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1 **Soil organic matter changes under experimental pedoclimatic modifications in**
2 **mountain grasslands of the French Alps**

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14 **Abstract**

15 Mountain grasslands contain large stocks of soil organic carbon (SOC), of which a good part is in
16 labile particulate form. This labile SOC may be protected by cold climate that limits microbial
17 activity. Strong climate change in mountain regions threatens to destabilize these SOC stocks.
18 However, so far the climate response of SOC stocks in mountain grasslands remains highly
19 uncertain, under either warming or cooling conditions. To overcome this knowledge gap, we
20 studied the effect of pedoclimatic regime changes on topsoil (0–10 cm) SOC in two
21 complementary experiments: 3 °C of warming or cooling by reciprocal transplanting to an alpine
22 (2450 m a.s.l.) and a subalpine (1950 m a.s.l.) grassland and 1 °C of warming by open-top
23 chambers in the same grasslands.

24 Topsoil SOC stocks were higher at the alpine site than at the subalpine site, and the
25 biogeochemical signature of the soil organic matter (SOM) also differed between the two study
26 sites. SOM was O-enriched, H-depleted, and more thermally stable at the warmer subalpine site.
27 After three years, abrupt warming by transplanting tended to decrease topsoil SOC content. The
28 remaining SOC was characterized by a more thermostable signature. This result suggests the
29 preferential depletion of labile SOC upon experimental topsoil warming. Cooling did not modify
30 overall SOC content but uphill transplanted topsoils showed a more thermolabile biogeochemical
31 signature. In contrast, open-top chamber warming of alpine and subalpine topsoils caused limited
32 changes to SOC stocks and SOM biogeochemical signature, possibly because the induced
33 pedoclimatic change was more limited and more gradual compared to the warming by
34 transplanting which reduced the annual snow cover period by around 60 days and increased

35 cumulative degree days by a factor of ten as compared to the OTC-induced warming. Gradual
36 temperature changes may take longer to become effective than a shock transplant treatment.
37 We conclude that SOC in mountain grassland topsoils can be highly reactive to climate shocks.

38

39 Keywords: soil organic carbon, thermal analysis, mountain soils, cooling experiment, warming
40 experiment

41 **Introduction**

42 Mountain ecosystems cover about 27% of the earth's continental surface and contribute benefits
43 to more than half of humanity (FAO, 2021; Grêt-Regamey et Weibel, 2020; Palomo, 2017). Climate
44 regulation through organic carbon sequestration in soils is one of these critical contributions (EEA,
45 2010; Jobbagy and Jackson, 2000; Schimel, 1995). Mountain soils in temperate regions are known
46 to store large amounts of soil organic carbon (SOC ; Doblas-Miranda et al., 2013; Martin et al.,
47 2011; Meersmans et al., 2012). The soils of grasslands in the European Alps can harbor between
48 53 and 260 Mg ha⁻¹ of SOC (Djukic et al., 2010; Leifeld et al., 2009), which is comparable with
49 those of European forests (Berninger et al., 2015; Liski et al., 2002). The strong climatic constraints
50 at high elevation (e.g. cold climate and frost) limit the decomposition activity of soil microbes and
51 thus result in a high residence time of soil organic matter (Körner, 2003; Sjögersten et al., 2011).
52 This is especially true in the upper soil horizons, where a large part of the SOC is often found in
53 particulate form, that is not stabilized by mineral interactions, but can show a mean ¹⁴C-age above
54 one century (Budge et al., 2011; Hou et al., 2019; Leifeld et al., 2009; Martinsen et al., 2011;
55 Saenger et al., 2015; Sjögersten, et al., 2011 but see Puissant et al., 2017). This particulate SOC is
56 climatically stabilized (Trumbore, 2009) and therefore potentially highly vulnerable to climate
57 changes predicted for the Alps, including rising temperatures and decreasing snow cover below
58 1500–2000 m above sea level (Gobiet et al., 2014; Jacob et al., 2014). In addition, soils of
59 mountain grasslands are more exposed to climate variability compared to forest soils because the
60 sparse vegetation cover has limited buffering capacity (Gavazov, 2013). The fate of the largely
61 labile SOC stocks of mountain grasslands in response to climate change is therefore a real
62 concern, but remains highly uncertain (Leifeld et al., 2009; Sjögersten et al., 2011).

63 Rising temperatures are expected to stimulate heterotrophic decomposition of organic matter
64 and increase its mineralization (Bond-Lamberty et al., 2018; Bond-Lamberty & Thomson, 2010).
65 However, warming effects on the SOC budget are difficult to predict due to a multitude of
66 interplaying processes : (i) the acclimation of vegetation to warming can result in quantitative and
67 qualitative changes of organic matter inputs (Melillo et al., 2002), (ii) the acclimation of microbial
68 community composition and/or functional strategies can affect decomposition (Conant et al.,
69 2011), (iii) warming is often accompanied by increasing water deficits which limits decomposition
70 (Davidson and Trumbore, 2000), and finally, (iv) the different SOC kinetic pools are prone to
71 respond in different ways to these different dynamics (Davidson & Janssens, 2006). As a result of
72 this multitude of processes acting in concert, experimental studies have shown very contrasting
73 response of topsoil SOC stocks to warming. Some studies found a limited or neutral effect of
74 warming on SOC content due to accompanying soil moisture limitation or acclimation of microbial
75 communities (Marty et al., 2019; Reynolds et al., 2015), while others found very significant effects
76 of warming on soil organic matter: Hicks Pries et al. (2017) observed an important increase of
77 whole-soil profile respiration with warming. A 35-years monitoring study in the German Alps
78 demonstrated a significant decrease in SOC stocks, especially at sites with high levels of
79 particulate SOC and those with the greatest temperature changes (Prietz et al., 2016). In
80 Western Himalaya alpine grasslands, Tiwari et al., (2021) found an increased net SOC uptake due
81 to enhanced plant growth in open-top chamber (OTC with warming of 1.5-2 °C). These results
82 highlight the variability of responses of SOC stocks and fluxes to both experimental and
83 observational warming studies depending on initial conditions and studied timeframes and
84 magnitude of temperature increase. The effect of cooling on SOC is even less studied and we thus

85 do not know whether cooling just leads to opposite effects on decomposition processes to
86 warming or to new responses. However, it would be interesting to understand the effect of cold
87 on SOC, especially in mountain where climatic stabilization maintains the stocks of labile SOC. The
88 few studies existing are based on reciprocal transplants along elevation gradients in forests and
89 in semi-arid shrub-steppe. They have shown no or limited effects of cooling on SOC content (Link
90 et al., 2003; Luan et al., 2014).

91 Several studies have shown the interest of separating SOC into fractions with different mean
92 turnover rates to better understand its vulnerability to climate change (*e.g.*, Lugato et al., 2021).
93 Thermal fractionation of SOC can be used to measure thermal and chemical properties that are
94 specific to biogeochemically stable SOC: stable SOC is thermally stable and depleted in hydrogen
95 (Barré et al., 2016 ; Gregorich et al., 2015; Plante et al., 2013). Due to the stabilization of mountain
96 SOC by climate and the correlation between altitude and SOC lability (Sjögersten et al., 2011),
97 warming is expected to result in the release of an important amount of labile SOC at high
98 elevations. An experimental warming of a shrub-steppe ecosystem showed preferential loss of
99 particulate SOC (Link et al., 2003) while Puissant et al. (2017) highlighted significant SOC losses in
100 the mineral associated fraction, which is the most stable form, on an experimentally warmed
101 subalpine grassland soil.

102 Here we studied the effects of soil warming and cooling on mountain grassland topsoil organic
103 matter, focusing on changes in SOC contents and on the biogeochemical signature of organic
104 matter. We compared two types of common warming experiments that simulate abrupt changes
105 of topsoil temperature: a reciprocal transplant along an elevational gradient that warms an alpine
106 grassland and cools a subalpine grassland and concurrently changes snow regimes, and an OTC

107 warming experiment at the same subalpine and alpine grasslands. Our specific hypotheses are:
108 (1) the SOC content of cooled topsoils increases and that of warmed topsoils decreases as the
109 magnitude of warming increases, (2) topsoil warming will especially cause the release of labile
110 SOC and cooling causes its enrichment and (3) SOC of the alpine topsoil is more sensitive to
111 warming than that of the subalpine topsoil.

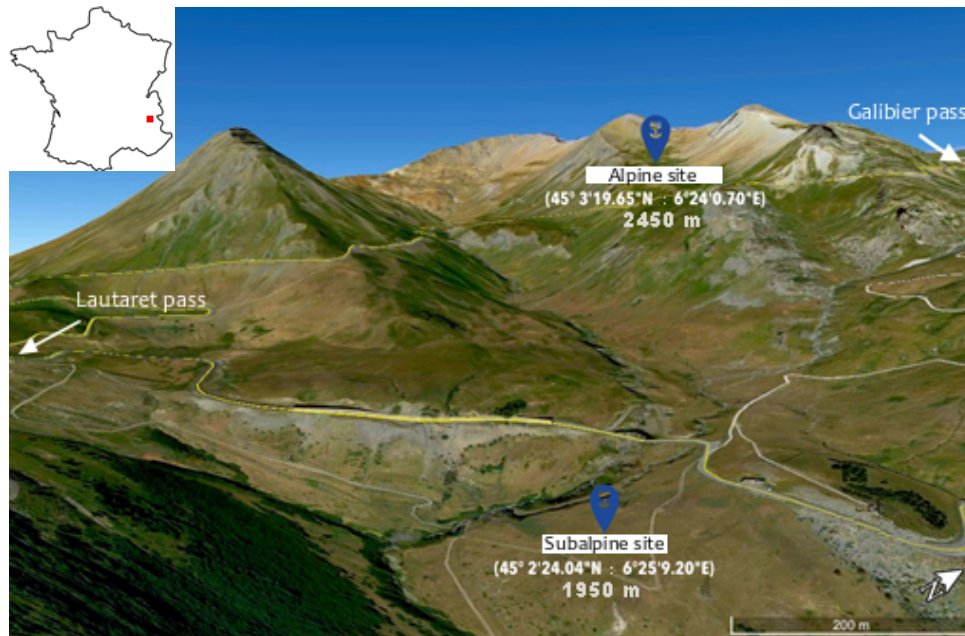
112

113 **Materials and methods**

114 **Study area**

115 The two study sites are located at the long-term Socio-Ecological Research platform Lautaret-
116 Oisans (Zone Atelier Alpes), Grand Galibier Massif in the French South-Western Alps at 2450 m
117 (alpine site, 45°03'19.65 "N 6°24'0.70 "E) on a South-East facing slope and at 1950 m (subalpine
118 site, 45°02'24.04 "N 6°25'09.20 "E) on a South-West facing slope (Figure 1). The meteorological
119 data used to characterize these two sites were extracted from the S2M re-analyses developed by
120 Météo France for the French Alps (Durand et al., 2009; Vernay et al., 2019; Vionnet et al., 2012).
121 Over the period 1988–2017, the yearly accumulation of growing degree days (GDD; from
122 snowmelt to end of July) at the subalpine site is 73% higher than at the alpine site. This difference
123 is largely due to contrasting snow melt dates. On average, snow melt occurs at the beginning of
124 June at the alpine site and at the end of April at the subalpine site. The decadal trend of growing
125 degree days (GDD) since 1959 is significantly positive for both sites. GDD have increased by 10%
126 between the period 1988-2017 and the period 1959–1988 for the subalpine site, and of 41% for
127 the alpine site.

128



129
 130 **Figure 1: Location of the two study sites in the French South-Western Alps (background**
 131 **picture modified from Google earth, 2018).**

132
 133 The soil parent material of the two sites is composed of flysch sediments, called "Flysch des
 134 Aiguilles d'Arves" (Deharveng et al., 1987). The subalpine grassland is dominated by a tall fescue
 135 (*Patzkea paniculata*); other abundant species are *Carex sempervirens*, *Festuca nigrescens*,
 136 *Centaurea uniflora*, *Helianthemum nummularium* and *Meum athamanticum*. The alpine grassland
 137 is dominated by *Carex sempervirens*, *Festuca nigrescens*, *Poa alpina*, *Potentilla aurea*, *Trifolium*
 138 *alpinum*, and *Geum montanum*. Both sites were used for grazing before the experiment but are
 139 fenced off. The subalpine site was used for hay making before the 1960s. Soils of both sites are
 140 silty and classified as Dystric Cambisols (FAO, 2014). They are composed of four soil horizons (see
 141 the photos and pedological description in the supplementary Figure S1). Soil bulk density to a
 142 depth of 10 cm is 0.77 g cm⁻³ at the subalpine site and 0.70 g cm⁻³ at the alpine site. Table 1

143 presents the physicochemical characteristics of the topsoil horizons found above 10 cm depth at
 144 the two sites (including two soil horizons for the alpine site and one soil horizon for the subalpine
 145 site). The topsoils of the two sites are quite similar regarding these physico-chemical
 146 characteristics. They are both acidic (pH in H₂O < 5.5), rich in clay (> 30%) with an exchangeable
 147 phosphorus (P) content corresponding to fairly high P soil availability in a context of natural
 148 grassland soils (> 0.01 g/kg).

149
 150 **Table 1: Physicochemical characteristics of the topsoil horizons found above 10 cm depth at the**
 151 **subalpine and alpine study sites.**

Site	Horizon WRB code	Depth (cm)	Clay (g/kg)	Silt (g/kg)	Sand (g/kg)	Corg (g/kg)	Ntot (g/kg)	P ₂ O ₅ (g/kg)	CaCO ₃ (g/kg)	pH H ₂ O soil	CEC (cmol+/kg)
Subalpine site	A	0–10	380	424	196	68.2	5.4	0.012	<1	5.4	13.3
	A	0–3	442	433	125	171	12.6	0.059	<1	5.0	18.9
Alpine site	A/Bw	3–20	324	459	217	38.7	3.4	0.011	<1	4.7	6.8

152
 153
 154 **Experimental design and topsoil sampling**

155 Two adjacent warming experiments were installed in 2016 at the two study sites.

156 *Reciprocal transplant*

157 In autumn 2016, ten alpine grassland plots were transplanted from the alpine to the subalpine
 158 site (hereafter “alpine warmed transplant”) and ten subalpine grassland plots from the subalpine
 159 to the alpine site (“subalpine cooled transplant”) using a helicopter. Each 4 m² plot consisted of
 160 turfs with above- and below-ground parts of the plant communities and a layer of their associated

161 soil of about 20 cm thickness. In order to account for the disturbing effect of the transplanting,
162 ten 1 m² plots were also transplanted (i.e. simply switched) at the alpine (“alpine control
163 transplant”) as well as the subalpine site (“subalpine control transplant”). Topsoil temperature
164 was monitored at both study sites using a thermal sensor implanted in the soil at 5 cm depth at
165 the beginning of the experiment. At the end of summer 2019, the topsoils of the twenty
166 transplanted plots and the twenty control plots were sampled at 10 cm depth. The topsoil
167 composites samples were dried at ambient temperature and sieved at 2 mm.

168 In addition to the warming, the reciprocal transplant decreased the period of snow cover and
169 increased the GDD of the alpine warmed transplant. Conversely, it increased the period of snow
170 cover and decreased the GDD of the subalpine cooled transplant.

171

172 *Open top chambers*

173 During the growing seasons of 2017, 2018 and 2019 (generally May until October), eight
174 hexagonal open-top chambers were used to experimentally warm the alpine (hereafter “alpine
175 warmed OTC”) and the subalpine (hereafter “subalpine warmed OTC”) soils and associated plant
176 communities. The chambers are based on the design of the International Tundra Experiment
177 (Molau and Mølgaard, 1996), with a 1.5 m diameter, 0.5 m height and covering an area of
178 approximately 2 m² and are arranged in a randomized design to take into account micro-
179 topographic and soil property variation. Paired control plots of 2 m² were also established some
180 2-3 meters away from each open topped chamber (“alpine control OTC” and “subalpine control
181 OTC”). We monitored soil temperature of controls and warmed plots over the period of the

182 growing season using thermal sensors (HOBO pendant UA1-64) implanted in soils at 10 cm depth.
183 During July and August 2019, four soil cores (0–5 cm deep, 2.5 cm diameter) were randomly
184 collected and mixed together to form a composite topsoil sample for each control and warmed
185 plot. The topsoil samples were dried at ambient temperature and sieved at 2 mm.

186

187 **Soil analyses and data treatment**

188 All topsoil samples were finely ground in a disc mill. The soil organic matter bulk chemistry and
189 the SOC thermal stability was characterized by Rock-Eval[®] thermal analysis (Rock-Eval[®] 6 Turbo,
190 Vinci Technologies). A detailed description of this method can be found in Behar et al., (2001) and
191 Disnar et al., (2003). It consists in carbon measurement as gaseous effluent during two phases.
192 The first one is a pyrolysis stage (3 minutes isotherm at 200°C followed by a 200 to 650 °C
193 temperature ramp with a heating rate of 30°C min⁻¹) in N₂ atmosphere during which CO and CO₂
194 were quantified with an infrared detector. Volatile hydrocarbon effluents (CH) were quantified
195 with flame ionization detector. The second phase is an oxidation stage (1 minute isotherm at
196 300°C followed by a 300 to 850 °C temperature ramp with a heating rate of 20°C min⁻¹ and a 5
197 minutes isotherm at 850°C) in laboratory air atmosphere during which CO and CO₂ were
198 quantified with an infrared detector. From each Rock-Eval[®] thermogram, we define three thermal
199 SOC fractions: (i) a small and highly thermolabile pyrolysable SOC fraction (hereafter termed POC
200 1), corresponding to the carbon evacuated as CH, CO or CO₂ at 200 °C over the first 200 s of the
201 pyrolysis phase (Khedim et al., 2021); (ii) pyrolysable organic carbon pool (PC), corresponding to
202 the carbon evacuated as CH, CO or CO₂ during the whole pyrolysis phase, (iii) pyrolysis-resistant

203 organic carbon pool (RC), evacuated as CO or CO₂ during the oxidation stage. The sum of the PC
204 pool and the RC pool inform on the total SOC content (Rock-Eval® parameter TOC). The organic
205 carbon yield of Rock-Eval® SOC quantification was on average 85% to 90% of SOC content
206 determined by elemental analysis, using respectively the Rock-Eval® parameter TOC or the sum
207 of Rock-Eval® parameters TOC and MinC (see Behar et al., 2001 for a definition of these
208 parameters) in these acidic topsoil samples free of carbonates (Table 1).

209 In the PC and RC thermal SOC fractions, we also determined the temperature corresponding to
210 the release of 30%, 50%, 70% and 90% of the CH, CO and CO₂ during the pyrolysis phase and of
211 the CO and CO₂ during the oxidation phase (T_{xx_CH_PYR}, T_{xx_CO_PYR}, T_{xx_CO2_PYR}, T_{xx_CO_OX}
212 and T_{xx_CO2_OX} in the following) in order to more accurately characterize the thermal stability of
213 the SOC released (Cécillon et al., 2018). We also coupled the CH, CO, CO₂ pyrolysis signals to
214 determine the temperature parameters T_{xx_PYR} of the full pyrolysis signal, and we couple the CO,
215 CO₂ oxidation signals to determine the temperature parameters T_{xx_OX} of the full oxidation signal
216 according to Khedim et al. (2021). The higher these indexes are, more thermally resistant the SOC
217 is. Respectively, the CH, CO and CO₂ evacuated during the pyrolysis phase represented on average
218 24%, 3% and 10% of the sum of TOC and MinC. The CO and CO₂ released during the oxidation
219 phase respectively contribute to 4% and 60% of TOC+MinC. Then, the integrated signal of the full
220 pyrolysis gases released represent 37% and that of oxidation represent 63% of TOC+MinC, on
221 average.

222 The oxygen released as CO and CO₂ during the pyrolysis phase and the hydrogen released as
223 hydrocarbons were quantified to respectively determine the oxygen index (OIRE6, mg O₂ g⁻¹ C)
224 and the hydrogen index (HI, mg CH g⁻¹ C). The OIRE6 is correlated with the elemental O : C ratio

225 of soil organic matter and the HI is correlated with the elemental H : C ratio of soil organic matter
226 (Espitalié et al., 1977; Lafargue et al., 1998). Then according to Sebag et al. (2016), the I index was
227 calculated, informing on the preservation of thermally labile SOC released as CH during the
228 pyrolysis phase, as well as the R index, assessing the contribution of thermally stable SOC released
229 as CH during the pyrolysis phase.

230 An elemental analysis (dry combustion; Flash EA1112, Thermo Scientific) was also performed to
231 quantify the SOC content of the transplanted and the OTC warmed topsoil samples and to
232 quantify the N_{tot} content of the transplanted topsoils. The C:N elemental ratio of soil organic
233 matter was calculated as SOC/N_{tot} for the transplanted topsoils. SOC stocks were calculated to
234 10 cm depth (for the reciprocal transplant experiment) or 5 cm depth (for the OTC experiment)
235 according to the equation (1) with t for soil thickness and BD for soil bulk density (initially
236 measured at each site at 10 cm depth).

$$237 \text{ SOC stock [kg/m}^2\text{]} = (\text{SOC[g/kg]} * t [\text{cm}] * \text{BD [kg/m}^3\text{]})/100 \quad (1)$$

238

239 **Statistical analysis**

240 We quantified the effects of the four climate manipulation treatments (warming alpine
241 transplant, cooling subalpine transplant, OTC warming of subalpine grassland and OTC warming
242 of alpine grassland) on all the above-mentioned soil organic matter parameters. We used a Mann-
243 Whitney rank test to compare alpine plots with alpine controls and subalpine plots with subalpine
244 controls, and to compare alpine and subalpine controls. In order to verify the absence of spatial

245 variability between OTC-control pairs, an ANOVA with a mixed effect on the pairs was performed.
246 The statistical tests and graphs were generated with R v.3.5 (R Core Team, 2018).

247 **Results**

248 **Soil temperature**

249 Both sites are seasonally snow covered. During winter, a deep snowpack insulated soil and the
250 topsoil freezing was limited (Table 2). Soil freezing was slightly more pronounced at the subalpine
251 site (lower Freezing Degree Day, FDD) and this was mainly due to early spring low temperature
252 under snow free conditions. The first snow free date occurred two months earlier at the subalpine
253 than at the alpine site (Table 2). Consequently, the yearly accumulation of GDD was 1.8 times
254 higher at the subalpine site. By the time snow melted at the alpine site, the subalpine site had
255 already accumulated 600°C GDD on average and reached flowering of its dominant grass species,
256 *Patzkea paniculata*. The mean daily temperature during summer was 3°C warmer at the subalpine
257 than the alpine site, and for both T_{min} and T_{max}.

258 Summer warming by the OTC was around 1°C irrespective of the site (Table S1). Noticeably, we
259 did not find a higher effect of OTC on daily minimum than maximum soil temperatures. Over the
260 two months of treatment until the sampling date, this OTC-induced warming represented a gain
261 of about 60°C GDD, *i.e.* a 4% increase of the annual GDD for the alpine soil and a 2% increase for
262 the subalpine site. By comparison, when the alpine grassland was transplanted in the subalpine
263 site, the earlier snow melting date represented a GDD gain of 600°C, *i.e.* 10 times more than the
264 OTC-induced warming.

265

266 **Table 2: Topsoil temperature parameters at the two study sites.** Data are averages over the
 267 three years of the experiment. Time series of soil temperatures are presented in Figure S2.
 268 GDDxxx date: date at which the accumulated GDD over the year reaches the xxx°C threshold.

	<i>Alpine control transplant</i>	<i>Subalpine control transplant</i>
Snowmelting date (sd)	31/05 (± 7)	31/03 (± 22)
GDD600 date (sd)	21/07 (± 5)	11/06 (± 9)
GDD1200 date (sd)	10/09 (± 9)	18/07 (± 9)
cumulated GDD (sd)	1490°C (± 121)	2654°C (± 34)
cumulated FDD (sd)	-18°C (± 30)	-32°C (± 36)
Tmax june (sd)	15.3°C (± 0.9)	18.8°C (± 2.0)
Tmin july (sd)	9.8°C (± 1.6)	12.8°C (± 9)
Tmean july (sd)	13.2°C (± 1.6)	16.3°C (± 1.5)
Tmax july (sd)	15.4°C (± 0.7)	18.8°C (± 0.5)

269
 270
 271 **Soil organic carbon content and stocks**
 272 Alpine grassland topsoils had higher SOC contents than subalpine grassland topsoils, especially in
 273 the transplant experiment (Table S2; p-value < 0.001). The 0–10 cm SOC stocks were also higher
 274 at the alpine site (7.8 kg/m²) compared to the subalpine site (5.6 kg/m²). This difference did not
 275 apply for SOC stocks of the 0–5 cm layer (OTC control plots), which for both sites were estimated
 276 at about 3.1 kg C/m².

277 In the transplant experiment, SOC content tended to decrease with warming and did not respond
 278 to cooling (Figure 2a; Table 3). In the OTC experiment, warming slightly decreased SOC content
 279 at the subalpine but not at the alpine site. Overall, no significant changes of SOC stocks were
 280 observed (Table S2).

281

282 **Soil organic matter biogeochemical signature**

283 The soil organic matter biogeochemical signature of control plots in both experiments
284 (transplants (0–10 cm) and OTC (0–5 cm)) were very similar (comparable values for most Rock-
285 Eval® parameters, Table S2). Conversely, topsoil soil organic matter characteristics of the alpine
286 and the subalpine sites differed strongly, with a higher C:N ratio and a higher proportion of
287 thermolabile SOC in the alpine site compared to the subalpine site, as shown by the different
288 Rock-Eval® parameters (i.e. a higher POC1 proportion (POC1/TOC), a higher PC proportion
289 (PC/TOC), a reduced thermal stability (lower values for Rock-Eval® temperature parameters and
290 R index, and a higher I index), higher HI and a lower OIRE6 at the alpine site than at the subalpine
291 site).

292 The values of Rock-Eval® parameters measured in the transplanted soils layed between the values
293 measured on the soils of the alpine and subalpine control plots. Thus, most of the changes in the
294 Rock-Eval® parameters induced by the pedoclimatic modifications were in the expected direction
295 even though not all responses were strong enough to significantly deviate from the controls
296 (Table 3).

297 As expected, POC1 content significantly decreased for the alpine warmed transplants and the
298 proportion of pyrolysis resistant carbone (RC/TOC) slightly increased (Figure 2b, c). The I index
299 decreased significantly, such as the C:N ratio which decreased very significantly for the alpine
300 warmed transplants (Figure 2d, Table 3). The Rock-Eval® temperature parameters that represent
301 the majority of the SOC analyzed ($T_{xx_CO2_OX}$, T_{xx_PYR} , T_{xx_OX}) showed a significant SOC
302 thermostability increase with warming (Figure 2f, Tables 3, S2). With cooling, we observed an

303 increase in POC1, PC and RC contents associated with a RC/TOC ratio decrease (Table 3, Figures
304 2b, c). The HI and the I indexes showed an increasing trend contrary to the R index, which
305 decreased (Figures 2d, e). The C:N ratio increased significantly. Moreover, the Rock-Eval®
306 temperature parameters showed a decreasing global trend (Figure 2f, Table 3).

307 No significant changes in the Rock-Eval® parameters were observed for the OTC warmed soils.
308 Overall, alpine and subalpine topsoils warmed by OTC showed weaker and more complex
309 warming responses of their soil organic matter biogeochemical signature compared with warmed
310 transplants (Table S2). The Rock-Eval® temperature parameters showed an increasing SOC
311 thermostability trend for the alpine OTC soils which did not appear for the subalpine OTC soils
312 (Figure 2f, Tables 3, S2).

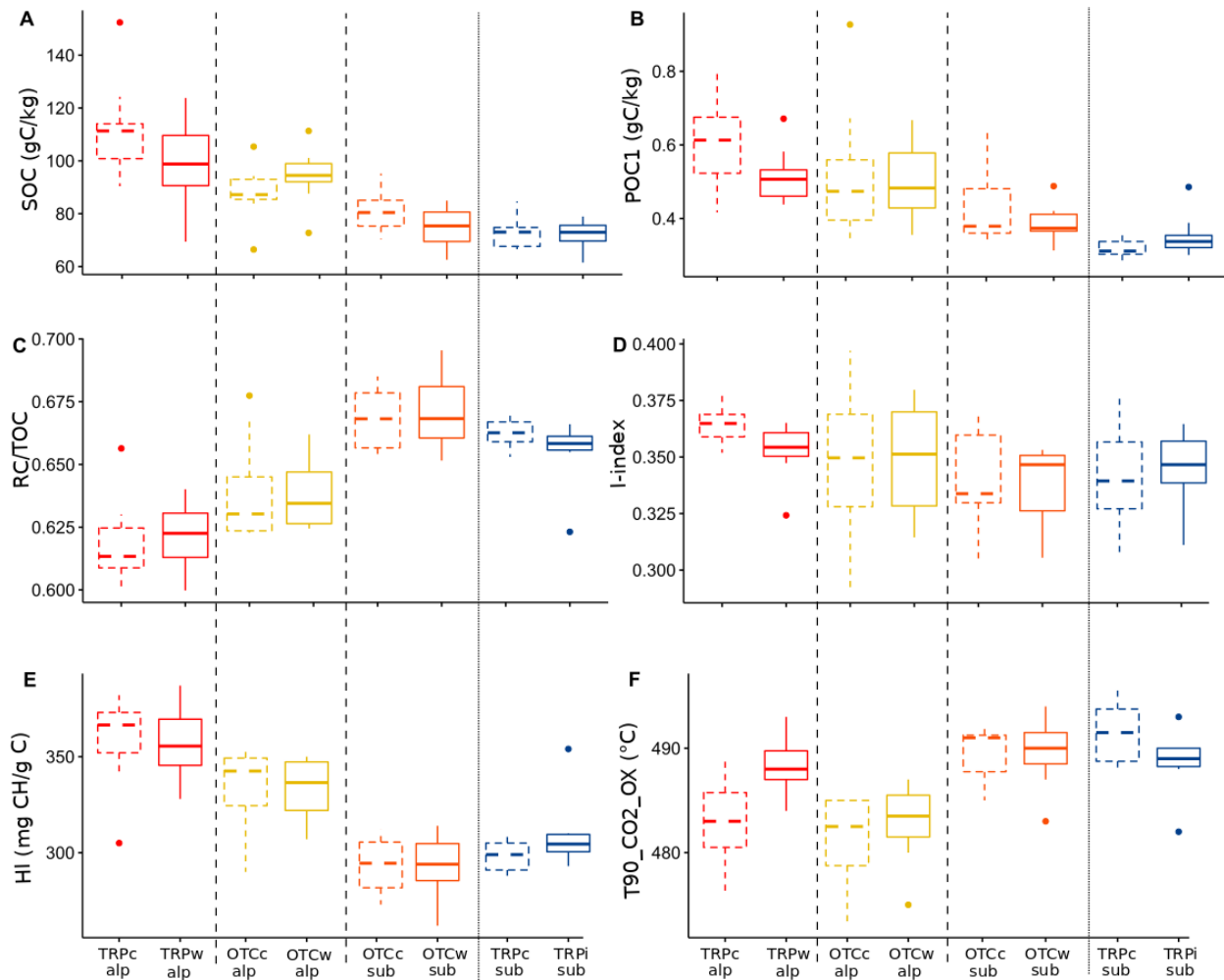
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314

315 **Table 3: Effect of the experimental treatment on soil parameters.** The significance was estimated
 316 using a non-parametric Mann-Whitney rank test. An ANOVA with mixed effect on pairs confirms
 317 the absence of spatial variability for OTC plots (Table S4). The orange color highlights the results
 318 that contradict our expectations (↑ increase, ↓ decrease, = no change). A complementary part
 319 of the results is presented in Table S3. Symbols for p-values: *** p < 0.001; ** p < 0.01; * p < 0.05;
 320 † p < 0.1; NS p > 0.1.

	WARMING							COOLING		
	Expectation	Alpine transplant		Alpine OTC		Subalpine OTC		Expectation	Subalpine transplant	
		observed	pvalue	observed	pvalue	observed	pvalue		observed	pvalue
SOC (gC/kg)	↓	↓	NS	↑	NS	↓	NS	↑	=	NS
Stock SOC (kg/m ²)	↓	↓	NS	↑	NS	↓	NS	↑	=	NS
POC1 (gC/kg)	↓	↓	†	↑	NS	↓	NS	↑	↑	†
POC1/TOC	↓	↓	NS	↑	NS	↓	NS	↑	↓	NS
PC (gC/kg)	↓	↓	NS	↓	NS	↑	NS	↑	↑	†
RC (gC/kg)	=	↓	NS	↓	NS	↑	NS	=	↑	†
PC/TOC	↓	↓	NS	↓	NS	=	NS	↑	↑	†
RC/TOC	↑	↑	NS	↑	NS	=	NS	↓	↓	†
HI (mg CH g/C)	↓	↓	NS	↓	NS	↓	NS	↑	↑	NS
OIRE6 (mg O ₂ g/C)	↑	↑	NS	↑	NS	↓	NS	↓	↓	NS
C:N	↓	↓	***					↑	↑	**
I index	↓	↓	*	↑	NS	↑	NS	↑	↑	NS
R index	↑	↑	NS	↓	NS	=	NS	↓	↓	NS
T30_CO2_OX (°C)	↑	↑	**	↑	NS	↑	NS	↓	=	NS
T50_CO2_OX (°C)	↑	↑	*	↑	NS	=	NS	↓	=	NS
T70_CO2_OX (°C)	↑	↑	*	↑	NS	↓	NS	↓	↓	NS
T90_CO2_OX (°C)	↑	↑	**	↑	NS	↓	NS	↓	↓	†
T50_PYR (°C)	↑	=	NS	=	NS	↓	NS	↓	↓	NS
T90_PYR (°C)	↑	↑	NS	↑	NS	↓	NS	↓	↓	NS
T50_OX (°C)	↑	↑	*	↑	†	=	NS	↓	↓	NS
T90_OX (°C)	↑	↑	**	↑	NS	↓	NS	↓	↓	†
<i>Consistent results</i>		27/38		16/37		13/37			23/38	

321



322
 323
 324 **Figure 2: Treatments effect comparisons between control soils (dashed lines) and treated soils**
 325 **(full lines) on (a) SOC content, (b) POC1 content, (c) RC/TOC ratio, (d) I-Index, (e) HI, (f)**
 326 **T₉₀_CO₂_OX parameter. With TRP: transplant, OTC: open-top chamber, c/w/i:**
 327 **control/warmed/cooled, alp: alpine site, sub: subalpine site.**

328

329 **Discussion**

330 SOC stocks in mountain grasslands are important but may be vulnerable under predicted climate
331 changes for the end of this century. So far studies in different regions, with different warming
332 treatments, and over different time scales do not concur on the risk climate warming is imposing
333 on these carbon stocks. Here, we compared two different types of warming experiments in the
334 French Alps. Over the short period of three years, the two pedoclimatic regime changes
335 experiments showed contrasted alpine and subalpine grassland topsoils responses according to
336 the experimental pedoclimate modifications. The abrupt warming by transplanting caused a
337 thermolabile SOC release and the cooling an overall modification of the SOC biogeochemical
338 signature, with enhanced SOC thermolability. Alpine and subalpine topsoils warmed by OTC
339 reacted differently to the same treatment, and also much less strongly than the transplanted
340 warmed soils. Our study underlines the importance of analyzing SOC stock responses with
341 complementary techniques and for different scenarios of climate change anticipated for the next
342 decades or until the end of this century.

343 We found higher amounts of SOC in the alpine grassland topsoils compared to the warmer
344 subalpine grassland topsoils. Following Lugato et al. (2021) and using a space-for-time approach
345 while such an approach on SOC dynamics may be controversial, this result could be interpreted
346 as a potential strong long-term warming-induced loss of SOC stocks (-30% under a *ca.* +3°C climate
347 change scenario; Abramoff et al., 2019; Cécillon, 2021a; Varney et al., 2020). Beyond the effect of
348 lower soil temperature, the climatic stabilization of topsoil soil organic matter at the alpine site is
349 probably also related to its lower topsoil pH, which limits soil organic matter degradation (Leifeld
350 et al., 2009; Smith et al., 2002; Trumbore et al., 1996), and its higher C/N ratio, commonly

351 negatively correlated with nitrogen soil mineralization and nitrification rates (Sahrawat, 2008 and
352 references therein; Zhang et al., 2012). The SOC stocks estimated around 78 t C/ha for the alpine
353 site and 56 t C/ha for the subalpine site over the first 10 cm are nevertheless higher than other
354 estimations on grassland soils at comparable altitudes and depths (50 t C/ha for a subalpine
355 grassland according to Leifeld et al., 2009; 53 t C/ha mean in grasslands between 1900 and 2100
356 m a.s.l for Saenger et al., 2013; 32 t C/ha for an alpine grassland in Budge et al., 2011).

357

358 **Experimental warming and cooling effects on soil organic carbon contents and stocks**

359 Our hypothesis that SOC content of mountain topsoil will decrease when exposed experimentally
360 to warmer conditions and will increase in colder conditions was only partly supported by the
361 results, after three years of treatment. On the one hand, we found a non-significant decrease of
362 *ca.* 11% in SOC content of the alpine warmed transplants. This result is consistent with other
363 findings in a subalpine warming transplantation experiment which showed after 5 years a non-
364 significant decreasing trend in topsoil SOC content warmed up by 2 or 4 °C (Puissant, 2015). In
365 another transplant experiment in a shrub-steppe ecosystem, Link et al. (2003) showed a 32% SOC
366 content loss after 5 years of 5°C warming in the first 5 cm of soil. Our results are also consistent
367 with the decrease of about 8% on topsoil SOC content (0–10 cm) observed by Marañón-Jiménez
368 et al. (2018) on subarctic silt-loam andosols after seven years of 1.8 °C warming. For the two OTC-
369 warmed topsoils, the SOC content responses were weak. Since the OTCs were only installed
370 during the growing season, this treatment had a different effect than a more drastic change in
371 thermal regime with soil transplanting. Tiwari et al. (2021) also noted a limited effect of OTC

372 warming (+1.5°C) on alpine grassland soil respiration in contrast to the increased total respiration,
373 suggesting an increase in carbon sequestration by plants. This highlights the effect of the
374 intensity, the time and the type of warming experiment, supporting our hypothesis that the
375 magnitude and time of soil organic matter response to warming is positively related to the
376 magnitude of warming. Our results of SOC content maintaining with cooling is inconsistent with
377 the results of Wu et al. (2017) who observed a significant decrease in SOC content on a soil cooling
378 transplant experiment.

379 In temperate mountains, the duration of the snow cover plays an important role in ecosystem
380 functioning (Choler, 2015). It is likely that the combined effect of the increasing soil temperature
381 and the extension of the growing season affected the microbial activity of the alpine warmed
382 transplants, which explains a slight decrease in SOC content. Microbial decomposition activity is
383 largely temperature-dependent and SOC is generally greater in cold and wet climates compared
384 to hot, dry climates because carbon loss is more limited than carbon input (Jobbágy & Jackson,
385 2000; Streit et al., 2014; Trumbore, 2000; von Lützow & Kögel-Knabner, 2009; Wiesmeier et al.,
386 2019). In addition to its effect on microbial activity, warming affects the physical protection of
387 organic matter within organo-mineral complexes and may increase its vulnerability (Conant et al.,
388 2011). Some authors who have observed the decline in SOC content with warming suggest that
389 SOC losses only occur early in warming processes and that carbon mineralization decreases over
390 time due to substrate limitation or a decline in microbial biomass (Allison et al., 2010; Li et al.,
391 2019; Walker et al., 2018). Here, the weaker topsoil soil organic matter stock in the warmer
392 subalpine site does not support this, suggesting a long-term sustained warming-induced SOC loss
393 (see above). Contrary to previous reports by Melillo et al. (2002) and Sistla et al. (2013) in other

394 ecosystems, the warming-induced increase in plant production observed on our alpine warmed
395 transplants soils by Bektaş et al. (2021) did not fully compensate SOC losses. There have been
396 conflicting results about SOC balance with ecosystem warming in a number of studies (Poeplau
397 et al., 2020; Qin et al., 2015; Tiwari et al., 2021; Zhou et al., 2016). Longer time-period of
398 experimentation is needed, to verify whether the trend of incomplete SOC output compensation
399 by increased SOC inputs by plants.

400

401 **Biogeochemical soil organic matter signature response to experimental climate change**

402 Consistent with other studies, our results indicate that the alpine site topsoil contains more
403 thermally labile soil organic matter than the warmer subalpine site (Budge et al., 2011; Hou et al.,
404 2019; Leifeld et al., 2009). Generally, our findings on the biogeochemical signature of SOM were
405 consistent with our hypotheses, especially for transplanted soils (Tables 3). The warming-induced
406 SOC loss upon transplanting increased the thermal stability of remaining SOC. Conversely,
407 transplanting soils from the subalpine site to the alpine site (*i.e.*, cooling) decreased the overall
408 SOC thermal stability. Our findings therefore indicate a preferential degradation of thermally
409 labile SOC when the alpine topsoil is abruptly exposed to warmer subalpine conditions, which is
410 consistent with the monitoring by Prietzel et al. (2016) in German Alps forest soils, and also with
411 our own observations of a more thermally stable topsoil SOC at the subalpine site than at the
412 alpine site. The fact that the proportion of pyrolysable carbon (POC1/TOC, PC/TOC) did not
413 decrease significantly in alpine warmed transplants does not mean that the labile SOC pool
414 remained unchanged. Indeed, no currently available SOC fractionation method can reliably isolate

415 non-composite SOC fractions in terms of soil carbon turnover time (Smith et al., 2002; von Lützow
416 et al., 2007), including Rock-Eval® thermal analysis (Cécillon et al., 2021b). On the other hand, our
417 results showed increased values of Rock-Eval® temperature parameters (accounting for the
418 majority of the SOC analyzed, *i.e.* T_{xx_CO2_OX} and T_{xx_OX}) with soil warming, indicating that the
419 SOC remaining after experimental warming is more thermally stable.

420 It is likely that more significant changes in the SOC biogeochemical signature will take longer to
421 establish. Poeplau et al. (2019) reported significant changes in the bulk chemistry and thermal
422 stability of the SOC after a six-and-a-half years intense warming of a high latitude grassland soil.
423 They showed that the warming-resistant SOC was thermally stable, and also depleted in
424 hydrocarbons and enriched in oxygen, a trend that is found in our experimental warming
425 treatment, although not significant. It is worth noting that our results showed that topsoil soil
426 organic matter was significantly H-depleted and O-enriched at the warmer subalpine site
427 compared with the alpine site. Our results are also consistent with the observations of several
428 authors, who had observed an initial preferential depletion of the labile SOC pool during soil
429 warming experiments (Eliasson et al., 2005; Link et al., 2003; Marañón-Jiménez et al., 2019). The
430 labile SOC fraction (thermally labile, H-enriched) is an easily available substrate providing more
431 energy to microorganisms than the biogeochemically stable SOC fraction (Barré et al., 2016; Li et
432 al., 2019). Thus, SOC resistant to warming is characterized by higher biological stability, which
433 would require higher energy budgets to be degraded (Barré et al. 2016, Marañón-Jiménez et al.,
434 2018). With cooling, we observed the opposite effect compared to warming (decrease in soil
435 organic matter thermal stability), indicating that the newly accumulated SOC is thermally more
436 labile. This result also points towards topsoil soil organic matter preservation from decomposition

437 by climatic conditions unfavorable to the mineralization activity of microorganisms at the colder
438 alpine site (Budge et al., 2011; Hou et al., 2019; Leifeld et al., 2009; Martinsen et al., 2011; Saenger
439 et al., 2015; Sjögersten et al., 2011).

440 Contrary to our hypothesis, we did not detect clear differences in the responses of alpine and
441 subalpine soil organic matter signature to OTC-warming. A possible explanation is that the
442 warming was not pronounced enough or implemented over a too short experimental period to
443 show significant changes. Poeplau et al. (2019) showed that a warming of 9.9 °C was necessary to
444 detect significant changes in the Rock-Eval[®] signature of soil organic matter. Nevertheless, there
445 was a consistent, though not significant, trend towards an increased SOC thermal stability for the
446 alpine warmed OTC soil, a trend that was not observed for the subalpine warmed OTC. This
447 suggests a greater sensitivity of alpine topsoil soil organic matter biogeochemical signature to
448 warming than the subalpine topsoil, but the lack of statistical significance prevents us from going
449 further in our conclusions.

450 **Conclusions**

451 Our results showed that the transplantation of high elevation alpine grassland soils to a warmer-
452 subalpine site led to the loss of thermally labile topsoil SOC after three years of experiment. These
453 warming-induced SOC losses modified the biogeochemical signature of the remaining SOC, which
454 was characterized by a more thermally resistant signature. This confirms the presence of an easily
455 mineralizable SOC fraction in alpine grassland topsoils that is sensitive to a three-years climate
456 change of +3 °C. Such warming intensity would, on long-term, decrease significantly SOC stocks
457 in this alpine grassland ecosystem, as reflected by the observed differences of SOC stocks
458 between the alpine and the subalpine sites. On the other hand, weak-intensity warming,
459 represented by OTC experiments, is not expected to have a short-term measurable impact on
460 SOC stocks. The continued monitoring of SOC stock and plant productivity in the study site will
461 provide further evidence on the dynamics of long-term carbon inputs and outputs.

462

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473 **References**

- 474 Abramoff, R. Z., Torn, M. S., Georgiou, K., Tang, J., & Riley, W. J. (2019). Soil Organic Matter
475 Temperature Sensitivity Cannot be Directly Inferred From Spatial Gradients. *Global*
476 *Biogeochemical Cycles*, 33(6), 761-776. <https://doi.org/10.1029/2018GB006001>
- 477 Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming
478 dependent on microbial physiology. *Nature Geoscience*, 3(5), 336-340.
479 <https://doi.org/10.1038/ngeo846>
- 480 Balesdent, J. (1996). The significance of organic separates to carbon dynamics and its modelling
481 in some cultivated soils. *European Journal of Soil Science*, 47(4), 485-493.
482 <https://doi.org/10.1111/j.1365-2389.1996.tb01848.x>
- 483 Barré, P., Plante, A. F., Cécillon, L., Lutfalla, S., Baudin, F., Bernard, S., Christensen, B. T., Eglin, T.,
484 Fernandez, J. M., Houot, S., Kätterer, T., Le Guillou, C., Macdonald, A., van Oort, F., &
485 Chenu, C. (2016). The energetic and chemical signatures of persistent soil organic
486 matter. *Biogeochemistry*, 130(1-2), 1-12. <https://doi.org/10.1007/s10533-016-0246-0>
- 487 Behar, F., Beaumont, V., & De B. Penteado, H. L. (2001). Rock-Eval 6 Technology: Performances
488 and Developments. *Oil & Gas Science and Technology*, 56(2), 111-134.
489 <https://doi.org/10.2516/ogst:2001013>
- 490 Bektaş, B., Thuiller, W., Saillard, A., Choler, P., Renaud, J., Colace, M., Della Vedova, R., &
491 Münkemüller, T. (2021). Lags in phenological acclimation of mountain grasslands after
492 recent warming. *Journal of Ecology*, 1365-2745.13727. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.13727)
493 [2745.13727](https://doi.org/10.1111/1365-2745.13727)

494 Berninger, F., Susiluoto, S., Gianelle, D., Bahn, M., Wohlfahrt, G., Sutton, M., Garcia-Pausas, J.,
495 Gimeno, C., Sanz, M. J., Dore, S., Rogiers, N., Furger, M., Balzarolo, M., Sebastià, M. T.,
496 Tenhunen, J., Staszewski, T., & Cernusca, A. (2015). Management and site effects on
497 carbon balances of European mountain meadows and rangelands. *20*, 14.

498 Bond-Lamberty, B., Bailey, V. L., Chen, M., Gough, C. M., & Vargas, R. (2018). Globally rising soil
499 heterotrophic respiration over recent decades. *Nature*, *560*(7716), 80-83.
500 <https://doi.org/10.1038/s41586-018-0358-x>

501 Bond-Lamberty, B., & Thomson, A. (2010). Temperature-associated increases in the global soil
502 respiration record. *Nature*, *464*(7288), 579-582. <https://doi.org/10.1038/nature08930>

503 Budge, K., Leifeld, J., Hiltbrunner, E., & Fuhrer, J. (2011). Alpine grassland soils contain large
504 proportion of labile carbon but indicate long turnover times. *Biogeosciences*, *8*(7),
505 1911-1923. <https://doi.org/10.5194/bg-8-1911-2011>

506 Cécillon, L. (2021a). A dual response. *Nat. Geosci.*, *14*, 262-263. [https://doi.org/10.1038/s41561-](https://doi.org/10.1038/s41561-021-00749-6)
507 [021-00749-6](https://doi.org/10.1038/s41561-021-00749-6)

508 Cécillon, L., Baudin, F., Chenu, C., Christensen, B. T., Franko, U., Houot, S., Kanari, E., Kätterer, T.,
509 Merbach, I., van Oort, F., Poeplau, C., Quezada, J. C., Savignac, F., Soucémarianadin, L.
510 N., & Barré, P. (2021b). Partitioning soil organic carbon into its centennially stable and
511 active fractions with statistical models based on Rock-Eval® thermal analysis
512 (PARTYSOCv2.0 and PARTYSOCv2.0EU). *Discuss. [preprint]*.
513 <https://doi.org/10.5194/gmd-2021-16>

514 Cécillon, L., Baudin, F., Chenu, C., Houot, S., Jolivet, R., Kätterer, T., Lutfalla, S., Macdonald, A.,
515 van Oort, F., Plante, A. F., Savignac, F., Soucémarianadin, L. N., & Barré, P. (2018). A

516 model based on Rock-Eval thermal analysis to quantify the size of the centennially
517 persistent organic carbon pool in temperate soils. *Biogeosciences*, 15(9), 2835-2849.
518 <https://doi.org/10.5194/bg-15-2835-2018>

519 Choler, P. (2015). Growth response of temperate mountain grasslands to inter-annual variations
520 in snow cover duration. *Biogeosciences*, 12(12), 3885-3897. [https://doi.org/10.5194/bg-](https://doi.org/10.5194/bg-12-3885-2015)
521 [12-3885-2015](https://doi.org/10.5194/bg-12-3885-2015)

522 Conant, R. T., Ryan, M. G., Ågren, G. I., Birge, H. E., Davidson, E. A., Eliasson, P. E., Evans, S. E.,
523 Frey, S. D., Giardina, C. P., Hopkins, F. M., Hyvönen, R., Kirschbaum, M. U. F., Lavellee, J.
524 M., Leifeld, J., Parton, W. J., Megan Steinweg, J., Wallenstein, M. D., Martin Wetterstedt,
525 J. Å., & Bradford, M. A. (2011). Temperature and soil organic matter decomposition
526 rates—Synthesis of current knowledge and a way forward. *Global Change Biology*,
527 17(11), 3392-3404. <https://doi.org/10.1111/j.1365-2486.2011.02496.x>

528 Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C., Machmuller, M.
529 B., Snoek, B. L., Fang, S., Zhou, G., Allison, S. D., Blair, J. M., Bridgman, S. D., Burton, A. J.,
530 Carrillo, Y., Reich, P. B., Clark, J. S., Classen, A. T., Dijkstra, F. A., Elberling, B., ... Bradford,
531 M. A. (2016). Quantifying global soil carbon losses in response to warming. *Nature*,
532 540(7631), 104-108. <https://doi.org/10.1038/nature20150>

533 Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition
534 and feedbacks to climate change. *Nature*, 440(7081), 165-173.
535 <https://doi.org/10.1038/nature04514>

536 Davidson, E., & Trumbore, S. E. (2000). Soil warming and organic carbon content. *Nature*, 408,
537 789-790.

538 Deharveng, L., Perriaux, J., & Ravenne, C. (1987). Sédimentologie du flysch des Aiguilles d'Arves
539 (Alpes françaises). insu-00514769

540 Disnar, J. R., Guillet, B., Keravis, D., Di-Giovanni, C., & Sebag, D. (2003). Soil organic matter
541 (SOM) characterization by Rock-Eval pyrolysis: Scope and limitations. *Organic*
542 *Geochemistry*, 34(3), 327-343. [https://doi.org/10.1016/S0146-6380\(02\)00239-5](https://doi.org/10.1016/S0146-6380(02)00239-5)

543 Djukic, I., Zehetner, F., Tatzber, M., & Gerzabek, M. H. (2010). Soil organic-matter stocks and
544 characteristics along an Alpine elevation gradient. *J. Plant Nutr. Soil Sci.*, 9.

545 Doblas-Miranda, E., Rovira, P., Brotons, L., Martínez-Vilalta, J., Retana, J., Pla, M., & Vayreda, J.
546 (2013). Soil carbon stocks and their variability across the forests, shrublands and
547 grasslands of peninsular Spain. 9.

548 Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B., & Mérindol, L. (2009).
549 Reanalysis of 44 Yr of Climate in the French Alps (1958–2002): Methodology, Model
550 Validation, Climatology, and Trends for Air Temperature and Precipitation. *Journal of*
551 *Applied Meteorology and Climatology*, 48(3), 429-449.
552 <https://doi.org/10.1175/2008JAMC1808.1>

553 European Environment Agency. (2010). Europe's ecological backbone : Recognising the true
554 value of our mountains. Publications Office. <https://data.europa.eu/doi/10.2800/43450>

555 Eliasson, P. E., McMurtrie, R. E., Pepper, D. A., Stromgren, M., Linder, S., & Agren, G. I. (2005).
556 The response of heterotrophic CO₂ flux to soil warming. *Global Change Biology*, 11(1),
557 167-181. <https://doi.org/10.1111/j.1365-2486.2004.00878.x>

558 Espitalié, J., Laporte, J. L., Madec, M., Marquis, F., Leplat, P., Paulet, J., & Boutefeu, A. (1977).
559 Rapid Method for Source Rocks Characterisation and for Determination of Petroleum
560 Potential and Degree of Evolution. *Rev. Inst. Fr. Pét.*, 32(1).

561 FAO. (2014). World reference base for soil resources (WRB) 2014: International soil classification
562 system for naming soils and creating legends for soil maps. FAO.

563 Gavazov, K. S. (2013). Subalpine Pasture-Woodlands in a Changing Climate: The Role of Land
564 Use Type in Ecosystem Resistance to Simulated Climate Change. *École polytechnique*
565 *fédérale de Lausanne*.

566 Grêt-Regamey, A., & Weibel, B. (2020). Global assessment of mountain ecosystem services using
567 earth observation data. *Ecosystem Services*, 46, 101213.
568 <https://doi.org/10.1016/j.ecoser.2020.101213>

569 Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2014). 21st century
570 climate change in the European Alps—A review. *Science of The Total Environment*, 493,
571 1138-1151. <https://doi.org/10.1016/j.scitotenv.2013.07.050>

572 Gregorich, E. G., Gillespie, A. W., Beare, M. H., Curtin, D., Sanei, H., & Yanni, S. F. (2015).
573 Evaluating biodegradability of soil organic matter by its thermal stability and chemical
574 composition. *Soil Biology and Biochemistry*, 91, 182-191.
575 <https://doi.org/10.1016/j.soilbio.2015.08.032>

576 Hicks Pries, C. E., Castanha, C., Porras, R. C., & Torn, M. S. (2017). The whole-soil carbon flux in
577 response to warming. *Science*, 355(6332), 1420-1423.
578 <https://doi.org/10.1126/science.aal1319>

579 Hitz, C., Egli, M., & Fitze, P. (2001). Below-ground and above-ground production of vegetational
580 organic matter along a climosequence in alpine grasslands. *Journal of Plant Nutrition and*
581 *Soil Science*, 164(4), 389 - 3979.

582 Hou, Y., He, K., Chen, Y., Zhao, J., Hu, H., & Zhu, B. (2019). Changes of soil organic matter
583 stability along altitudinal gradients in Tibetan alpine grassland. *Plant and Soil*. 458, 21–
584 40. <https://doi.org/10.1007/s11104-019-04351-z>

585 Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O. B., Bouwer, L. M., Braun, A., Colette,
586 A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L., Nikulin, G.,
587 Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., ... Yiou, P. (2014). EURO-
588 CORDEX : New high-resolution climate change projections for European impact research.
589 *Regional Environmental Change*, 14(2), 563-578. [https://doi.org/10.1007/s10113-013-](https://doi.org/10.1007/s10113-013-0499-2)
590 [0499-2](https://doi.org/10.1007/s10113-013-0499-2)

591 Jobbágy, E. G., & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its
592 relation to climate and vegetation. *Ecological Applications*, 10(2), 423-436.
593 [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOSO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2)

594 Khedim, N., Cécillon, L., Poulénard, J., Barré, P., Baudin, F., Marta, S., Rabatel, A., Dentant, C.,
595 Cauvy-Fraunié, S., Anthelme, F., Gielly, L., Ambrosini, R., Franzetti, A., Azzoni, R. S.,
596 Caccianiga, M. S., Compostella, C., Clague, J., Tielidze, L., Messenger, E., Choler, P.,
597 Ficetola, G. F. (2021). Topsoil organic matter build-up in glacier forelands around the
598 world. *Global Change Biology*, 27(8), 1662-1677. <https://doi.org/10.1111/gcb.15496>

599 Körner, C. (2003). *Alpine plant life : Functional plant ecology of high mountain ecosystems*.
600 Springer Science&Business Media.

601 Lafargue, E., Marquis, F., & Pillot, D. (1998). Rock-Eval 6 Applications in Hydrocarbon
602 Exploration, Production, and Soil Contamination Studies. *Revue de l'Institut Français Du*
603 *Pétrole*, 53(4), 421-437. <https://doi.org/10.2516/ogst:1998036>

604 Leifeld, J., Zimmermann, M., Fuhrer, J., & Conen, F. (2009). Storage and turnover of carbon in
605 grassland soils along an elevation gradient in the Swiss Alps. *Global Change Biology*,
606 15(3), 668-679. <https://doi.org/10.1111/j.1365-2486.2008.01782.x>

607 Li, Y., Lv, W., Jiang, L., Zhang, L., Wang, S., Wang, Q., Xue, K., Li, B., Liu, P., Hong, H., Renzen, W.,
608 Wang, A., Luo, C., Zhang, Z., Dorji, T., Taş, N., Wang, Z., Zhou, H., & Wang, Y. (2019).
609 Microbial community responses reduce soil carbon loss in Tibetan alpine grasslands
610 under short-term warming. *Global Change Biology*, 25(10), 3438-3449.
611 <https://doi.org/10.1111/gcb.14734>

612 Link, S. O., Smith, J. L., Halvorson, J. J., & Bolton, H. B. (2003). A reciprocal transplant experiment
613 within a climatic gradient in a semiarid shrub-steppe ecosystem: Effects on bunchgrass
614 growth and reproduction, soil carbon, and soil nitrogen. *Global Change Biology*, 9.

615 Liski, J., Perruchoud, D., & Karjalainen, T. (2002). Increasing carbon stocks in the forest soils of
616 western Europe. *Forest Ecology and Management*, 17.

617 Luan, J., Liu, S., Chang, S. X., Wang, J., Zhu, X., Liu, K., & Wu, J. (2014). Different effects of
618 warming and cooling on the decomposition of soil organic matter in warm-temperate
619 oak forests : A reciprocal translocation experiment. *Biogeochemistry*, 121(3), 551-564.
620 <https://doi.org/10.1007/s10533-014-0022-y>

621 Lugato, E., Lavalley, J. M., Haddix, M. L., Panagos, P., & Cotrufo, M. F. (2021). Different climate
622 sensitivity of particulate and mineral-associated soil organic matter. *Nature Geoscience*,
623 14(5), 295-300. <https://doi.org/10.1038/s41561-021-00744-x>

624 Lutfalla, S., Chenu, C., & Barré, P. (2014). Are chemical oxidation methods relevant to isolate a
625 soil pool of centennial carbon? *Biogeochemistry*, 118(1-3), 135-139.
626 <https://doi.org/10.1007/s10533-013-9910-9>

627 Molau, U. & Mølgaard, P. (1996), International tundra experiment (ITEX) manual. Danish Polar
628 Center, Copenhagen, Denmark.

629 Marañón-Jiménez, S., Peñuelas, J., Richter, A., Sigurdsson, B. D., Fuchslueger, L., Leblans, N. I.
630 W., & Janssens, I. A. (2019). Coupled carbon and nitrogen losses in response to seven
631 years of chronic warming in subarctic soils. *Soil Biology and Biochemistry*, 134, 152-161.
632 <https://doi.org/10.1016/j.soilbio.2019.03.028>

633 Marañón-Jiménez, S., Soong, J. L., Leblans, N. I. W., Sigurdsson, B. D., Peñuelas, J., Richter, A.,
634 Asensio, D., Fransen, E., & Janssens, I. A. (2018). Geothermally warmed soils reveal
635 persistent increases in the respiratory costs of soil microbes contributing to substantial C
636 losses. *Biogeochemistry*, 138(3), 245-260. <https://doi.org/10.1007/s10533-018-0443-0>

637 Martin, M. P., Wattenbach, M., Smith, P., Meersmans, J., Jolivet, C., Boulonne, L., & Arrouays, D.
638 (2011). Spatial distribution of soil organic carbon stocks in France. *Biogeosciences*, 8(5),
639 1053-1065. <https://doi.org/10.5194/bg-8-1053-2011>

640 Martinsen, V., Mulder, J., Austrheim, G., & Mysterud, A. (2011). Carbon storage in low-alpine
641 grassland soils: Effects of different grazing intensities of sheep. *European Journal of Soil
642 Science*, 62(6), 822-833. <https://doi.org/10.1111/j.1365-2389.2011.01393.x>

643 Marty, C., Piquette, J., Morin, H., Bussi eres, D., Thiffault, N., Houle, D., Bradley, R. L., Simpson,
644 M. J., Ouimet, R., & Par e, M. C. (2019). Nine years of in situ soil warming and topography
645 impact the temperature sensitivity and basal respiration rate of the forest floor in a
646 Canadian boreal forest. PLOS ONE, 14(12), e0226909.
647 <https://doi.org/10.1371/journal.pone.0226909>

648 Meersmans, J., Martin, M. P., Lacarce, E., De Baets, S., Jolivet, C., Boulonne, L., Lehmann, S.,
649 Saby, N. P. A., Bispo, A., & Arrouays, D. (2012). A high resolution map of French soil
650 organic carbon. Agronomy for Sustainable Development, 32(4), 841-851.
651 <https://doi.org/10.1007/s13593-012-0086-9>

652 Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Magill,
653 A., Ahrens, T., & Morrisseau, S. (2002). Soil Warming and Carbon-Cycle Feedbacks to the
654 Climate System. Science, 298(5601), 2173-2176.
655 <https://doi.org/10.1126/science.1074153>

656 Palomo, I. (2017). Climate Change Impacts on Ecosystem Services in High Mountain Areas : A
657 Literature Review. Mountain Research and Development, 37(2), 179-187.
658 <https://doi.org/10.1659/MRD-JOURNAL-D-16-00110.1>

659 Plante, A. F., Beaupr e, S. R., Roberts, M. L., & Baisden, T. (2013). Distribution of Radiocarbon
660 Ages in Soil Organic Matter by Thermal Fractionation. Radiocarbon, 55(2), 1077-1083.
661 <https://doi.org/10.1017/S0033822200058215>

662 Poeplau, C., Barr e, P., C ecillon, L., Baudin, F., & Sigurdsson, B. D. (2019). Changes in the Rock-
663 Eval signature of soil organic carbon upon extreme soil warming and chemical

664 oxidation—A comparison. *Geoderma*, 337, 181-190.
665 <https://doi.org/10.1016/j.geoderma.2018.09.025>

666 Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., Cotrufo, M. F., Derrien, D.,
667 Gioacchini, P., Grand, S., Gregorich, E., Griepentrog, M., Gunina, A., Haddix, M.,
668 Kuzyakov, Y., Kühnel, A., Macdonald, L. M., Soong, J., Trigalet, S., ... Nieder, R. (2018).
669 Isolating organic carbon fractions with varying turnover rates in temperate agricultural
670 soils – A comprehensive method comparison. *Soil Biology and Biochemistry*, 125, 10-26.
671 <https://doi.org/10.1016/j.soilbio.2018.06.025>

672 Poeplau, C., Sigurðsson, P., & Sigurdsson, B. D. (2020). Depletion of soil carbon and aggregation
673 after strong warming of a subarctic Andosol under forest and grassland cover. *SOIL*, 6(1),
674 115-129. <https://doi.org/10.5194/soil-6-115-2020>

675 Prietzel, J., Zimmermann, L., Schubert, A., & Christophel, D. (2016). Organic matter losses in
676 German Alps forest soils since the 1970s most likely caused by warming. *Nature*
677 *Geoscience*, 9(7), 543-548. <https://doi.org/10.1038/ngeo2732>

678 Puissant, J. (2015). Effets des changements climatiques sur la dynamique de décomposition
679 microbienne du carbone organique du sol en prairie subalpine calcaire. Université
680 Grenoble Alpes.

681 Puissant, J., Mills, R. T. E., Robroek, B. J. M., Gavazov, K., Perrette, Y., De Danieli, S.,
682 Spiegelberger, T., Buttler, A., Brun, J.-J., & Cécillon, L. (2017). Climate change effects on
683 the stability and chemistry of soil organic carbon pools in a subalpine grassland.
684 *Biogeochemistry*, 132(1-2), 123-139. <https://doi.org/10.1007/s10533-016-0291-8>

685 Qin, Y., Yi, S., Chen, J., Ren, S., & Wang, X. (2015). Responses of ecosystem respiration to short-
686 term experimental warming in the alpine meadow ecosystem of a permafrost site on the
687 Qinghai–Tibetan Plateau. *Cold Regions Science and Technology*, 115, 77-84.
688 <https://doi.org/10.1016/j.coldregions.2015.03.012>

689 R Core Team (2018). R: A language and environment for statistical computing. R Foundation for
690 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

691 Reynolds, L. L., Johnson, B. R., Pfeifer-Meister, L., & Bridgman, S. D. (2015). Soil respiration
692 response to climate change in Pacific Northwest prairies is mediated by a regional
693 Mediterranean climate gradient. *Global Change Biology*, 21(1), 487-500.
694 <https://doi.org/10.1111/gcb.12732>

695 Saenger, A., Cécillon, L., Sebag, D., & Brun, J.-J. (2013). Soil organic carbon quantity, chemistry
696 and thermal stability in a mountainous landscape: A Rock–Eval pyrolysis survey. *Organic
697 Geochemistry*, 54, 101-114. <https://doi.org/10.1016/j.orggeochem.2012.10.008>

698 Saenger, A., Cécillon, L., Poulénard, J., Bureau, F., De Daniéli, S., Gonzalez, J.-M., & Brun, J.-J.
699 (2015). Surveying the carbon pools of mountain soils: A comparison of physical
700 fractionation and Rock-Eval pyrolysis. *Geoderma*, 241-242, 279-288.
701 <https://doi.org/10.1016/j.geoderma.2014.12.001>

702 Sahrawat, K. L. (2008). Factors Affecting Nitrification in Soils. *Communications in Soil Science
703 and Plant Analysis*, 39(9-10), 1436-1446. <https://doi.org/10.1080/00103620802004235>

704 Schimel, D. S. (1995). Terrestrial ecosystems and the carbon cycle. *Global Change Biology*, 16.

705 Sebag, D., Verrecchia, E. P., Cécillon, L., Adatte, T., Albrecht, R., Aubert, M., Bureau, F., Cailleau,
706 G., Copard, Y., Decaens, T., Disnar, J.-R., Hetényi, M., Nyilas, T., & Trombino, L. (2016).
707 Dynamics of soil organic matter based on new Rock-Eval indices. *Geoderma*, 284,
708 185-203. <https://doi.org/10.1016/j.geoderma.2016.08.025>

709 Shaver, G. R., Canadell, J., Chapin, F. S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson,
710 S., Melillo, J., Pitelka, L., & Rustad, L. (2000). Global Warming and Terrestrial
711 Ecosystems : A Conceptual Framework for Analysis. *BioScience*, 50(10), 871.
712 [https://doi.org/10.1641/0006-3568\(2000\)050\[0871:GWATEA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0871:GWATEA]2.0.CO;2)

713 Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., & Schimel, J. P. (2013). Long-
714 term warming restructures Arctic tundra without changing net soil carbon storage.
715 *Nature*, 497(7451), 615-618. <https://doi.org/10.1038/nature12129>

716 Sjögersten, S., Alewell, C., Cécillon, L., Hagedorn, F., Jandl, R., Leifeld, J., Martinsen, V.,
717 Schindlbacher, A., Sebastià, M.-T., & Van Mieghroet, H. (2011). Mountain Soils in a
718 Changing Climate – Vulnerability of Carbon Stocks and Ecosystem Feedbacks. In *Soil*
719 *Carbon in Sensitive European Ecosystems : From Science to Land Management* (p.
720 118-148).

721 Smith, J. L., Halvorson, J. J., & Bolton, H. (2002). Soil properties and microbial activity across a
722 500m elevation gradient in a semi-arid environment. *Soil Biology and Biochemistry*,
723 34(11), 1749-1757. [https://doi.org/10.1016/S0038-0717\(02\)00162-1](https://doi.org/10.1016/S0038-0717(02)00162-1)

724 Smith, J. U., Smith, P., Monaghan, R., & MacDonald, A. J. (2002). When is a measured soil
725 organic matter fraction equivalent to a model pool? *European Journal of Soil Science*,
726 53(3), 405-416. <https://doi.org/10.1046/j.1365-2389.2002.00458.x>

727 Streit, K., Hagedorn, F., Hiltbrunner, D., Portmann, M., Saurer, M., Buchmann, N., Wild, B.,
728 Richter, A., Wipf, S., & Siegwolf, R. T. W. (2014). Soil warming alters microbial substrate
729 use in alpine soils. *Global Change Biology*, 20(4), 1327-1338.
730 <https://doi.org/10.1111/gcb.12396>

731 Tasser, E., Tappeiner, U., Cernusca, A. (2005). Ecological effects of land use changes in the European
732 Alps. In: Huber UM, Bugmann H, Reasoner MA, editors. *Global Change and Mountain Regions:
733 An Overview of Current Knowledge*. Dordrecht, The Netherlands, Springer, 413–425.

734 Tiwari, P., Bhattacharya, P., Rawat, G. S., Rai, I. D., & Talukdar, G. (2021). Experimental warming
735 increases ecosystem respiration by increasing above-ground respiration in alpine
736 meadows of Western Himalaya. *Scientific Reports*, 11(1), 2640.
737 <https://doi.org/10.1038/s41598-021-82065-y>

738 Trumbore, S. (2009). Radiocarbon and Soil Carbon Dynamics. *Annual Review of Earth and
739 Planetary Sciences*, 37(1), 47-66.
740 <https://doi.org/10.1146/annurev.earth.36.031207.124300>

741 Trumbore, S. (2000). Age of soil organic matter and soil respiration: Radiocarbon constraint on
742 belowground carbon dynamics. *Ecological Applications*, 10(2), 13.

743 Trumbore, S., Chadwick, O. A., & Amundson, R. (1996). Rapid Exchange Between Soil Carbon
744 and Atmospheric Carbon Dioxide Driven by Temperature Change. *Science*, 272(5260),
745 393-396. <https://doi.org/10.1126/science.272.5260.393>

746 van Gestel, N., Shi, Z., van Groenigen, K. J., Osenberg, C. W., Andresen, L. C., Dukes, J. S.,
747 Hovenden, M. J., Luo, Y., Michelsen, A., Pendall, E., Reich, P. B., Schuur, E. A. G., &

748 Hungate, B. A. (2018). Predicting soil carbon loss with warming. *Nature*, 554(7693),
749 E4-E5. <https://doi.org/10.1038/nature25745>

750 Varney, R. M., Chadburn, S. E., Friedlingstein, P., Burke, E. J., Koven, C. D., Hugelius, G., & Cox, P.
751 M. (2020). A spatial emergent constraint on the sensitivity of soil carbon turnover to
752 global warming. *Nature Communications*, 11(1), 5544. [https://doi.org/10.1038/s41467-](https://doi.org/10.1038/s41467-020-19208-8)
753 020-19208-8

754 Vernay, M., Lafaysse, M., Hagenmuller, P., Nheili, R., Verfaillie, D., & Morin, S. (2019). The S2M
755 meteorological and snow cover reanalysis in the French mountainous areas (1958—
756 Present). <https://doi.org/10.25326/37>

757 Vionnet, V., Brun, E., Morin, S., Boone, A., Faroux, S., Le Moigne, P., Martin, E., & Willemet, J.-M.
758 (2012). The detailed snowpack scheme Crocus and its implementation in SURFEX v7.2.
759 *Geoscientific Model Development*, 5(3), 773-791. [https://doi.org/10.5194/gmd-5-773-](https://doi.org/10.5194/gmd-5-773-2012)
760 2012

761 von Lützow, M., & Kögel-Knabner, I. (2009). Temperature sensitivity of soil organic matter
762 decomposition—What do we know? *Biology and Fertility of Soils*, 46(1), 1-15.
763 <https://doi.org/10.1007/s00374-009-0413-8>

764 von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., &
765 Marschner, B. (2007). SOM fractionation methods: Relevance to functional pools and to
766 stabilization mechanisms. *Soil Biology and Biochemistry*, 39(9), 2183-2207.
767 <https://doi.org/10.1016/j.soilbio.2007.03.007>

768 Walker, T. W. N., Kaiser, C., Strasser, F., Herbold, C. W., Leblans, N. I. W., Wuebken, D., Janssens,
769 I. A., Sigurdsson, B. D., & Richter, A. (2018). Microbial temperature sensitivity and

770 biomass change explain soil carbon loss with warming. *Nature Climate Change*, 8(10),
771 885-889. <https://doi.org/10.1038/s41558-018-0259-x>

772 Wang, X., Dong, S., Gao, Q., Zhou, H., Liu, S., Su, X., & Li, Y. (2014). Effects of short-term and
773 long-term warming on soil nutrients, microbial biomass and enzyme activities in an
774 alpine meadow on the Qinghai-Tibet Plateau of China. *Soil Biology and Biochemistry*, 76,
775 140-142. <https://doi.org/10.1016/j.soilbio.2014.05.014>

776 Wiesmeier, M., Urbanski, L., Hobbey, E., Lang, B., von Lützow, M., Marin-Spiotta, E.,
777 van Wesemael, B., Rabot, E., Ließ, M., Garcia-Franco, N., Wollschläger, U., Vogel, H.-J., &
778 Kögel-Knabner, I. (2019). Soil organic carbon storage as a key function of soils—A review
779 of drivers and indicators at various scales. *Geoderma*, 333, 149-162.
780 <https://doi.org/10.1016/j.geoderma.2018.07.026>

781 Wu, L., Yang, Y., Wang, S., Yue, H., Lin, Q., Hu, Y., He, Z., Van Nostrand, J. D., Hale, L., Li, X.,
782 Gilbert, J. A., & Zhou, J. (2017). Alpine soil carbon is vulnerable to rapid microbial
783 decomposition under climate cooling. *The ISME Journal*, 11(9), 2102-2111.
784 <https://doi.org/10.1038/ismej.2017.75>

785 Zhang, S., Chen, D., Sun, D., Wang, X., Smith, J. L., & Du, G. (2012). Impacts of altitude and
786 position on the rates of soil nitrogen mineralization and nitrification in alpine meadows
787 on the eastern Qinghai–Tibetan Plateau, China. *Biology and Fertility of Soils*, 48(4),
788 393-400. <https://doi.org/10.1007/s00374-011-0634-5>

789 Zhang, Y., Zhang, N., Yin, J., Zhao, Y., Yang, F., Jiang, Z., Tao, J., Yan, X., Qiu, Y., Guo, H., & Hu, S.
790 (2020). Simulated warming enhances the responses of microbial N transformations to

791 reactive N input in a Tibetan alpine meadow. *Environment International*, 141, 105795.

792 <https://doi.org/10.1016/j.envint.2020.105795>

793 Zhou, Y., Hagedorn, F., Zhou, C., Jiang, X., Wang, X., & Li, M.-H. (2016). Experimental warming of

794 a mountain tundra increases soil CO₂ effluxes and enhances CH₄ and N₂O uptake at

795 Changbai Mountain, China. *Scientific Reports*, 6(1), 21108.

796 <https://doi.org/10.1038/srep21108>

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798