

1 **No solid evidence of soil carbon loss under warming in tropical**
2 **forests along a 3000 m elevation gradient**

3 **Running head:** SOC under warming in tropical forests

4 **Authors:** Zhongkui Luo¹, Xiaowei Guo², Osbert Jianxin Sun²

5 **Affiliations:** ¹College of Environmental and Resource Sciences, Zhejiang University,
6 Zhejiang 310086, China. ²College of Ecology and Nature Conservation, Beijing Forestry
7 University, Beijing 100083, China.

8 **Correspondence:** Zhongkui Luo, email: luozk@zju.edu.cn

9 **Keywords:** Soil carbon composition, soil translocation, chemical fractions, ¹³C NMR
10 spectroscopy, tropical forest, warming

11 **Abstract**

12 Soil organic carbon (SOC) decomposition is inherently sensitive to temperature. As such, a
13 big concern is the potential SOC loss under climatic warming, but field empirical
14 evidences are lacking, particularly in tropical forest soils in which ~10% of global SOC is
15 stored. Recently Nottingham et al. (2019) assessed the data collected from a novel
16 experiment translocating soils across a 3000 m tropical forest elevation gradient to mimic
17 temperature changes *in situ*, and concluded that warming caused considerable SOC loss.
18 However, this conclusion was based on a metric with a strong assumption that soil cores
19 translocated to other elevations on average had the same initial SOC content to control soil
20 cores reinstalled at their original elevation. Because of limited replicates ($n = 3$) in the data, an
21 approach ignoring spatial heterogeneity of SOC content may undermine the credibility of the
22 results. Here, we used a nonparametric bootstrap approach to re-analyze the data, explicitly
23 taking data variability into account. Contrary to Nottingham et al. (2019), we found that SOC

24 content did not show significant differences among translocated soils from the same elevation
25 origin. Further looking into six chemical fractions determined by ^{13}C NMR spectroscopy
26 shown that they had similar, insignificant response to translocation-induced temperature
27 changes, which also does not support the conclusion of Nottingham et al (2019) that labile
28 SOC is more sensitive to warming. We concluded that temperature changes did not
29 significantly alter either total SOC content or its six chemical fractions after five years of
30 shift of temperature regimes in tropical forests. This may largely due to thermal adaptation of
31 microbial decomposition and environmental constrains (e.g., low pH) which suppress the
32 effect of temperature changes. Longer term experiment with more sampling replicates are
33 required to maximize the value of soil translocation experiments to address the effect of
34 warming on SOC dynamics.

35 **Introduction**

36 Soil organic carbon (SOC) pool in tropical forest soils accounts for ~40% of SOC stock in
37 global forests (Pan et al., 2011) and ~10% in global soils (Batjes, 2016; Le Quere et al., 2016).
38 As the inherent temperature sensitivity of SOC decomposition (Davidson & Janssens, 2006),
39 it is vital to understand how SOC in tropical forests responds to climatic warming. Earth
40 system models usually predict SOC loss under warming including in tropical forest soils,
41 rising a big concern of positive SOC loss - climatic warming feedbacks (Allison, Wallenstein,
42 & Bradford, 2010). Nevertheless, there are no solid, consistent empirical evidences to prove
43 those model projections. Results from field warming experiments are inconclusive; the
44 effects of warming on SOC balance are observed to be positive, neutral or negative,
45 depending on study-specific ecosystems, experimental manipulation (such as duration), local
46 soil and climatic conditions, and other confounding factors (e.g., Sistla et al., 2013; Pries,
47 Castanha, Porras, & Torn, 2017; and two data syntheses by Crowther et al., 2016 and van
48 Gestel et al., 2018). A 26-year soil warming experiment at Harvard forest (a temperate forest)

49 indeed observed three multiyear phases of soil microbial respiration: from the first phase of
50 decreasing respiration, to the second phase of stable respiration, to the third phase of
51 increasing respiration, due to changes in substrate availability and microbial community
52 functioning (Melillo et al., 2017). In tropics, the data is particularly lacking (Crowther et al.,
53 2016; van Gestel et al., 2018), inhibiting our understanding and quantification of the fate of
54 SOC under climatic warming in tropical areas.

55 By conducting a field experiment in tropical forests, recently Nottingham et al. (2019)
56 addressed the effects of long-term (5 years) soil warming on SOC content and a series of
57 microbial properties. Intriguingly, to do so, they translocated soils among four tropical forest
58 sites along a 3000 m elevation gradient in Peru to generate an average temperature change of
59 ± 15 °C. After five years of the translocation, they measured SOC content and a suite of other
60 soil chemical and biological properties. By assessing the data (hereafter we call it
61 “Nottingham dataset”), they concluded that “warming caused a considerable loss of soil
62 carbon” (Nottingham et al. 2019). They also measured six chemical fractions including
63 carbonyl (165-190 ppm), O-aryl (140-165 ppm), aryl (110-140 ppm), di-O-alkyl (92-110
64 ppm), O-alkyl (46-92 ppm), and alkyl (0-46 ppm), using ^{13}C NMR spectroscopy. By
65 assessing the fraction data, they concluded that SOC loss was related to the lability of SOC
66 component fractions. Particularly, labile SOC fractions were more sensitive to temperature
67 changes and their loss was the major contributor to total SOC loss.

68 In Nottingham et al. (2019), however, there was a strong assumption underlying the
69 estimation of the effects of temperature change. That is, soil cores translocated to other
70 elevations on average have the same initial SOC content to control soil cores reinstalled at
71 their original elevation. As there are only three replicates in the data, an approach ignoring
72 spatial heterogeneity of SOC content may over- or under-estimate the effect of warming.
73 Focusing on total SOC content and its chemical component fractions, in this study we

74 reassessed the Nottingham dataset by explicitly taking into account data variability, and
75 found that neither total SOC content nor its six chemical fractions was significantly affected
76 by elevation shift-induced temperature changes.

77 **Reassessment of Nottingham dataset**

78 In Nottingham et al. (2019), relative response ratios (RR) were calculated to estimate the
79 effect of temperature change (which was represented by elevation shift in Nottingham et al.
80 2019 due to its close correlation with temperature change, $R^2 = 0.99$):

$$81 \quad RR_{i,des} = \ln \left(\frac{C_{i,des}}{\overline{C_{ori}}} \right), i = 1,2,3. \quad (1)$$

82 where $C_{i,des}$ is the variable of interest (i.e., total SOC content and its six chemical component
83 fractions in this study) of the i^{th} replicate of soils translocated to other elevation destination,
84 and $\overline{C_{ori}}$ is the average of three replicates of the interested variable in the control soil cores
85 reinstalled at original elevation. As such, three RRs were obtained for each destination of
86 each soil origin (a total of four soil origins from four elevations). Based on these RRs,
87 Nottingham et al (2019) conducted a series of statistical analyses such as regression and
88 ANOVA. However, their analyses ignored the potential effect of data variability on the
89 results.

90 In this re-analysis, we first conducted pair-wise comparisons of total SOC and its
91 chemical fractions (the data were natural log-transformed before conducting the comparison)
92 among translocated soils of the same origin using ANOVA (pair-wise Tukey post-hoc test,
93 which controls for Type I error). This analysis enables us to directly assess whether or not
94 soil translation has induced significant changes in SOC content and in its chemical fractions.
95 Embracing the benefit of RR for quantifying “the relative effect of translocation (warming or
96 cooling) on each property independently to soil type” (Nottingham et al. 2019), and

97 meanwhile taking into account the potential effect of data variability on results, here we used
98 a non-parametric bootstrap approach to quantify the relationship between RR and
99 temperature changes due to soil translocation along the 3000 m elevation gradient. The non-
100 parametric approach is not only robust to departures from the normal distribution but also
101 explicitly take data variability into account (Fox & Weisberg, 2011). As there are three
102 replicates for both control soils at the origin location and soils translocated to other
103 destinations, we can calculate nine estimations of RR for each destination. Based on this, we
104 conducted 200 bootstrapping simulations. For each simulation, RR was randomly selected
105 from the nine RR for each translocated soil. A linear regression model was fitted treating RR
106 and temperature change (due to soil translocation) as response and independent variables,
107 respectively. Then, we calculated the average of RR for each translocated soil based on the
108 200 random draws, and a linear regression model was fitted using the average RRs. The
109 significance of all regressions (i.e., a total of 201 regressions including 200 bootstrapping
110 regressions plus one average regression) was tested at $P < 0.05$.

111 It should be noted that Nottingham et al (2019) focused on the relationship of RR of soil
112 C with elevation shift rather than directly with temperature change, albeit the close
113 correlation between temperature change and elevation shift ($R^2=0.99$). As elevation shift may
114 include changes of a series of other ecosystem properties (e.g., radiation, humidity, rainfall
115 regimes although total amount of rainfall entering to the experimental soils was controlled in
116 their study, see discussions below) other than temperature, our reassessment directly used the
117 elevation shift-induced average temperature changes as a predictor variable of RR. The data
118 is available from Nottingham et al. (2019).

119 **Total SOC changes**

120 The ANOVA results indicated that total SOC content did not show significant difference

121 among translocated soils of the same origin for all four soil origins (Fig. 1). It is apparent that
122 great variability existed for SOC content in some translocated soils of the same origin (Fig. 1).
123 The bootstrapping regression simulations indicated that only 16 of the 200 simulations were
124 significant ($P < 0.05$) for RR of soil C content (Fig. 2). When specifically assessing the
125 relationship of average RR of SOC content with temperature changes, the relationship was
126 also insignificant ($P = 0.14$) with a R^2 of 0.21 (Fig. 2). In Nottingham et al (2019), a 3.86%
127 significant ($P < 0.05$) decline of SOC content per 1 °C temperature increase was estimated.
128 Based on the result in this reassessment, however, this decline was insignificant and only 1.4%
129 per 1 °C temperature increase (i.e., the regression coefficient for the temperature change).
130 These results demonstrate that five years of translocation did not significantly changed SOC
131 content in soils from the same origin, and is consistent with a global data synthesizing of
132 forest soil respiration in mineral soils (Giardina & Ryan, 2000). Expanding the dataset used
133 in (Crowther et al., 2016), a recent global data synthesis of field warming experiments also
134 indicated that SOC stock does not significantly respond to warming (van Gestel et al., 2018),
135 although no tropical data was included.

136 Why is total SOC tolerant towards temperature changes (both warming and cooling)?
137 Although limitations of the data itself (see the discussion below) may result in that the real
138 temperature response of SOC cannot be detected (i.e., Type II error from the perspective of
139 statistics), we discuss the possibility of four mechanisms to explain such persistent SOC
140 content under different temperature regimes: 1) microbial thermal adaptation, 2) substrate
141 depletion, 3) nutrient limitation for microbial carbon acquisition, and 4) environmental
142 constraints such as low pH.

143 The thermal adaptation hypothesis suggests that microbial community may gradually
144 adapt to warming via adjusting microbial physiology and/or shifting community composition
145 (Bradford, 2013; Luo, Wan, Hui, & Wallace, 2001). Although microbial respiration is

146 sensitive to temperature shift at onset, it will decline towards the pre-warmed/cooled rates
147 over time due to microbial adaptation to temperature shift. A laboratory incubation of three
148 contrasting soils under temperatures ranging from 5 to 25 °C indicated that soil respiration
149 was only significantly different at the start several days of the incubation and gradually
150 reached to a similar rate, regardless of substrate availability and initial microbial community
151 composition (Tang, Sun, Luo, He, & Sun, 2018). For this reason, the long-term effect of
152 warming on total SOC content could be negligible, although significant short-term changes in
153 soil respiration at the start of an experiment. Indeed, microbial measurements after five years
154 of the translocation in Nottingham et al. (2019) indicated that microbial community
155 composition was not significantly different evidenced by the observation that the majority of
156 microbial taxa was unaffected by temperature changes (please see Fig. 2 in Nottingham et al.
157 2019). If microbes do not adapt to temperature changes, it is reasonable to infer that
158 microbial community composition may be significant different among the translocated soils.
159 Other studies at the same sites also suggested that microbial respiration was adapted to
160 warming (Nottingham, Bååth, Reischke, Salinas, & Meir, 2019).

161 Besides potential microbial adaptation, microbial activity and functioning could be
162 constrained by other environmental factors (Manzoni, Taylor, Richter, Porporato, & Agren,
163 2012). The low pH in the studied soils (pH < 4 for all soils, Nottingham et al. 2019) could
164 play a critical role in regulating microbial growth and activity in the studied soils. A number
165 of studies have demonstrated that microbial activity and growth are inhibited in acidic soils
166 (Jones et al., 2009; Rousk, Brookes, & Bååth, 2010). A field study in a silty loam soil at
167 Rothamsted research demonstrated that all microbial variables including fungal and bacterial
168 growth were universally inhibited below pH 4.5 (Rousk, Brookes, & Baath, 2009). It is
169 highly probably that microbial processes are less sensitivity to warming at low pH soils, as
170 pH rather than temperature is the limiting factor of microbial carbon decomposition.

171 It is less possible for substrate depletion and nutrient limitation for microbial carbon
172 acquisition to take effective in the studied soils. Substrate availability and quality (e.g., the
173 carbon: nitrogen ratio of soil organic matter) are substantially different among soils from
174 different elevations (see Table S1 in Nottingham et al. 2019). If substrate depletion does
175 occur, total SOC as well as its six chemical fractions should be to some extent different in
176 terms of their temperature response in soils from different elevations (i.e., different origin).
177 However, in all soils, none of the six chemical fractions shown significant difference (see
178 results below), although substrate availability is substantially different among the soils. For
179 the same reason, nutrient limitation would be not the reason, as the soils studied from
180 different elevations have distinct nutrient reserve. For example, soil carbon: nitrogen ratios
181 range from 4.07 to 19.17, carbon: phosphorus ratios from 41.52 to 253.71, and resin-
182 extractable phosphorus ranges from less than 0.8 mg kg⁻¹ soil to more than 79.99 mg kg⁻¹ soil.
183 If nutrient is a limiting factor, temperature response of SOC should present some significant
184 difference among the soils due to the distinct nutrient availability.

185 **Changes in SOC chemical composition**

186 Fig. 3 shows the ANOVA results of the effect of elevation shift on six chemical component
187 fractions in soils from four elevation origins. Except Carbonyl, O-Aryl and Aryl contents in
188 the soil from the 3300 m elevation at its original elevation were significantly different from
189 that in corresponding soils translocated to other elevations, translocation did not significantly
190 influence the content of all six chemical fractions in all four soils. Large data variability also
191 existed for the chemical fractions, particularly in soils with relatively high SOC content. It is
192 interesting to note that both total SOC content and its six chemical fractions shown greater
193 variability in cooler climate at the 3300 m elevation (Figs. 1 and 3). Bootstrapping
194 regressions on the relationship between temperature changes and the RR of the contents of
195 six chemical fractions indicated that only were 2 of 200 simulations significant for Carbonyl

196 (Fig. 4a) and Aryl (Fig. 4c), 11 for Alkyl (Fig. 4f), 24 for O-Alkyl and Di-Alkyl (Fig. 4d and
197 e), and 26 for O-Aryl (Fig. 4b), demonstrating the importance of quantifying data variability.
198 When assessing the relationship of average RR of SOC chemical fractions with temperature
199 changes, the relationship was only marginal ($P = 0.086$) for O-Aryl with a R^2 of 0.27 (Fig. 4).

200 Nottingham et al (2019) interpreted that the detected soil C loss using their approach
201 “primarily originated from labile C pools”. Our re-analysis demonstrated that neither total
202 SOC content nor its chemical fractions was significantly affected by translocation, while their
203 correlations with temperature changes were highly variable and also insignificant on average.
204 Nottingham et al (2019) found that carbonyl content was significantly and positively
205 correlated to temperature changes (Fig. 2 therein), which is difficult to explain (i.e., why
206 carbonyl increases under warming without any external inputs) and opposite to our re-
207 assessment as shown in Fig. 4a. It is clear that all the six chemical fractions were negatively
208 correlated to temperature changes, although none of the correlations was significant at $P <$
209 0.05 (Fig. 4). The result of the similar temperature response of six chemical fractions is in
210 line with prevailing recognitions.

211 In a review paper, Dungait, Hopkins, Gregory, & Whitmore (2012) has concluded that
212 SOC turnover is governed by accessibility rather than chemical recalcitrance. A data-model
213 integration study synthesizing global incubation dataset also found that $> 90\%$ of SOC is
214 physically protected against microbial decomposition, and the dynamic physical protection
215 process is the limiting step of overall SOC decomposition (Luo et al., 2017). Empirical
216 evidence also shown that the response of SOC decomposition to temperature is constrained
217 by substrate availability to microbial decomposers rather than SOC chemical recalcitrance
218 (Zimmermann, Leifeld, Conen, Bird, & Meir, 2012, Moinet et al. 2018). Using ^{14}C
219 techniques, Vaughn & Torn (2019) separated SOC in an Alaska soil into new and old carbon

220 with distinct chemical structures, and found that the two pools shown similar temperature
221 sensitivities. Above all, growing studies have converged on that chemical SOC fractions exert
222 similar temperature sensitivity to decomposition, and physical accessibility rather than
223 chemical structure of SOC is the limiting step. There may be no exception for SOC in
224 tropical forest soils. It will be interesting to identify that whether different chemical fractions
225 are involved in different physical protection processes (i.e., adsorption to and desorption from
226 minerals, occlusion within soil aggregates, and organo-mineral interactions).

227 **Limitations of Nottingham dataset and future research**

228 Soil translocation experiment is invaluable for mimicking climate change *in situ*, but there are
229 several limitations in the Nottingham dataset. First, as abovementioned, there are only three
230 replicates in the data. Considering the spatial heterogeneity of soil properties including SOC
231 (Garten, Kang, Brice, Schadt, & Zhou, 2007; Stursova, Barta, Santruckova, & Baldrian, 2016;
232 the data in the Appendix of Nottingham *et al.* 2019 can also demonstrate this), more
233 replicates would enable us to provide more accurate estimations of the temperature response
234 of soil C and its chemical components. Second, the experimental design cannot eliminate the
235 effect of soil moisture discrepancies among the translocated soils from the same origin, albeit
236 translocated tubes were capped with reduction collars or expansion funnels to maintain the
237 same rainfall per square meter (Zimmermann, Meir, Bird, Malhi, & Cahuana, 2010).
238 Nevertheless, absolute rainfall amount is not the only factor influencing soil moisture. Both
239 rainfall regimes (e.g., the time, frequency and intensity of rainfall events) and upward soil
240 water movement may have marked effects on soil moisture including its temporal dynamics.
241 Different rainfall regimes among the destinations may result in complex soil moisture-
242 temperature interactions and relevant consequences on soil carbon decomposition (Rodrigo,
243 Recous, Neel, & Mary, 1997; Zhou, Hui, & Shen, 2014). Upward movement of water
244 through the open bottom of soil tubes (although a 63 μm nylon mesh at the base of the tubes

245 was installed) may be substantial due to capillary action. In order to avoid potential
246 confounding effects of soil moisture, we suggest that both soil moisture and temperature
247 should be monitored over time, making it possible to explicitly separate the effects of soil
248 moisture and temperature changes as well as quantifying their interactions. Third, the
249 duration of the experiment is five years. Considering normal funding cycles and the difficulty
250 to reach the remote areas of the tropical forests, the experiment should be appreciated.
251 However, five years are too short to observe statistically significant trends of soil carbon
252 changes, particularly for recalcitrant pools (if these pools really exist) which usually have
253 residence times of decades or centuries (Luo, Wang, & Wang, 2019; Schmidt et al., 2011).
254 We would suggest to last the experiment as long as possible to detect clear response of SOC
255 to temperature changes.

256 Another significant confounding factor influencing the results is that plant carbon inputs
257 to the translocated soils were excluded. As pointed out by Nottingham et al (2019), plant
258 carbon inputs to the soil may offset the changes in SOC (although this change is insignificant
259 according to our reassessment) as plant biomass and thus carbon input is generally higher
260 under lower elevation sites where have higher temperature. Except this direct offsetting effect,
261 the absence of carbon inputs has other two kinds of potential consequences on SOC dynamics
262 under temperature changes. First, the absence of carbon input weakens the priming effect.
263 The priming effect is a key process regulating the interaction between new and old SOC
264 (Kuzyakov, 2010; Luo, Wang, & Smith, 2015). Weakening priming effect may have
265 significant consequences on net SOC balance (Rousk, Hill, & Jones, 2015). More importantly,
266 there was no living roots in the soil cores, resulting in the absence of rhizosphere priming
267 effect, which is much more important than the priming effect in the bulk soil as root
268 rhizosphere is a hotspot of microbial growth and activity (Cheng et al., 2014; Zhu et al.,
269 2014). Second, it is unclear whether and how new carbon inputs interact with temperature to

270 affect SOC dynamics. Some evidences from laboratory incubations implied that microbial
271 community structure and functioning respond distinctly to temperature changes under
272 treatments with and without new carbon inputs (e.g., Abro et al., 2011). For these reasons, it
273 should take care when extrapolating results obtained from experiments excluding plant-soil
274 interactions.

275 **Conclusions**

276 Based on the data collected from translocated soils across a 3000 m tropical forest elevation
277 gradient with ± 15 °C temperature changes, Nottingham et al. (2019) concluded that soil
278 carbon declines 4% per 1 °C warming. Reassessing their data, particularly focusing on
279 measurements of total SOC and its chemical fractions, we did not find significant changes in
280 SOC content, and only found an insignificant decline of ~1.4% per 1 °C warming. This
281 insignificant response of SOC dynamics to warming may be likely explained by microbial
282 adaptation to temperature changes and/or environmental constrains (such as low pH of the
283 studied soils) which inhibit microbial growth and activity. We also did not find significant
284 changes in six chemical fractions although they potentially reflect distinct chemical
285 recalcitrance, supporting the proposition that chemical SOC fractions may have similar
286 temperature sensitivity, and SOC dynamics are governed by accessibility of substrates to
287 microbial attack rather than the recalcitrance of SOC chemical compounds. Overall, the
288 unique Nottingham dataset fills a gap of data availability in tropical areas, and provides
289 evidence that SOC in tropical soils may be neutral in terms of its response to warming, which
290 is in line with the results in other ecosystems (van Gestel et al., 2018).

291 **Acknowledgements**

292 We thank the funding support from the National Natural Science Foundation of China (Grant
293 Nos. 31870426, 31470623).

294 **Authorship**

295 ZL assessed the data and wrote the manuscript. XG and OJS contributed to interpretation and
296 writing.

297 **References**

- 298 Abro, S., Tian, X. H., You, D. H., Ba, Y. L., Li, M., & Wu, F. Q. (2011). Influence of
299 microbial inoculants on soil response to properties with and without straw under different
300 temperature regimes. *African Journal of Microbiology Research*, 5(19), 3054-3061.
- 301 Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to
302 warming dependent on microbial physiology. *Nature Geoscience*, 3(5), 336-340.
303 doi:10.1038/ngeo846
- 304 Batjes, N. H. (2016). Harmonized soil property values for broad-scale modelling (WISE30sec)
305 with estimates of global soil carbon stocks. *Geoderma*, 269, 61-68.
306 doi:<https://doi.org/10.1016/j.geoderma.2016.01.034>
- 307 Bradford, M. A. (2013). Thermal adaptation of decomposer communities in warming soils.
308 *Frontiers in Microbiology*, 4, 16. doi:10.3389/fmicb.2013.00333
- 309 Chen, J., Luo, Y. Q., Garcia-Palacios, P., Cao, J. J., Dacal, M., Zhou, X. H., . . . van
310 Groenigen, K. J. (2018). Differential responses of carbon-degrading enzyme activities to
311 warming: Implications for soil respiration. *Global Change Biology*, 24(10), 4816-4826.
312 doi:10.1111/gcb.14394
- 313 Cheng, W., Parton, W. J., Gonzalez-Meler, M. A., Phillips, R., Asao, S., McNickle, G. G., . . .
314 Jastrow, J. D. (2014). Synthesis and modeling perspectives of rhizosphere priming. *New
315 Phytologist*, 201(1), 31-44. doi:10.1111/nph.12440
- 316 Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C.,
317 Machmuller, M. B., . . . Bradford, M. A. (2016). Quantifying global soil carbon losses in

- 318 response to warming. *Nature*, 540(7631), 104-+. doi:10.1038/nature20150
- 319 Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon
320 decomposition and feedbacks to climate change. *Nature*, 440(7081), 165-173.
321 doi:<https://xs.scihub.ltd/https://doi.org/10.1038/nature04514>
- 322 Dungait, J. A., Hopkins, D. W., Gregory, A. S., & Whitmore, A. P. (2012). Soil organic
323 matter turnover is governed by accessibility not recalcitrance. *Global Change Biology*,
324 18(6), 1781-1796. doi:<https://doi.org/10.1111/j.1365-2486.2012.02665.x>
- 325 Fox, John, and Sanford Weisberg. "Multivariate linear models in R." *An R Companion to*
326 *Applied Regression*. Los Angeles: Thousand Oaks (2011).
- 327 Garten, C. T., Kang, S., Brice, D. J., Schadt, C. W., & Zhou, J. (2007). Variability in soil
328 properties at different spatial scales (1m–1km) in a deciduous forest ecosystem. *Soil*
329 *Biology and Biochemistry*, 39(10), 2621-2627.
330 doi:<https://doi.org/10.1016/j.soilbio.2007.04.033>
- 331 Giardina, C. P., & Ryan, M. G. (2000). Evidence that decomposition rates of organic carbon
332 in mineral soil do not vary with temperature. *Nature*, 404(6780), 858-861.
- 333 Jones, R. T., Robeson, M. S., Lauber, C. L., Hamady, M., Knight, R., & Fierer, N. (2009). A
334 comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone
335 library analyses. *The ISME Journal*, 3(4), 442-453. doi:10.1038/ismej.2008.127
- 336 Kuzyakov, Y. (2010). Priming effects: Interactions between living and dead organic matter.
337 *Soil Biology & Biochemistry*, 42(9), 1363-1371. doi:10.1016/j.soilbio.2010.04.003
- 338 Le Quere, C., Andrew, R. M., Canadell, J. G., Sitch, S., Korsbakken, J. I., Peters, G. P., . . .
339 Zaehle, S. (2016). Global Carbon Budget 2016. *Earth System Science Data*, 8(2), 605-649.
340 doi:10.5194/essd-8-605-2016
- 341 Luo, Y., Wan, S., Hui, D., & Wallace, L. L. (2001). Acclimatization of soil respiration to
342 warming in a tall grass prairie. *Nature*, 413(6856), 622-625. doi:10.1038/35098065

- 343 Luo, Y., Xia, J., Ahlström, A., Zhou, S., Huang, Y., Shi, Z., . . . Lu, X. (2017). *Matrix*
344 *approach to uncertainty assessment and reduction for modeling terrestrial carbon cycle*.
345 Paper presented at the AGU Fall Meeting Abstracts.
346 <https://ui.adsabs.harvard.edu/abs/2017AGUFM.B34A..01L>
- 347 Luo, Z., Wang, E., & Smith, C. (2015). Fresh carbon input differentially impacts soil carbon
348 decomposition across natural and managed systems. *Ecology*, 96(10), 2806-2813.
349 doi:10.1890/14-2228.1.sm
- 350 Luo, Z., Wang, G., & Wang, E. (2019). Global subsoil organic carbon turnover times
351 dominantly controlled by soil properties rather than climate. *Nature Communications*,
352 10(1), 3688. doi:10.1038/s41467-019-11597-9
- 353 Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Agren, G. I. (2012). Environmental and
354 stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*,
355 196(1), 79-91. doi:10.1111/j.1469-8137.2012.04225.x
- 356 Melillo, J. M., Frey, S. D., DeAngelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F.
357 P., . . . Grandy, A. S. (2017a). Long-term pattern and magnitude of soil carbon feedback
358 to the climate system in a warming world. *Science*, 358(6359), 101-104.
359 doi:10.1126/science.aan2874
- 360 Moinet, G. Y. K., Hunt, J. E., Kirschbaum, M. U. F., Morcom, C. P., Midwood, A. J., &
361 Millard, P. (2018). The temperature sensitivity of soil organic matter decomposition is
362 constrained by microbial access to substrates. *Soil Biology and Biochemistry*, 116, 333-
363 339. doi:<https://doi.org/10.1016/j.soilbio.2017.10.031>
- 364 Nottingham, A. T., Bååth, E., Reischke, S., Salinas, N., & Meir, P. (2019). Adaptation of soil
365 microbial growth to temperature: Using a tropical elevation gradient to predict future
366 changes. *Global Change Biology*, 25(3), 827-838.
- 367 Nottingham, A. T., Whitaker, J., Ostle, N. J., Bardgett, R. D., McNamara, N. P., Fierer,

- 368 N., . . . Meir, P. (2019). Microbial responses to warming enhance soil carbon loss
369 following translocation across a tropical forest elevation gradient. *Ecology Letters*, 22(11),
370 1889-1899. doi:10.1111/ele.13379
- 371 Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., . . . Hayes, D.
372 (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, 333(6045),
373 988-993. doi:10.1126/science.1201609
- 374 Pries, C. E. H., Castanha, C., Porras, R., & Torn, M. (2017). The whole-soil carbon flux in
375 response to warming. *Science*, 355(6332), 1420-1423.
- 376 Rodrigo, A., Recous, S., Neel, C., & Mary, B. (1997). Modelling temperature and moisture
377 effects on C–N transformations in soils: comparison of nine models. *Ecological*
378 *Modelling*, 102(2), 325-339. doi:[https://doi.org/10.1016/S0304-3800\(97\)00067-7](https://doi.org/10.1016/S0304-3800(97)00067-7)
- 379 Rousk, J., Brookes, P. C., & Baath, E. (2009). Contrasting Soil pH Effects on Fungal and
380 Bacterial Growth Suggest Functional Redundancy in Carbon Mineralization. *Applied and*
381 *Environmental Microbiology*, 75(6), 1589-1596. doi:10.1128/aem.02775-08
- 382 Rousk, J., Brookes, P. C., & Bååth, E. (2010). Investigating the mechanisms for the opposing
383 pH relationships of fungal and bacterial growth in soil. *Soil Biology and Biochemistry*,
384 42(6), 926-934. doi:<https://doi.org/10.1016/j.soilbio.2010.02.009>
- 385 Rousk, J., Hill, P. W., & Jones, D. L. (2015). Priming of the decomposition of ageing soil
386 organic matter: concentration dependence and microbial control. *Functional Ecology*,
387 29(2), 285-296. doi:10.1111/1365-2435.12377
- 388 Schmidt, M. W., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., . . .
389 Manning, D. A. (2011). Persistence of soil organic matter as an ecosystem property.
390 *Nature*, 478(7367), 49-56. doi:<https://xs.scihub.ltd/https://doi.org/10.1038/nature10386>
- 391 Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., & Schimel, J. P. (2013).
392 Long-term warming restructures Arctic tundra without changing net soil carbon storage.

- 393 *Nature*, 497(7451), 615-618. doi:10.1038/nature12129
- 394 Stursova, M., Barta, J., Santruckova, H., & Baldrian, P. (2016). Small-scale spatial
395 heterogeneity of ecosystem properties, microbial community composition and microbial
396 activities in a temperate mountain forest soil. *Fems Microbiology Ecology*, 92(12).
397 doi:10.1093/femsec/fiw185
- 398 Tang, Z., Sun, X., Luo, Z., He, N., & Sun, O. J. (2018). Effects of temperature, soil substrate,
399 and microbial community on carbon mineralization across three climatically contrasting
400 forest sites. *Ecology and Evolution*, 8(2), 879-891.
- 401 van Gestel, N., Shi, Z., van Groenigen, K. J., Osenberg, C. W., Andresen, L. C., Dukes, J.
402 S., . . . Hungate, B. A. (2018). Predicting soil carbon loss with warming. *Nature*,
403 554(7693), E4-E5. doi:10.1038/nature20150
- 404 Vaughn, L. J. S., & Torn, M. S. (2019). ¹⁴C evidence that millennial and fast-cycling soil
405 carbon are equally sensitive to warming. *Nature Climate Change*, 9(6), 467-471.
406 doi:10.1038/s41558-019-0468-y
- 407 Zhou, W. P., Hui, D. F., & Shen, W. J. (2014). Effects of Soil Moisture on the Temperature
408 Sensitivity of Soil Heterotrophic Respiration: A Laboratory Incubation Study. *Plos One*,
409 9(3). doi:10.1371/journal.pone.0092531
- 410 Zhu, B., Gutknecht, J. L. M., Herman, D. J., Keck, D. C., Firestone, M. K., & Cheng, W.
411 (2014). Rhizosphere priming effects on soil carbon and nitrogen mineralization. *Soil*
412 *Biology & Biochemistry*, 76, 183-192. doi:10.1016/j.soilbio.2014.04.033
- 413 Zimmermann, M., Leifeld, J., Conen, F., Bird, M. I., & Meir, P. (2012). Can composition and
414 physical protection of soil organic matter explain soil respiration temperature sensitivity?
415 *Biogeochemistry*, 107(1-3), 423-436.
- 416 Zimmermann, M., Meir, P., Bird, M. I., Malhi, Y., & Ccahuana, A. J. (2010). Temporal
417 variation and climate dependence of soil respiration and its components along a 3000 m

418 altitudinal tropical forest gradient. *Global Biogeochemical Cycles*, 24(4).

419

420 **Figure Legends**

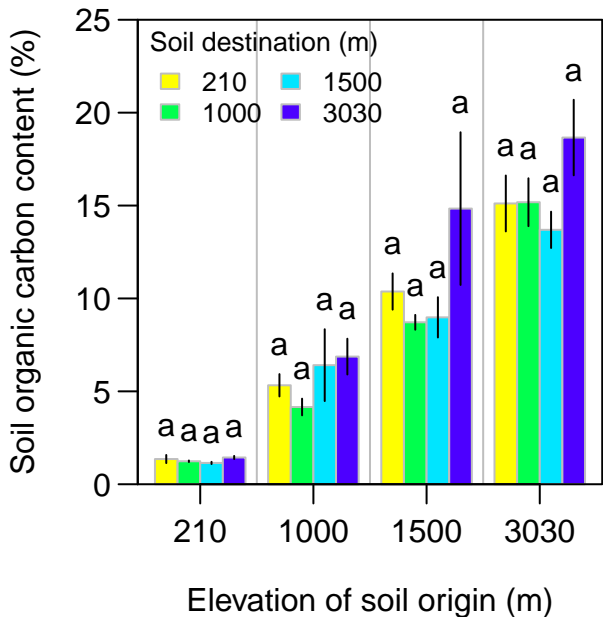
421 **Fig. 1. Effects of soil translocation on soil carbon content.** Different letters above the bars
422 for the same soil origin group indicate significant difference at $P < 0.05$. Error bars show one
423 standard error. Please note that the increasing pattern just shows that soil carbon increases
424 with elevation and does not relate to the effect of temperature changes.

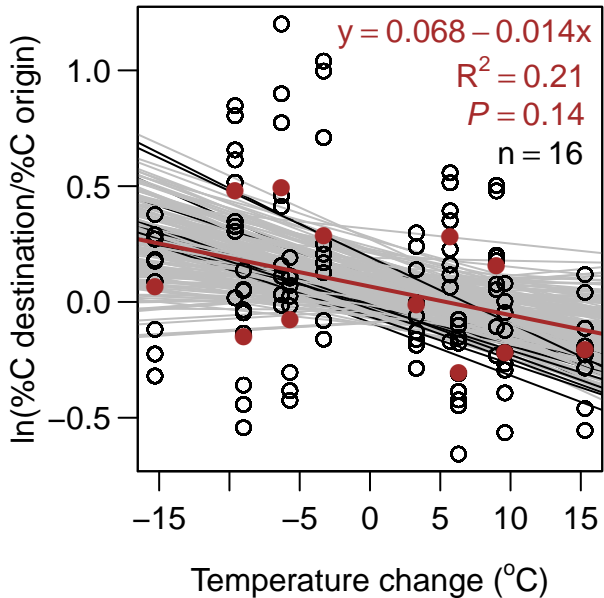
425 **Fig. 2. Relationship of the log relative response ratio (RR) of soil carbon content with**
426 **temperature changes.** Circles show nine possible RR taking into account combinations of
427 three replicates at soil destination and origin. Thin lines show 200 bootstrapping regression
428 lines with RR randomly selected from the nine RR values, while black and grey ones indicate
429 that the regression is significant ($P < 0.05$) and insignificant ($P > 0.05$), respectively. n shows
430 the number of significant regression lines. Brown solid points are the average of the nine RR
431 values, while brown lines are the corresponding regression lines and brown texts in the plots
432 show the statistics of the regression lines based on average values.

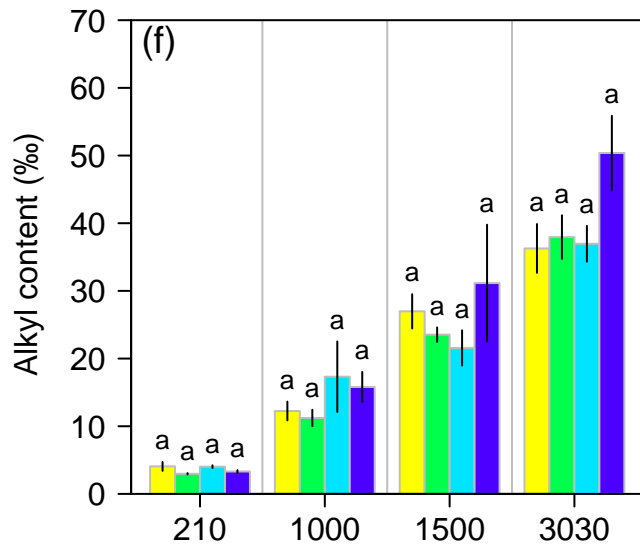
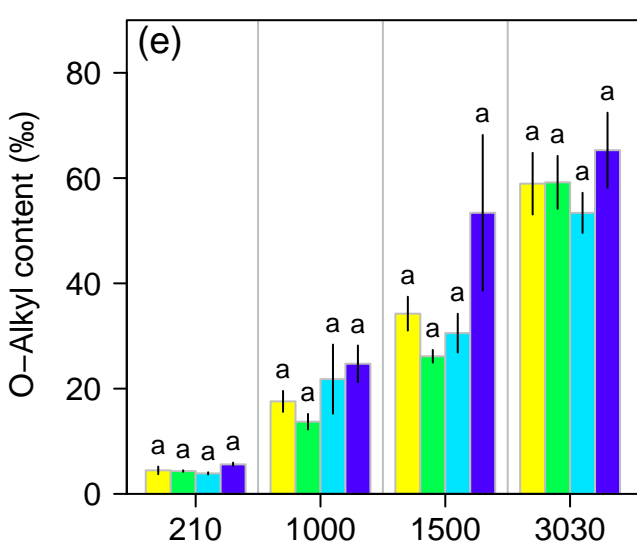
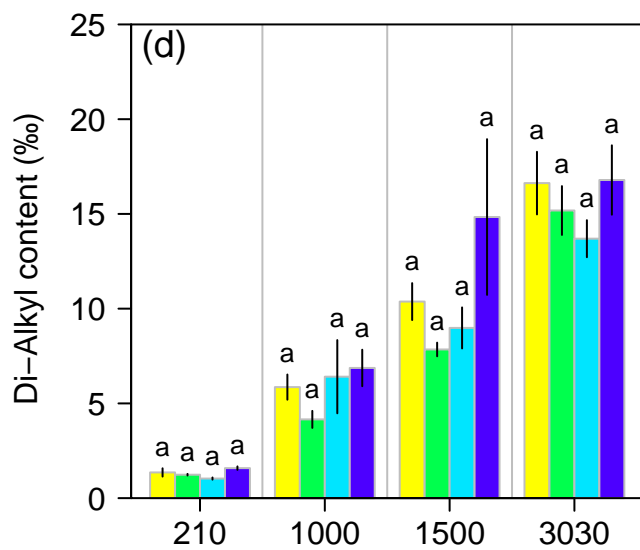
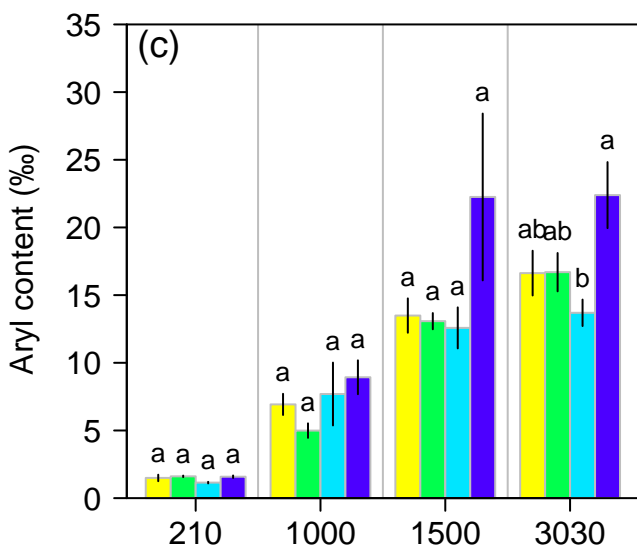
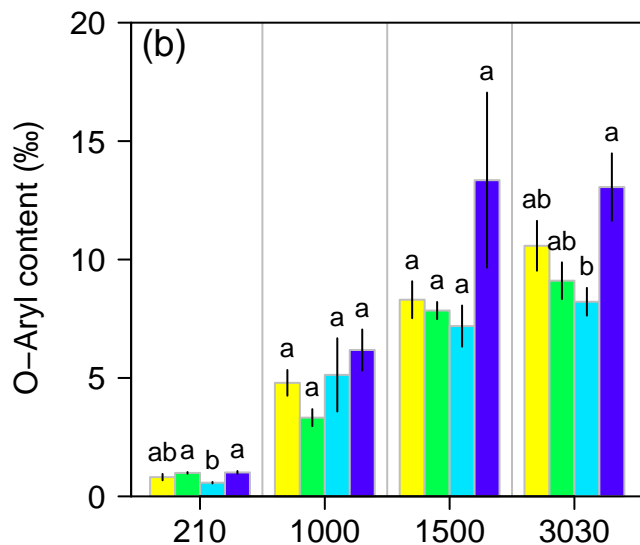
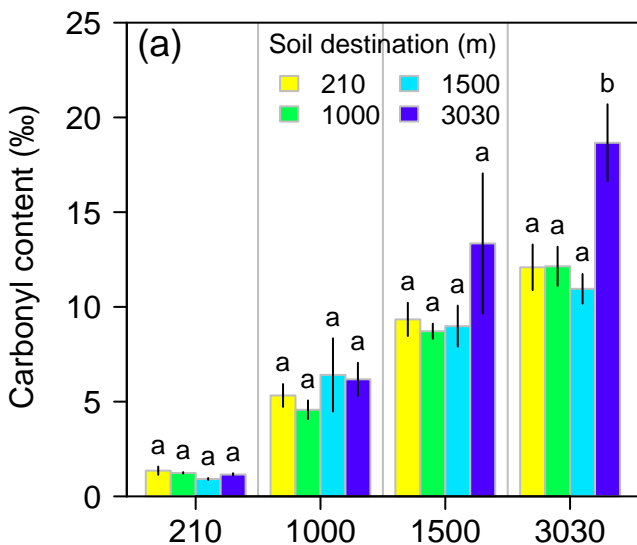
433 **Fig. 3. Effects of soil translocation on six chemical fractions of soil carbon.** Six chemical
434 fractions are carbonyl (165-190 ppm, a), O-aryl (140-165 ppm, b), aryl (110-140 ppm, c), di-
435 O-alkyl (92-110 ppm, d), O-alkyl (46-92 ppm, e), and alkyl (0-46 ppm, f), determined by ^{13}C
436 NMR spectroscopy. See Nottingham et al (2019) for details of the six chemical fractions.
437 Different letters above the bars for the same soil origin group indicate significant difference
438 at $P < 0.05$. Error bars show one standard error. Please note that the increasing pattern just
439 shows that soil carbon from different elevations are different.

440 **Fig. 4. Relationship of log relative response ratio (RR) of six chemical soil carbon**
441 **fractions with temperature changes.** Six chemical fractions are carbonyl (165-190 ppm, a),
442 O-aryl (140-165 ppm, b), aryl (110-140 ppm, c), di-O-alkyl (92-110 ppm, d), O-alkyl (46-92
443 ppm, e), and alkyl (0-46 ppm, f), determined by ^{13}C NMR spectroscopy. See Nottingham et al

444 (2019) for details of the six chemical fractions. Lines, points and legends share the same
445 explanation to that in Fig. 2.







Elevation of soil origin (m)

Elevation of soil origin (m)

