. This is important because plant species adapted to different temperatures can have contrasting effects on carbon cycle processes[11], raising the potential for migrating species to have qualitatively different impacts on carbon dynamics from resident plants. For example, studies of non-native species invasions have revealed that the arrival of novel species in a community can alter carbon cycling in recipient ecosystems[12,13], while woody plant expansions into treeless Arctic ecosystems can reverse the direction of carbon cycle feedbacks to climate warming[14,15]. However, the majority of warming-induced range expansions do not involve non-native species or novel growth forms, but occur among native communities of similar species (e.g. ref [9]). In particular, we know remarkably little about how migrations of herbaceous plants into predominantly herbaceous ecosystems will affect soil carbon stocks, and so the magnitude and direction of resulting climate feedbacks are unknown.

Alpine ecosystems occur in the uppermost elevations of the planet as cool islands within warmer landscapes that are bounded by steep gradients in temperature[16]. They are experiencing both rapid temperature change[17] and faster-than-average species immigration[18], the latter of which mainly involves an influx of herbaceous warm-adapted species from lowlands into herbaceous cold-adapted communities at higher elevations[7–9]. Coupled to this, alpine ecosystems are globally relevant reservoirs of soil carbon and hold more than 90% of their total ecosystem carbon in the soil[1–3,19,20]. As such, alpine ecosystems are not only themselves important for climate feedbacks, but are also sentinels for climate warming impacts on other terrestrial ecosystems. Here, we used alpine ecosystems as a model system to determine how the establishment of range expanding native plant species affects soil carbon storage in warming ecosystems. We first used two whole-community transplant experiments in different alpine regions (western/central Swiss Alps) to establish the effects of simulated warming and lowland plant arrival on alpine soil carbon loss. Second, we used

these experiments plus glasshouse and laboratory studies to elucidate potential mechanisms through which lowland plants influence the alpine soil carbon cycle, testing the hypothesis that they act *via* changes to root exudation[21,22].

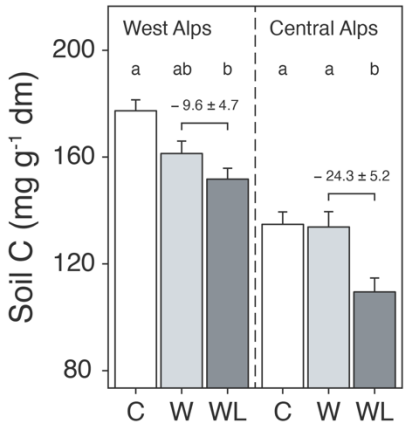

Figure 1 | Warming and lowland plant effects on alpine soil carbon loss. Mean ± SE soil carbon content (mg C g^{-1} dry mass) in alpine turfs exposed to warming (W; light grey), warming plus lowland plants (WL; dark grey) or an ambient control (C; white). Data are displayed for two experiments in the western (left) and central (right) Alps, with letters indicating treatment differences (LMEs; N = 58).

Results & Discussion

<u>Lowland plants amplify warming-induced soil carbon loss</u>

We exploited two independent field experiments in which alpine plant communities plus rooting zone soil were transplanted from high to low elevation to simulate warming, or back into a high elevation site as a negative control (Supplementary Fig. S1). Half of the alpine communities at low elevation were planted with seedlings of local lowland plant species to simulate the arrival of lowland plants in the ecosystem. Remaining communities at low elevation and all control communities at high elevation were instead subjected to a planting disturbance control (see Methods for a full account of control treatments and validation exercises). We found that warming of less than one year caused a small decline in alpine soil carbon content, but in both regions this effect was stronger and only became statistically significant when lowland plants were also present (Fig. 1; Table S1; $P < 0.001$). Indeed, considering field data from both experiments together, we estimate that the arrival of lowland plants in the ecosystem amplified warming-induced soil carbon loss by 52% ± 31% (mean ± 95%

91 confidence intervals) per ºC relative to warming alone (Supplementary Fig. S3; P = 0.001). These
92 findings collectively show that once lowland plants establish in alpine communities they can amplify
93 warming-induced soil carbon loss. We thus suggest that uphill migrations of lowland plants, which
94 are already globally common[8,18], have a hitherto unrecognised bearing over alpine soil carbon
95 storage and could ultimately yield a positive climate feedback.
96
97 Lowland and alpine plants have distinct effects on soil microbial respiration
98 Soil carbon loss occurs due to the activity of soil microorganisms, which break down soil organic
99 matter and release a portion as CO_2 through respiration[23]. We therefore hypothesised that the
100 observed impact of lowland plants on alpine soil carbon loss was mediated *via* lowland plant effects
101 on soil microbial respiration. To test this, we performed a glasshouse experiment in which we grew
102 lowland plants (*Bromus erectus*, *Salvia pratensis*, *Medicago lupulina*) or alpine plants (*Phleum*
103 *alpinum*, *Anthyllis vulneraria* subsp. *alpestris*, *Plantago alpina*) in alpine soil collected from the
104 western Alps region. We found that lowland plants accelerated soil microbial respiration relative to
105 alpine plants (Fig. 2a; treatment × time: LR = 147.99, $P < 0.001$). Accelerated microbial activity was
106 also reflected in spectral analyses of soil pore water, which showed that soil under lowland plants
107 contained more dissolved organic matter (Fig. 2d,e; Table S2; a_{350}: $P < 0.001$, F_{tot}: $P < 0.001$) with a
108 higher proportion of microbially-derived products (Fig. 2f; Table S2; FI; P = 0.002) than soil under
109 alpine plants. Importantly, microbial respiration was enhanced despite no changes to microbial
110 biomass between treatments (Fig. 2g; Table S2; P = 0.693), showing that microbes respired
111 intrinsically faster (that is, per unit of biomass) in the presence of lowland plants. These findings
112 together imply that lowland plants accelerate alpine soil carbon loss by stimulating the activity of
113 alpine soil microbes and the associated release of CO_2 through respiration.
114
115 We posit that lowland plants accelerated microbial activity by increasing the quantity of root exudates
116 released into the soil, for four reasons. First, two-pool models of microbial respiration revealed that
117 soils supporting any plant contained a soil carbon pool that was effectively absent from a bare soil
118 control, and which was 1.5 ± 0.7 (mean ± SE) times larger under lowland plants than alpine plants
119 (Fig. 2b; Table S2; P = 0.046). This carbon pool decayed at a similar rate between treatments (Fig.

2c; Table S2; $P = 0.631$), indicating that it differed in size, but likely not composition, between lowland and alpine treatments. Second, the same carbon pool was consumed rapidly by soil microbes (half-life = 5.1 ± 0.4 days), and we also found that lowland plant effects on microbial respiration were lost after nine days of incubation without plants (Fig. 2a). Plants thus supplied compounds to microbes that were depleted within this timeframe. A nine-day decay period corresponds to the time expected for newly photosynthesised CO_2 to be released through root exudation and respired by soil microbes[21,22], suggesting that this carbon pool was mostly root exudates. Third, lowland plant effects on the alpine soil system were rapid, occurring within a period of weeks in the glasshouse experiment and months in the field experiments. It is unlikely that lowland plants influenced microbial activity *via* litter inputs within this timeframe[24,25]. Finally, dissolved organic matter contained a higher relative abundance of protein-like substances than humic-like and fulvic acid-like substances (Supplementary Fig. S5; Table S2; $P < 0.01$ in all cases) under lowland plants than alpine plants, also suggesting that lowland plants caused an enrichment in exudate-derived compounds[26]. Together, these findings suggest that lowland plants induce soil carbon loss from alpine ecosystems by increasing root exudation relative to resident alpine plants, which accelerates soil microbial activity and the associated degradation and release of soil carbon as CO_2[27,28].

Plants adapted to different temperatures can possess distinct traits that have opposing effects on carbon cycle processes[11]. We thus investigated whether lowland plants acted on the alpine soil system by introducing novel traits into the ecosystem. Publicly available trait data[29] relating to all species in the field experiments revealed that lowland plants on average possessed more productive traits than alpine plants (Supplementary Fig. S2a; $P = 0.025$). This was also the case in the glasshouse experiment, whereby trait measurements from all plants showed that lowland plants displayed more productive traits overall (Supplementary Fig. S2b; $P = 0.001$). Coupled to this, while lowland plants were planted at low abundance in the field experiments (mean ± SE relative cover: 4.7% ± 0.7%), the magnitude of soil carbon loss caused by lowland plant presence was greater in plots where lowland plants were more abundant overall (Supplementary Fig. S2e; $F_{1,14} = 5.79$, $P = 0.030$). By contrast, we found no evidence that soil carbon loss in the field was alternatively related

148 to individual lowland species identity (Supplementary Fig. S2c,d) or the composition of the recipient
149 alpine plant community (Supplementary Fig. S2,g).
150
151 Taken together, these findings confirm that lowland plants are functionally distinct from alpine
152 plants. As a result, our results suggest that their establishment leads to a shift in plant community
153 functioning that alters carbon cycle processes, with effects that intensify as lowland plants become
154 more abundant in the community[24,25]. However, it is also possible that lowland plants acted on the
155 alpine soil system simply by introducing more biomass into the ecosystem. We investigated this
156 possibility by summarising traits from the glasshouse experiment at the pot scale using a principal
157 components analysis and testing for relationships between resulting axes of trait variation and
158 alpine soil microbial respiration (Methods). We found that descriptors of plant biomass represented
159 the most important axis of trait variation (Supplementary Fig. 4c) and were positively related to
160 microbial respiration (Supplementary Fig. 4a; PC1: LR = 4.43, N = 20, P = 0.035). However, this
161 relationship did not differ between lowland and alpine treatments (treatment × PC1: LR = 0.28, N =
162 20, P = 0.596), ruling it out as the mechanism through which lowland plants uniquely alter the
163 alpine soil system. Instead, we found that trait variation represented by the second principal axis
164 (for example, specific leaf area; Supplementary Fig. 4d) had opposing effects on microbial
165 respiration between lowland and alpine treatments (Supplementary Fig. 4b; treatment × PC2: LR =
166 5.98, N = 20, P = 0.015). Lowland plants thus displayed relationships with the alpine soil system
167 that were qualitatively distinct from resident alpine plants. While focussed work is now needed to
168 pinpoint the specific physiological mechanism behind these differences, the existence of such a
169 distinction reveals that the arrival of lowland plants in alpine ecosystems has the capacity to initiate
170 a step-change in plant community functioning, with potential consequences for carbon cycle
171 processes[24,25].

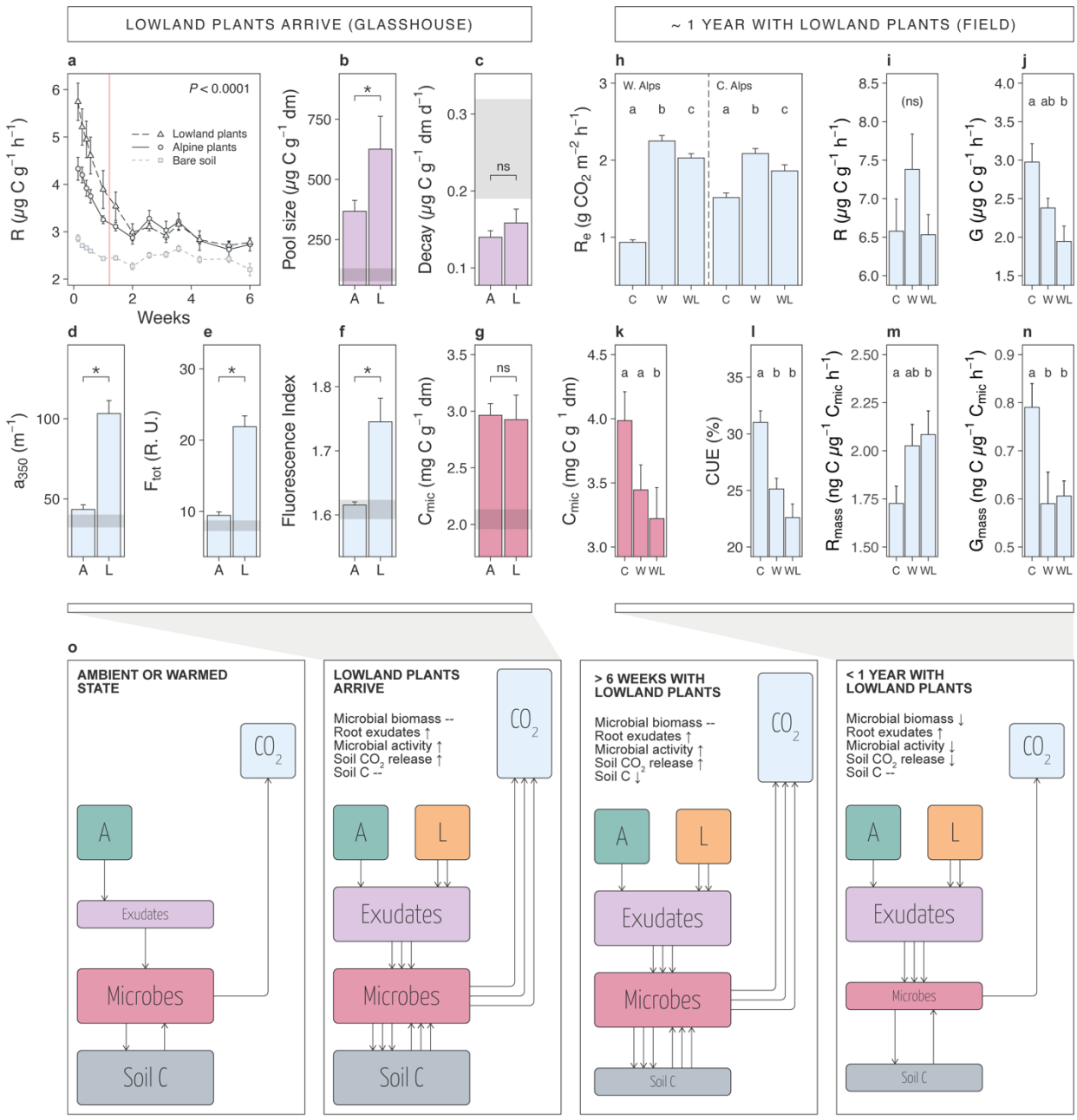

Fig. 2 | Lowland plants and alpine soil carbon cycling. (a-g) Effects of lowland (L) or alpine (A) plants on alpine soil in a glasshouse experiment (mean ± SE; grey points/ribbons: SEs for bare soil). (a) Total microbial respiration (R; μg C g^{-1} h^{-1}) during follow-up incubations without plants (N = 260). Vertical line indicates time before which A-L comparison differed (LME, Tukey). (b) Size (μg C g^{-1}) and (c) decay rate (μg C g^{-1} d^{-1}) of a carbon pool identified using two-pool models (N = 16). (d) Absorbance (a_{350}; m^{-1}), (e) total fluorescence (F_{tot}; Raman Units) and (f) fluorescence index (FI) of soil pore water (N = 20). (g) Microbial biomass carbon (C_{mic}; mg C g^{-1} dry mass) (N = 18). (h-m) Effects of field warming (W), warming plus lowland plants (WL) or an ambient control (C) on alpine soil (means ± SEs) after one season. (h) Total ecosystem respiration (R_e; g CO_2 m^{-2} h^{-1}) averaged over multiple dates in the western and central Alps field experiments (N = 196, N = 90). (i) Total microbial respiration (μg C g^{-1} h^{-1}), (j) total microbial growth (μg C g^{-1} h^{-1}), (k) C_{mic} (μg C g^{-1}), (l) microbial carbon use efficiency (CUE; %), (m) biomass-specific microbial respiration (R_{mass}; ng C μg^{-1} C_{mic} h^{-1}) and (n) biomass-specific microbial growth (G_{mass}; ng C μg^{-1} C_{mic} h^{-1}) in the western Alps experiment (N = 28). Treatment effects ($P < 0.05$) are indicated by asterisks (b-g; LMEs) or letters (h-n; LMEs, Tukey). Fills correspond to pools in a conceptual model (o) proposing a timeline for how lowland (L) versus alpine (A) plants impact alpine soil carbon loss.

186 Lowland plant-induced carbon loss is pulsed

187 Soil microbial processes are constrained by multiple feedbacks within the soil system, such as
188 substrate availability[30,31] and microbial acclimation[32–34], that over time can slow, and eventually
189 arrest, amplified soil carbon loss[31,33,34]. We thus interrogated the state of the soil system in the field
190 experiments after one season to explore the possible duration of lowland plant effects on alpine soil
191 carbon loss. We focussed particularly on intrinsic rates (that is, per unit of biomass) of microbial
192 respiration and growth as processes that promote soil carbon loss and gain, respectively[28,35], as well
193 as microbial biomass as the scalar through which these processes affect soil carbon[30,31]. We found
194 that biomass-specific rates of microbial respiration in the field increased under warming in the
195 presence, but not absence, of lowland plants (Fig. 2m; Table S1; $P = 0.038$). By contrast, biomass-
196 specific rates of microbial growth were slower under warming but remained unaffected by lowland
197 plant presence (Fig. 2n; Table S1; $P = 0.016$). These findings support observations from the
198 glasshouse experiment that lowland plants accelerate intrinsic rates of microbial respiration (Fig.
199 2a,g), while also confirming that this persists for at least one season of field exposure. Moreover, by
200 stimulating respiration, but not growth, lowland plants increased the capacity for alpine soils to lose
201 carbon, but not to gain carbon *via* accumulation into microbial biomass[28,35].

202

203 Faster microbial respiration can only yield a loss of soil carbon if it occurs on a per unit of soil
204 basis[31,34,36], which was the case in the glasshouse experiment (Fig. 2g). However, in the field we
205 found that lowland plants caused a reduction of microbial biomass carbon in warmed plots (Fig. 2k;
206 Table S1; $P < 0.001$). As such, although microbes always respired intrinsically faster in the presence
207 of lowland plants, in the field they had become less abundant and so we observed no change to
208 microbial respiration when expressed per unit of soil (Fig. 2i; Table S1; $P = 0.550$). Depressed
209 microbial respiration per unit of soil was also evident at the ecosystem scale, in that warming
210 accelerated total ecosystem respiration (that is, plant plus soil respiration) but its effect was
211 dampened in plots containing lowland plants (Fig. 2h; Table S1; $P < 0.001$). The decline in microbial
212 biomass likely took place because soil microbes are chiefly carbon limited, making their abundance
213 tightly coupled to soil carbon content (here: $r_{26} = 0.61$, $P = 0.001$)[31]. Moreover, since intrinsic rates

214 of microbial growth were unaffected by lowland plants, a reduction in microbial biomass translated
215 into a decline in microbial growth per unit of soil (Fig. 2j; Table S1; P = 0.009) – preventing any
216 recovery of microbial biomass *via* growth[35]. We thus suggest that as soil carbon was lost, microbial
217 biomass also declined, and at the time of measurement this had entirely eliminated the influence of
218 accelerated biomass-specific microbial respiration over the soil system. In short, the soil carbon loss
219 observed in warmed field plots containing lowland plants must have both started and stopped within
220 one season.
221
222 Our findings collectively suggest that the establishment of lowland plants in warming alpine
223 ecosystems accelerates intrinsic rates of microbial respiration (Fig. 2a), which leads to a pulse of
224 soil carbon release at baseline levels of microbial biomass (Fig. 1, Fig. 2g). However, resulting soil
225 carbon loss leads to a decline in microbial biomass (Fig. 2k), a decrease in microbial respiration per
226 unit of soil (Fig. 2i) and a cessation of further carbon loss from the ecosystem within a one-year
227 timeframe (Fig. 2o)[31]. Here, we simulated a single event of lowland plant establishment, and at
228 relatively low abundance in the community (mean ± SE relative cover: 4.7% ± 0.7%). Future work
229 should thus address whether increases in lowland plant cover or repeated establishment events
230 could induce additional pulses of alpine soil carbon loss. It is important to note that this interpretation
231 does not consider the possibility that soil microbes acclimate to the presence of lowland plants, which
232 could also yield a deceleration in microbial processes over time[32–34]. Nevertheless, it remains true
233 that biomass-specific microbial growth and respiration affect the soil system as a function of their
234 biomass, and here changes to microbial biomass were sufficient to explain the behaviour of the soil
235 system in both glasshouse and field experiments. We also found no evidence that soil microbes
236 instead changed their resource use strategy in the presence versus absence of lowland plants (that
237 is, carbon use efficiency; Fig. 2l; Table S1; P < 0.001; Tukey: P = 0.996), pointing away from
238 microbial acclimation as an alternative mechanism.
239
240 Conclusions
241 In summary, we show that uphill migrations of native lowland plants can rapidly amplify the direct
242 effects of climate warming on soil carbon loss from alpine ecosystems. This is important because it

demonstrates that plant range expansions between herbaceous plant communities have the potential to yield a positive feedback to climate warming, at least in the short term. These results contrast with expectations from woody species expansions in the Arctic, where shrubs with recalcitrant litter can slow carbon turnover in herbaceous communities and potentially yield a negative climate feedback[14,15]. We thus suggest that the influence of range expanding species on ecosystem carbon dynamics depends on the relative trait composition of migrating species versus the recipient community[37], as well as subsequent effects on environmental processes[14]. While our findings demonstrate that lowland plants affect the rate of soil carbon loss in the short term, short-term experiments, such as ours, cannot resolve whether lowland plants will also affect the total amount of soil carbon lost in the long term. However, here soil carbon loss occurred despite a low abundance of lowland plants, and increased with total lowland plant cover. Given that both warming and associated plant migrations will intensify over time[8,9], our estimates of lowland plant impacts may be conservative – particularly if increases in lowland plant cover or repeated establishment events cause recurrent pulses of soil carbon loss. Moreover, while alpine ecosystems store only a small fraction of total global soil carbon[1,2], redistributions among herbaceous plant communities are occurring globally[4–9], including in similarly cool ecosystems in the Arctic that contain vast soil carbon stocks[38]. This raises the potential for resulting climate feedbacks to also be widespread. Future work should focus on testing the conditions under which this feedback could occur in other ecosystems experiencing influxes of range expanding plant species, on quantifying how deeply it occurs in shallow alpine soils, and on estimating the magnitude of the climate feedback given both ongoing warming and variation in rates of species range shifts.

Materials & Methods

Field site description, experimental design. We made use of two independent alpine grassland transplant experiments that were established in Switzerland in the western Alps (46°12′40″N, 7°03′13″E)[39] and central Alps (46°52′20″N, 9°28′58″E) in autumn 2016. The experiments examine effects of climate warming on alpine ecosystems, including the arrival of lowland plants due to warming-induced uphill plant migrations (Supplementary Fig. S1). In the western Alps experiment the plant community is dominated by *Sesleria caerulea*, *Carex sempervirens* and *Vaccinium vitis-idea*. In the central Alps experiment the dominant species are *Nardus stricta*, *Alchemilla xanthochlora*, *Trifolium pratense* and *Anthyllis vulneraria*. Broadly, the experiments share the same design. Turfs (area = 1 m^2, depth = 20 cm) of intact alpine vegetation plus rhizosphere soil were removed from a high elevation control site (western Alps: 2200 m, MAT = 0.7 ºC, TAP = 1448 mm; central Alps: 2000 m, MAT = 1.6 ºC, TAP = 1151 mm; ref. [40]) and replanted either at a low elevation site to simulate climate warming (western Alps: 1400 m, MAT = 6.0 ºC, TAP = 1236 mm, N = 10; central Alps: 1400 m, MAT = 4.4 ºC, TAP = 1010 mm, N = 20; ref. [40]) or back into a high elevation site as a transplantation control (see below). At the low elevation site, we created an additional treatment to simulate the arrival of lowland plants under warming by planting a low abundance of lowland plant species in a grid design (13 cm between individuals), creating a lowland plant density of approximately 56 individuals per m^2 (4.7% ± 0.7% total cover) in a background alpine plant community. Lowland plants were positioned randomly in the grid, but with the same number of individuals per species per plot, and we controlled for planting disturbance in all remaining plots using alpine plants in place of lowland plants (see below). In the western Alps region, lowland plant species were *Achillea millefolium, Bellis perennis, Bromus erectus, Dactylis glomerata, Medicago lupulina, Plantago media* and *Salvia pratensis*, and individuals were planted into one side of each plot in a split-plot design (n = 10). In the central Alps experiment, lowland plant species were *Brachypodium pinnatum, Carex flacca, Carum carvi, Dactylis glomerata, Hypericum perforatum, Plantago lanceolata*, *Primula veris, Ranunculus bulbosus, Salvia pratensis*, *Silene vulgaris*, *Trifolium montanum* and *Viola hirta*, and individuals were planted into half of the transplanted turfs (n = 10). In the western Alps experiment, lowland individuals were pre-grown in a greenhouse in steam-sterilized field soil and planted into the plots in May 2017. In the central Alps experiment, lowland

individuals were taken from the surrounding vegetation and planted into the plots in autumn 2016. In both regions, soil was partially removed from lowland individuals prior to planting, and we performed an additional experiment to eliminate the possibility that small contaminations of lowland soil biota during planting could have modified alpine soil microbial community composition (see Supplementary Methods). Overall, the experimental design in both regions yielded three treatments (n = 10 for each) arranged in a block design: warming only (W); warming plus low elevation plants (WL); and a high elevation control (C). One turf at the low elevation site in the western Alps experiment failed, leaving a total sample size of N = 28 and N = 30 in the western Alps and central Alps, respectively.

Field experiment controls and validation. We controlled for transplantation disturbance in both experiments by moving alpine control turfs back into a high elevation control site. In the western Alps experiment, alpine turfs were planted into different positions at their origin high elevation site. In the central Alps experiment, alpine turfs were planted into a new high elevation site at the same elevation. As such, we eliminated the possibility that alpine turfs changed simply because they were disturbed or were moved to a different location (that is, irrespective of elevation). The transplantation process had no effect on alpine soil carbon content, in that we found no difference in soil carbon content between replanted alpine control turfs at high elevation sites and undisturbed alpine soil in the surrounding area (LR = 2.27, N = 16, P = 0.132). We also controlled for potential effects of planting disturbance in all turfs not planted with lowland plants (that is, remaining turfs at low elevation and all control turfs at high elevation). In the western Alps experiment, we planted alpine species from the high elevation control site into the other side of alpine turfs at the low elevation site, as well as into all control turfs at the high elevation site. This was done in autumn 2016 using the same approach and randomized hexagonal grid design. In the central Alps experiment, we mimicked planting disturbance by digging up and replanting existing individuals in alpine turfs at the low elevation site not containing lowland plants, as well as all control turfs at the high elevation site. This was done in spring 2017 using the same grid design. It is important to note that we did not perform a reverse transplantation (that is, from low to high elevation), so we cannot entirely rule out the possibility that transplantation of any community to any new environment could yield a loss of soil

322 carbon. Nevertheless, it is well established that climate warming promotes soil carbon loss[27,41,42],
323 and we found that soil from low elevation sites (that is, the potential end-member for warming alpine
324 ecosystems) contained less carbon than soil from the alpine sites (70.1 ± 3.05 mg C g^{-1} soil dry mass
325 compared to 145.0 ± 5.29 mg C g^{-1} soil dry mass; LR = 37.2, N = 27, $P < 0.001$), validating our
326 expectation that alpine soil would lose carbon under warming. Elevation-based transplant
327 experiments are a powerful approach for assessing warming effects on ecosystems[11,43], especially
328 when they include rigorous disturbance controls (see above) and are performed in multiple locations
329 where the common change from high to low elevation is temperature – here warming of between 2.8
330 ºC (central alps) and 5.3 ºC (western alps). While small variations in experimental design between
331 regions, such in the order of planting in W and WL treatments, likely introduced some error when
332 comparing experiments, we used both regions together so that we could identify treatment effects
333 that were consistent among them and were thus not artefacts of experimental design.
334
335 **Field plant community composition.** We surveyed the composition of alpine communities in
336 summer 2017. This was done by dividing each plot into 5 × 5 cm cells and visually estimating the
337 canopy cover of all species rooted in every grid cell. Species cover was approximated with an ordinal
338 scale in which the first three cover categories correspond to 1/16, 1/8, and 1/4 of the grid cell area
339 (25 cm^2), and subsequent cover categories were constant increases of 1/4 of the grid cell area.
340 Plants were identified to species level whenever possible, although some taxa were identified only
341 to genus or subfamily levels when species identity was unclear based on vegetative traits. Species
342 cover (cm^2) was then calculated as the species-wise sum of cover estimates across all grid cells in
343 the quarter of the plot used for soil and ecosystem respiration measurements (see below).
344
345 **Field soil carbon content, microbial physiology, microbial biomass.** We collected soil samples
346 from all treatments in both field experiments (N = 58) in August 2017. In each plot, we created a
347 composite sample from three cores (ø = 1 cm, approx. *d* = 7 cm) no closer than 7 cm from a planted
348 individual and from the same quarter of the plot used for ecosystem respiration measurements (see
349 below; Supplementary Fig. S1). We focused on rhizosphere soil for two reasons. First, alpine soils
350 are shallow and alpine plants are shallow-rooting, making the rhizosphere the most logical target for

351 a first assessment of warming and lowland plant effects on alpine soil carbon cycling. Second, we
352 wanted to avoid any potential contamination from the base of the turf (depth = 20 cm). Soils were
353 kept cool, transported immediately to the laboratory, sieved (2 mm mesh size), adjusted to 60% of
354 water holding capacity (WHC) and pre-incubated for three days at field temperature prior to
355 measurements. We measured microbial biomass carbon (mg per g dry mass) *via* chloroform
356 fumigation extraction followed by analysis on a TOC-VCPH/CPNTNM-1 analyzer (Shimadzu; 48h
357 incubation period; 1 M KCl extraction for fumigated and non-fumigated samples; conversion factor
358 0.45)[44]. While this approach also yielded measurements of dissolved organic carbon (DOC; mg C
359 per g dry mass), treatment effects on this variable echoed those of microbial biomass carbon (Table
360 S1) so we did not interpret them separately. Soil organic carbon content (%) was measured on dry
361 soil (60 ºC for 48h) with a Carlo Erba 1110 elemental analyzer (EA, CE Instruments) coupled to a
362 Delta Plus IRMS via a Conflo III (Thermo Fisher). We additionally quantified microbial growth,
363 respiration and carbon use efficiency in soils from the western Alps experiment (N = 28) using the
364 incorporation of ^{18}O into DNA[31]. Briefly, we incubated 500 mg of soil for 24h at field temperature
365 following addition of either ^{18}O-H_2O to 20 atom% enrichment and 80% of WHC or the same volume
366 of molecular grade non-labelled H_2O as a natural abundance control. Gas samples were taken at
367 the start and end of the 24h incubation and analyzed for CO_2 concentration with a Trace GC Ultra
368 (Thermo Fisher) to determine microbial respiration (µg C per g dry mass per h). At the end of the
369 incubation, soil was snap-frozen in liquid nitrogen, and DNA was extracted (FastDNA SPIN Kit for
370 Soil, MP Biomedical), quantified (Quant-iT PicoGreen dsDNA Assay Kit, Thermo Fisher) and
371 analyzed for ^{18}O abundance and total oxygen content using a thermochemical EA coupled to a Delta
372 V Advantage IRMS via a Conflo III (Thermo Fisher). Following ref. [31], we calculated total DNA
373 production during the 24h incubation (µg DNA per gram dry mass) and coupled it with measures of
374 microbial biomass carbon content to derive microbial growth (µg C per gram dry mass per h) and
375 carbon use efficiency (%).
376
377 **Field ecosystem respiration.** We measured rates of ecosystem respiration (g CO_2 per m^2 per h)
378 on multiple dates (western Alps: 7 dates; central Alps: 3 dates) between July and August 2017. One
379 month prior to the first measurement, we installed permanent gas sampling collars (*h* = 10 cm, ø =

380 30 cm) in each plot to a depth of 5 cm to create an airtight seal at the soil surface[11]. Measurements
381 were made by enclosing plants and soil within the collars with an opaque chamber (*h* = 50 cm, ø =
382 30 cm) and, following a 30s equilibration period, monitoring the increase in CO_2 concentration at 5s
383 intervals over a 60s period (Vaisala GMP343 CO_2 probe attached to an HM70 meter, Vaisala).
384 Chambers contained a fan to mix the headspace during measurements and a small sealable hole
385 on the top that was opened when placing the chamber on sampling collars to avoid pressurization
386 inside the chamber. Soil temperature and moisture were recorded for each measurement and used
387 alongside measurements of air temperature, air pressure, enclosure volume and soil surface area
388 to calculate the CO_2 flux[11]. Where necessary, we repeated measurements in the field to attain a
389 visually consistent CO_2 change over time, and during data processing we discarded fluxes with an
390 *r*-squared of less than 0.9 for this relationship.
391
392 **Glasshouse experiment design.** We established a six-week pot experiment to test for effects of
393 lowland plants on the alpine soil system. Specifically, we filled pots (ø = 10 cm, depth = 9 cm) with
394 sieved soil (mesh size 4 mm) from the high elevation site of the western Alps field experiment, and
395 planted them with lowland species (*Bromus erectus*, *Salvia pratensis*, *Medicago lupulina*) or alpine
396 species (*Phleum alpinum*, *Anthyllis vulneraria* ssp. *alpestris*, *Plantago alpina*) to create a lowland
397 only treatment, an alpine only treatment and a bare soil control (N = 30). We selected a grass, herb
398 and legume species for each treatment, all of which were found naturally at the low (lowland
399 treatment) or high (alpine treatment) elevation sites in the western Alps field experiment. Vegetated
400 treatments contained two individuals of each species planted in a circular pattern such they were
401 never adjacent to conspecifics or plants of the same functional type (i.e. grass, herb, legume). The
402 original design also included a mixed community treatment containing one individual of each lowland
403 and alpine species. However, the mixed treatment had double the species richness of other
404 vegetated treatments and contained an equal cover of lowland and alpine plants (compared to < 5%
405 lowland plant cover in field plots), so we focused our analyses on the comparison between alpine
406 and lowland plant treatments to understand how lowland plants affect the soil differently from alpine
407 plants. All plants were pre-grown from seed provided by commercial suppliers (www.hauenstein.ch,
408 www.schutzfilisur.ch, www.saatbau.at) in steam-sterilized potting soil for two to three weeks to

409 approximately the same biomass and root-washed immediately prior to planting. Pots were arranged
410 in a randomized block design (n = 10) in a greenhouse under standardized growing conditions (22
411 ºC; 50% humidity; no artificial light), and were watered every two to three days as needed. After six
412 weeks, we destructively harvested the plants and soil to characterize treatment effects on plant
413 physiology and the soil system.
414
415 **Glasshouse plant physiology.** We measured maximum leaf-level photosynthesis (photosynthetic
416 capacity; A_{max}; µmol CO_2 per m^2 per s) and stomatal conductance (g_s; µmol H_2O per m^2 per s) under
417 optimum conditions on one individual per species per pot using an open path infrared gas analyzer
418 connected to a 2.5 cm chamber (CIRAS-2 and PLC-6, PP Systems)[11]. Readings were taken once
419 for each individual and corrected using measurements of leaf area (cm^2) on the same leaf, which we
420 also dried and weighed to determine specific leaf area (SLA; cm^2 per gram). Following soil pore
421 water sampling (below), we quantified total, aboveground and belowground biomass of all individuals
422 in the experiment by destructively sampling, washing, drying (60 ºC for 48h) and weighing all plant
423 tissue.
424
425 **Glasshouse soil pore water analysis.** We collected soil pore water from all pots prior to soil
426 sampling (see below) to determine treatment effects on dissolved organic matter (DOM) quality. Soil
427 water was sampled by leaching pots twice with 50 mL sterile tap water, combining and filtering
428 leached water (filter pore size 0.2 µm) and measuring absorbance (200-900 nm with a 1nm
429 increment; 1 cm quartz cuvette; UV-vis spectrophotometer, Shimadzu) and fluorescence intensity
430 (excitation: 240-450 nm with a 5 nm increment; emission: 290-550 nm with a 2.5 nm increment;
431 Fluorolog-3 spectrometer, Horiba). We corrected absorbance spectra against a milli-Q water blank,
432 calculated Napierian absorption coefficients and used these data to derive absorbance at 350 nm
433 (a_{350}; a proxy for DOM content). We expressed fluorescence data as total fluorescence (F_{tot}; Raman
434 Units) and the fluorescence index (FI), i.e. the ratio of emission intensity at 470 nm versus 520 nm
435 at an excitation wavelength of 370 nm (a proxy for microbially-derived DOM[45]). We also derived
436 excitation-emission matrices (EEMs) to quantify the relative abundance of different components of
437 DOM through PARAFAC algorithms[46]. Following preprocessing (i.e. Raman scattering removal and

438 standardization to Raman Units) and normalization[47], we used the drEEM toolbox[48] in MATLAB
439 (Mathworks) to obtain a six-component PARAFAC model. The model was validated with split-half
440 analysis, random initialization and visualization of EEM residuals, after which we calculated the
441 relative abundance of each component as the maximum fluorescence signal of the component
442 against the total maximum fluorescence signal of all components. Finally, we classified components
443 against classical EEM nomenclature (Table S4; refs [49,50]). While PARAFAC modelling provides a
444 means to discriminate between DOM sources (e.g. components C3 and C4; Table S4), we did not
445 physically separate plant- and microbe-derived DOM when sampling soil pore water. As such,
446 observed changes to DOM composition were likely a result of changes to both plant and microbial
447 processes (see Main Text).
448
449 **Glasshouse soil carbon pools, microbial respiration.** We took soil cores (ø = 1 cm, *d* = 7 cm)
450 from the center of each pot (i.e. equidistant from all individuals) to quantify soil carbon pools and
451 microbial respiration. Soils were sieved (2 mm mesh size), adjusted to 60% of their WHC and pre-
452 incubated at 22 ºC for three days prior to measurements. We quantified concentrations of microbial
453 biomass carbon in all soils as for field soil (see above; mg C per g dry mass). We determined
454 microbial respiration by incubating 8 g sieved soil in the dark at 22 ºC for a further six-week period
455 without plants. We measured microbial respiration daily for the first four days, then approximately
456 biweekly until the end of the six-week period. We measured CO_2 concentrations (EGM-4, PP
457 Systems) of gas samples taken approximately 24h after flushing enclosed vials (*v* = 126 mL) with
458 CO_2-free air, and calculated microbial respiration (µg C per g dry mass per h) using accompanying
459 measurements of enclosure volume, air pressure and soil mass[11]. After each measurement, soils
460 were weighed and, when necessary, re-adjusted to 60% of their WHC.
461
462 **Two-pool mixed models of soil carbon mineralization.** We described the kinetics of soil carbon
463 mineralization during the follow-up incubation of glasshouse soil by employing a two-pool mixed
464 model to microbial respiration data[51]. Specifically, we constructed a model that considered a first
465 pool that followed first-order decomposition kinetics (i.e. a small soil carbon pool with a fast turnover)

466 and a second pool that followed zero-order kinetics (i.e. decay rate was constant over the incubation
467 period, representing a large soil carbon pool with a slow turnover):
468
469 $$C_{min} = C_l\left(1 - e^{-tk_l}\right) + B \cdot t$$
470
471 where C_{min} is the cumulative CO_2 respired (µg C g^{-1}) over the incubation time t (d), C_l and k_l are the
472 size (µg C g^{-1}) and decomposition constant (d^{-1}) of the first-order kinetics carbon pool, respectively,
473 and B is the basal respiration rate (µg C g^{-1} d^{-1}) of the zero-order kinetics carbon pool. Given that
474 C_{min} and t were known, we ran the two-pool mixed model with the nlsList function (maxiter = 100, tol
475 = 1×10^{-5}, minFactor = 1/1024) in R[52] using the package "nlme"[53] for each pot separately to estimate
476 values for C_l, k_l and B. Models failed to converge for one sample, and we excluded four additional
477 samples for which models made negative pool estimates (N = 25).
478
479 **Statistical analysis.** The majority of statistical test outputs appear as *P*-values in the Main Text,
480 with full outputs being provided in Tables S1 to S3. See text below for exceptions. Data analyses
481 and visualization were undertaken in R[52] using the packages "cowplot"[54], "drake"[55], "emmeans"[56],
482 "nlme"[53], "tidyverse"[57] and "vegan"[58]. Where necessary, region was accounted for in statistical
483 models as a fixed effect, since two levels was too few to be included as a random intercept term. As
484 such, region effects are presented (Tables S1, S3), but not interpreted. Statistical methods are
485 described as they appear in the Main Text.
486
487 <u>Warming and warming plus lowland plant effects on soil carbon content:</u> we used field data to test
488 for treatment (C, W, WL) effects on soil carbon content using an LME model including region as a
489 fixed effect and block as a random intercept term (see Table S1 for test output). We also calculated
490 how much more soil carbon loss occurred in the presence versus absence of lowland plants by fitting
491 a single LME testing for effects of soil temperature (plot means of all sampling dates), the presence
492 or absence of lowland plants and their interaction on soil carbon content (see Supplementary Fig.
493 S2 for test outputs). In order to compare slopes between C-W and C-WL treatment combinations,
494 we duplicated C treatment values, assigned one set to each C-W and C-WL pair and accounted for

495 this using a random intercept term. We also included region as a random slope term. We then tested
496 how much more soil carbon loss would occur per ºC of warming when lowland plants are present by
497 calculating the relative difference (% ± 95% confidence intervals) between the C-WL and C-W
498 slopes.
499
500 Plant mechanisms for soil carbon loss: we expressed soil carbon content as the block-wise percent
501 changes between WL and W treatments to derive a metric for lowland plant induced soil carbon loss
502 (i.e. % soil carbon remaining). We tested for lowland species identity effects on soil carbon remaining
503 using separate LMEs for each region (due to different lowland species pools) that tested for individual
504 species cover (cm^2) effects on soil carbon remaining in WL plots, including species as a random
505 intercept term (see Supplementary Fig. S2 for test outputs). We also performed separate linear
506 models including species as fixed effects, none of which were statistically significant (Table S3). We
507 tested for effects of total lowland species cover (cm^2) on soil carbon remaining in WL plots using a
508 linear model also including region as a fixed effect. We summarized alpine community composition
509 in W and WL treatments using an NMDS (Hellinger distance matrix, two axes), following which we
510 expressed NMDS scores as the block-wise percent changes between W and WL treatments to
511 derive metrics for lowland plant induced alpine plant community change, and used a linear model
512 that tested for effects of changes to NMDS scores on soil carbon remaining in WL plots including
513 region as a fixed effect (see Supplementary Fig. S3 for test outputs). For reference, raw NMDS
514 scores did not significantly differ between W and WL treatments (LME: NMDS #1: LR = 1.57, P =
515 0.210; NMDS #2: LR = 2.67, P = 0.102). Finally, we tested for differences between alpine and
516 lowland species traits in the field experiment using a PERMANOVA on a PCA of species mean trait
517 values ($\log_{10}$ plant height, $\log_{10}$ leaf area, $\log_{10}$ seed mass, SLA, leaf carbon, leaf nitrogen) from the
518 TRY database[29] for all species present (where necessary, missing values were gap-filled
519 following[59]), and in the glasshouse experiment using a PERMANOVA on a PCA of physiological
520 measurements (total biomass, leaf biomass, root biomass, SLA, A_{max}, g_s) for all plants (see
521 Supplementary Fig. S3 for test outputs). Traits were selected to explore broad life history differences
522 between alpine and lowland plant species[60], but were not used to identify the specific trait(s)
523 responsible for lowland plant effects on alpine soil carbon loss. We used TRY traits for field species

524 due to the large number of species present in the communities (N = 118), but used measured traits
525 in the glasshouse experiment to provide direct evidence of physiological differences between alpine
526 and lowland species.
527
528 Lowland versus alpine plant effects on the soil system: we used the glasshouse experiment to test
529 for lowland versus alpine plant effects on soil microbial biomass carbon, the size (C_l) and decay rate
530 (k_l) of the first modelled soil carbon pool and all variables relating to soil DOM quality using LMEs
531 including block as a random intercept term. We tested for effects of treatment, time and their
532 interaction on soil microbial respiration using the same LME structure but including the bare soil
533 treatment. In all cases, including/excluding the bare soil treatment had no effect over model
534 outcomes, but mean ± SE values for this treatment are included in figures for reference. Finally, we
535 explored how plant physiology in lowland and alpine treatments affected initial rates of soil microbial
536 respiration. We defined initial microbial respiration as the pot-wise mean respiration rates of the first
537 nine days of soil incubation (that is, while treatment effects persisted; see Fig. 2a), and expressed
538 pot-level plant physiology using scores from the first two axes of a principal components analysis
539 performed on sums of total, root and shoot biomass and biomass-weighted means of SLA, A_{max} and
540 g_s. We then tested for effects of treatment, PC1 and PC2 scores and their interaction on initial
541 microbial respiration using an LME including block as a random intercept term. Statistical test outputs
542 for LMEs are provided in Table S2, except for treatment and plant physiology effects on microbial
543 respiration, which appear in the Main Text.
544
545 Sequence of warming and lowland plant effects on alpine soil carbon loss: we used field data to test
546 for treatment (C, W, WL) effects on soil microbial biomass carbon and soil DOC using LME models
547 including region as a fixed effect and block as a random intercept term. We tested for treatment
548 effects on ecosystem respiration using an LME that included region as a fixed effect and sampling
549 date nested in block as a random intercept term. We tested for treatment effects on soil microbial
550 growth and respiration (per unit of soil and per unit of microbial biomass) and carbon use efficiency
551 in the western Alps experiment using LMEs including block as a random intercept term. Statistical
552 test outputs for these variables are provided in Table S1. We also used Pearson Product Moment

correlations to test for associations between soil microbial biomass and soil carbon content, microbial respiration and growth in the western Alps experiment, irrespective of experimental treatment.

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Author contributions

TWNW, AB and JMA conceived the study. AR, AB and JMA provided resources for field and laboratory experiments. SB, TM and HN established and maintained field experiments. TWNW, KG and TG undertook the field work. TWNW, KG, TG, PM, CS, AB and JMA undertook the glasshouse experiment. TWNW, KG, TG, PM, CS and AR did the laboratory work. TL performed the soil pore water sampling and associated analyses. SB and TM performed the soil inoculation experiment and associated analyses. TWNW did the data analysis, with support from DR, TWC and JMA. TWNW wrote the manuscript in close collaboration with JMA, and with support from all co-authors.

Competing interests

The authors declare no competing financial interests.

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