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Temperature response of soil respiration largely unaltered with experimental warming

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### Authors

Carey, Joanna C  
Tang, Jianwu  
Templer, Pamela H  
[et al.](#)

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6

7 **Authors:** Joanna C. Carey<sup>a\*</sup>, Jianwu Tang<sup>a\*</sup>, Pamela H. Templer<sup>b</sup>, Kevin D. Kroeger<sup>c</sup>, Thomas W.  
8Crowther<sup>d,e</sup>, Andrew Burton<sup>f</sup>, Jeffrey S. Dukes<sup>g</sup>, Bridget Emmett<sup>h</sup>, Serita Frey<sup>i</sup>, Mary Heskell<sup>a</sup>, Lifen Jiang<sup>j</sup>,  
9Megan Machmuller<sup>k</sup>, Jacqueline E. Mohan<sup>l</sup>, Anne Marie Panetta<sup>m</sup>, Peter B. Reich<sup>n,o</sup>, Sabine Reinsch<sup>h</sup>, Xin  
10Wang<sup>p</sup>, Steven D. Allison<sup>q</sup>, Christopher Bamminger<sup>r</sup>, Scott D. Bridgham<sup>s</sup>, Scott L. Collins<sup>t</sup>, Giovanbattista  
11 de Dato<sup>u</sup>, William C. Eddy<sup>v</sup>, Brian J. Enquist<sup>w</sup>, Marc Estiarte<sup>x,y</sup>, John Harte<sup>z</sup>, Amanda Henderson<sup>w</sup>, Bart  
12R. Johnson<sup>aa</sup>, Klaus S. Larsen<sup>bb</sup>, Yiqi Luo<sup>j</sup>, Sven Marhan<sup>r</sup>, Jerry Melillo<sup>a</sup>, Josep Peñuelas<sup>x,y</sup>, Laurel Pfeifer-  
13 Meister<sup>s,cc</sup>, Christian Poll<sup>r</sup>, Edward B. Rastetter<sup>a</sup>, Andy Reinmann<sup>b</sup>, Lorien L. Reynolds<sup>s</sup>, Inger K.  
14 Schmidt<sup>bb</sup>, Gaius R. Shaver<sup>a</sup>, Aaron L. Strong<sup>dd</sup>, Vidya Suseela<sup>ee</sup>, Albert Tietema<sup>ff</sup>

15

16**Affiliations:**

17<sup>a</sup>The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543.

18<sup>b</sup>Department of Biology, Boston University, Boston, MA 02215.

19<sup>c</sup>United States Geological Survey, Woods Hole, MA 02543.

20<sup>d</sup>Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, The  
21Netherlands

22<sup>e</sup>School of Forestry & Environmental Studies, Yale University, New Haven, CT 06511

23<sup>f</sup>School of Forest Resources and Environmental Science, Michigan Technological University, Houghton,  
24MI 49931

25<sup>g</sup>Department of Forestry and Natural Resources, Department of Biological Sciences, and Purdue Climate  
26Change Research Center, Purdue University, West Lafayette, IN, 47907, USA.

27<sup>h</sup>Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor, LL57 2 UW, UK

28<sup>i</sup>Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH  
2903824 USA

30<sup>j</sup>Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019.

31<sup>k</sup>Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523

32<sup>l</sup>Odum School of Ecology, University of Georgia, Athens, GA 30601

33<sup>m</sup>Department of Evolution and Ecology, University of California Davis, Davis, CA 95616

34<sup>n</sup>Department of Forest Resources, University of Minnesota St. Paul, MN 55108

35<sup>o</sup>University of Minnesota Institute on the Environment, St. Paul, MN 55108

36<sup>p</sup>State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese  
37Academy of Sciences, Beijing 100093.

38<sup>q</sup>Department of Ecology and Evolutionary Biology, Department of Earth System Science, University of  
39California Irvine, Irvine, CA 92697

40<sup>r</sup>Institute of Soil Science and Land Evaluation, University of Hohenheim, 70593 Stuttgart, Germany

41<sup>s</sup>Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403

42<sup>t</sup>Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM 87131 USA

43<sup>u</sup>Council for Agricultural Research and Economics - Forestry Research Centre (CREA-SEL), Arezzo  
44(AR), Italy

45<sup>v</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota St. Paul, MN 55108

46<sup>w</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona

47<sup>x</sup>CSIC, Global Ecology Unit CREAM-CSIC-UAB, Cerdanyola del Vallès, 08193 Catalonia, Spain.

48<sup>y</sup>CREAF, Cerdanyola del Vallès, 08193 Catalonia, Spain

49<sup>z</sup> Energy and Resources Group and Department of Environmental Science, Policy and Management,  
50University of California, Berkeley, CA 94720  
51<sup>aa</sup> Department of Landscape Architecture, University of Oregon, Eugene, OR 97403  
52<sup>bb</sup> Department of Geosciences and Natural Resource Management, University of Copenhagen,  
53Rolighedsvej 23, DK-1958 Frederiksberg, Denmark  
54<sup>cc</sup> Environmental Science Institute, University of Oregon, Eugene, OR 97403  
55<sup>dd</sup> Emmett Interdisciplinary Program in Environment and Resources, Stanford University, Stanford, CA  
5694305  
57<sup>ee</sup> Department of Agricultural & Environmental Sciences, Clemson University. Clemson, SC 29634  
58<sup>ff</sup> Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O.Box 94240, 1090 GE  
59Amsterdam, Netherland  
60  
61\*Correspondence authors: jcarey@mbl.edu, jtang@mbl.edu

62  
63Keywords: soil respiration, experimental warming, climate change, temperature sensitivity, temperature  
64response

65  
66**Abstract:**

67The respiratory release of carbon dioxide (CO<sub>2</sub>) from soil is a major and yet, poorly understood flux in the  
68global carbon cycle. Climatic warming is hypothesized to increase rates of soil respiration, potentially  
69fueling further increases in global temperatures. However, despite considerable scientific attention in  
70recent decades, the overall response of soil respiration to anticipated climatic warming remains unclear.  
71We synthesize the largest global dataset to date of soil respiration, moisture, and temperature  
72measurements, totaling >3800 observations representing 27 temperature manipulation studies, spanning  
73nine biomes and over two decades of warming. Our analysis reveals no differences in the temperature  
74sensitivity of soil respiration between control and warmed plots in all biomes, with the exception of  
75deserts and boreal forests. Thus, our data provide limited evidence of acclimation of soil respiration to  
76experimental warming in several major biome types, contrary to the results from multiple single-site  
77studies. Moreover, across all non-desert biomes, respiration rates with and without experimental warming  
78follow a Gaussian response, increasing with soil temperature up to a threshold of ~25°C, above which,  
79respiration rates decrease with further increases in temperature. This consistent decrease in temperature  
80sensitivity at higher temperatures demonstrates that rising global temperatures may result in regionally  
81variable responses in soil respiration, with colder climates being considerably more responsive to  
82increased ambient temperatures compared to warmer regions. Our analysis adds a unique cross-biome

83perspective on the temperature response of soil respiration, information critical to improving our  
84mechanistic understanding of how soil carbon dynamics change with climatic warming.

85

86**Significance Statement:** One of the greatest challenges in projecting future shifts in the global climate is  
87to understand how soil respiration rates will change with warming. Multiple experimental warming  
88studies have been conducted to explore this response, but no consensus has been reached. Based on a  
89global synthesis of 27 experimental warming studies spanning nine biomes, we find that although  
90warming increases soil respiration rates, there is limited evidence for a shifting respiration response with  
91experimental warming. We also note a universal decline in the temperature sensitivity of respiration at  
92soil temperatures  $>25^{\circ}\text{C}$ . Together, our data indicate that future respiration rates will often follow the  
93current temperature response function, but higher latitudes will be more responsive to warmer  
94temperatures.

95

96**Text:**

97**body**

98Compared to anthropogenic emissions, roughly nine times more carbon dioxide ( $\text{CO}_2$ ) is released from  
99soils to the atmosphere via soil respiration on an annual basis (1). Both plant root respiration and  
100microbial respiration during the decomposition of organic matter contribute to this efflux of carbon (C)  
101from soils, cumulatively estimated at  $\sim 90 \text{ Pg C yr}^{-1}$ (2). Rising temperatures are expected to stimulate soil  
102respiration (3), both by accelerating rates of C cycling via autotrophic respiration and by providing a  
103potentially powerful positive feedback to climatic warming via heterotrophic decomposition of organic  
104matter. However, due to a suite of factors beyond temperature that control soil respiration rates (e.g., soil  
105moisture, C substrate quality and quantity, nutrient availability), the interaction between temperature and  
106respiration remains uncertain (3–5). As such, soil respiration is a major and poorly understood flux in the  
107global C cycle.

108

109Experimental warming of soils is one approach used to understand the complex relationship between  
110respiration and temperature, as it allows scientists to separate the effects of warming from confounding  
111environmental variation (e.g., soil type, plant species composition). Results of experimental studies reveal  
112a range of responses of soil respiration to warming, with few unifying trends observed across biomes (6–  
1138). Although warming has been shown to stimulate soil respiration within many sites, several studies  
114show neutral, or even negative responses to warming, often attributed to moisture limitation (9, 10), shifts  
115in microbial physiological response or composition (11–13), or depletion of labile C pools (14–17). As  
116such, multiple single-site analyses find evidence of acclimation (sometimes termed thermal adaptation) of  
117soil respiration to experimental warming (10–14, 16, 17), although others report no evidence for such  
118shifts in respiration response over time (18–20). Moreover, the response of soil respiration to temperature  
119is not consistent across all temperature ranges, as the temperature sensitivity of respiration typically  
120decreases under warmer conditions (21, 22). As a result, the interaction between soil respiration and  
121climate warming remains one of the greatest sources of uncertainty in climate projections, despite being  
122an important boundary condition in current Earth system models (ESMs) (4, 23, 24).

123

124Current understanding of how soil respiration responds to experimental warming stems from single-site  
125warming experiments, or traditional meta-analyses based on average or cumulative soil respiration values  
126in control versus warmed plots. To date, no cross-biome synthesis efforts of experimental warming have  
127evaluated how temperature and moisture interact at high temporal frequencies to determine rates of soil  
128respiration. Therefore, the goals of this study were to: (i) synthesize the results of experimental warming  
129studies to understand how the temperature response function of soil respiration changes with experimental  
130warming treatments across biomes, with respect to both warming duration and seasonality; (ii) investigate  
131the role of soil moisture in driving these responses; and (iii) examine whether a uniform model exists that  
132can describe the response of soil respiration to temperature across all biomes. To do this, we generated an  
133unprecedented global dataset of >3800 observations of instantaneous soil respiration, soil temperature,  
134and soil moisture based on data from 27 individual warming experiments spanning nine biomes and up to  
13522 years of experimental warming. Our analysis is unique among soil respiration synthesis efforts focused

136on warming experiments, in that we used instantaneous observations (i.e., plot-scale measurements of soil  
137respiration averaged from individual sampling events) rather than annual or monthly averaged values to  
138evaluate the temperature response function of soil respiration and the interaction with soil moisture at the  
139global scale.

140

## 141Results and Discussion

### 142Evaluating Differences in Temperature Response Function with Experimental Warming

143We first sought to determine whether respiration responses from experimentally warmed plots paralleled  
144those of control plots over the seasonal range of temperature variation at the biome scale. After evaluating  
145multiple functional forms, we used a log-quadratic temperature response function, as this was the best  
146supported model for most biomes (Table S3):

147

148(1)

$$\ln(R) = \gamma_0 + \gamma_1 T + \gamma_2 T^2$$

149

150where  $R$  is soil respiration ( $\mu\text{mol C m}^2 \text{s}^{-1}$ ) and  $T$  is soil temperature ( $^{\circ}\text{C}$ ). Using this basic model, we  
151included warming treatment as an interaction term in order to evaluate differences in the temperature  
152response between warmed versus control plots (Table 1). We used this log-quadratic model for all biomes  
153(Model d in Table S3), except the boreal forest and northern shrublands, where a log-linear model ( $\ln(R)$   
154=  $\beta_0 + \beta_1 T$ ) was the better fit when including the warming treatment interaction term (Model c in Table  
155S3). We evaluated two specific features of the temperature response function: (i) the temperature

156sensitivity (i.e., the shape of the curve denoted by the first derivative of Eq. 1:  $\frac{d \ln(R)}{dT}$ , Table 1)

157and (ii) the magnitude of the respiration response when  $T = 0$  (i.e., the y-intercept of Eq. 1:  $\beta_0$ , Table 1).

158

159Including data from all warming durations and seasons, we observed no significant differences in the  
160temperature sensitivity of soil respiration between warmed or control treatments within each individual  
161biome, with the exception of boreal forest and desert (Table 1, Fig. 1). In the boreal forest and desert  
162biomes, where significant differences in the temperature sensitivities between warmed versus control  
163plots were observed, trends between treatments were not consistent; compared to control plots, warmed

164plots in the boreal forest had consistently lower temperature sensitivity, while in the desert warmed plots  
165had slightly higher temperature sensitivity at temperatures  $<24^{\circ}\text{C}$ , but lower sensitivity at temperatures  
166 $>24^{\circ}\text{C}$  (SI Appendix, Fig. S1, Fig. 2).  
167  
168The lack of difference in the temperature sensitivity of respiration between control and warmed plots in  
169all biomes except the desert and boreal forests cannot be attributed to an insufficient magnitude of  
170warming. Across our studies, the desert plots were subjected to a relatively small degree of warming ( $0.34$   
171 $^{\circ}\text{C}$  on average), but showed the largest differences in sensitivity between treatments. By contrast,  
172grasslands experienced larger amounts of experimental warming ( $1.9^{\circ}\text{C}$  on average) (Table S1), but did  
173not display altered sensitivity between treatments.  
174  
175In addition to evaluating changes in the temperature sensitivities with respiration, (i.e., the shape of the  
176temperature response function denoted by  $\beta_1$  and  $\beta_2$  in Table 1), we also evaluated differences in the  
177magnitude of respiration rates between treatments (denoted by the y-intercept,  $\beta_0$ , in Table 1). The desert  
178was the only biome to display a significantly different y-intercept between warmed versus control plots,  
179with warmed plots having a lower y-intercept than control plots. Thus, compared to desert control plots,  
180warmed plots emitted less  $\text{CO}_2$  at a given temperature, despite being generally more sensitive to changes  
181in soil temperature (Fig. 2C). Similar to the desert, temperate forests showed a marginally significant  
182( $p=0.06$ ) trend of emitting less  $\text{CO}_2$  from warmed plots compared to control plots at a given temperature  
183( $\beta_0$  in Table 1, Fig. 2D). Therefore, although the shapes of the temperature response functions with and  
184without experimental warming were similar in temperate forests, the magnitude of respiration from  
185warmed plots was typically lower than from control plots. In turn, despite little difference in temperature  
186sensitivities between treatments, the reduced fluxes from warmed plots provide evidence of acclimation to  
187experimental warming in the temperate forest.  
188  
189The lack of difference in temperature response between warmed and control plots in most biomes persists  
190regardless of warming duration or season. For example, by partitioning the observations into categories of  
191warming duration ( $<2$ ,  $2-5$ ,  $5-10$ , and  $>10$  years) and season (growing, non-growing, and shoulder) and  
192running the model described by Eq. 1, we continued to find no differences in the temperature response

193function between warmed and control plots, except in the boreal forest and desert. We then ran two  
194additional multivariate regression models that added duration or season as predictors of soil respiration  
195with interactions with warming treatment to our temperature response functions (Table S3). Here we  
196found similar outcomes, with significant interactions between season and warming treatment observed  
197only in the boreal forest and desert. Significant interactions between duration and warming treatment  
198were also observed in the boreal forest and desert, in addition to the temperate forest and northern  
199shrubland. Thus, over time respiration from warmed plots appears to respond differently to temperature  
200compared to respiration from control plots in these four biomes (see SI Appendix).  
201  
202Together, our results show a similar temperature response of soil respiration from warmed and control  
203plots across several major biome types, providing limited support of acclimation with experimental  
204warming at the biome scale, across seasons and often independent of warming duration. However, the  
205pronounced difference in the temperature response of respiration between treatments in the boreal forest  
206and desert ecosystems suggests that acclimation of soil communities to warmer conditions is likely to  
207have greater consequences for soil C dynamics in these biomes.

208

#### 209*Changes in Soil Moisture with Experimental Warming*

210Reductions in soil moisture that accompany experimental warming can influence the soil respiration  
211response to elevated temperatures (25, 26). Using log response ratios as our index of effect size, we found  
212that soil moisture was significantly ( $p < 0.05$ ) reduced in warmed plots across all sites, with the magnitude  
213of this soil drying being weakly correlated to the amount of soil warming at each site ( $p = 0.08$ ;  $r = -0.32$ ;  
214SI Appendix, Fig. S2A). In situations of severe soil drying, we found evidence that soil respiration  
215becomes limited by moisture, which in turn changes the respiration-temperature relationship. For  
216example, not only are the lowest moisture quartiles typically associated with a depressed temperature  
217response function (Fig. S3,  $\square_1$ ,  $\square_2$  in Table S4), but the magnitude of the respiration response to  
218warming decreased linearly with the degree of soil drying across our entire dataset ( $p < 0.05$ , Fig. 3). In  
219fact, when moisture of warmed plots dropped by at least 30% relative to control plots, respiration rates



220 were actually lower from warmed plots, despite experiencing higher soil temperatures (Fig. 3; see SI  
221 Appendix).  
222  
223 *A Universal Decline in Temperature Sensitivity at Seasonally Elevated Temperatures*  
224 Our dataset of instantaneous soil respiration and temperature measurements allowed us to evaluate the  
225 temperature response function of soil respiration across biomes. We observed a similar Gaussian response  
226 pattern (expressed as a log-quadratic function, Eq. 1) in the soil respiration response across temperature  
227 gradients in most non-desert biomes, with respiration rates increasing with temperature up to ~25°C (23-  
228 34°C, depending on the biome), above which respiration rates level off and decrease (Table 1, Fig. 1, Fig.  
229 S4). This common functional form applies to all the non-desert biomes that reach temperatures above  
230 25°C (thus, excluding boreal forests and northern shrublands), despite variation in temperature response  
231 function parameters among biomes (Table 1, Fig. S4). Low soil moisture at high temperatures partially  
232 explains this decreasing sensitivity at elevated temperatures (Fig. S3). Nevertheless, respiration rates  
233 continue to reach a plateau or even slightly decrease at elevated soil temperatures, even under the wettest  
234 conditions in most biomes (Fig. S3, Table S4). In turn, we hypothesize that decreased autotrophic demand  
235 for ATP and enzyme capacity (27), in addition to microbial enzymatic activities reaching their  
236 physiological thermal limit (13, 28), play important roles in the reduced temperature sensitivity under  
237 warmer conditions. The desert was again unique among biomes in that control plots did not display  
238 decreased sensitivity at such high temperatures, and warmed plots displayed dramatically higher  
239 temperature threshold for reduced respiration (55°C) (Table 1, Fig. 1). The fundamentally different  
240 response of soil respiration to temperature in deserts could be due to several factors, namely higher  
241 respiration temperature optima and maxima of plant and microbial communities in the desert compared to  
242 other ecosystems (28), or the importance of abiotic (i.e., UV-driven) decomposition as a major component  
243 of litter decomposition in deserts (29).

244

245 *Regionally Variable Response to Global Change*

246The reversal in the direction of the temperature response at temperatures greater than  $\sim 25^{\circ}\text{C}$  observed in  
247most non-desert biomes suggests that warmer global temperatures will result in regionally variable  
248responses in soil respiration rates, as different regions occupy different positions on the shared  
249temperature-response function. Compared to lower latitudes, higher latitude sites more often experience  
250soil temperatures  $< 25^{\circ}\text{C}$ , where the relationship between soil respiration and temperature is nearly  
251exponential. As such, our data indicate that higher latitude sites will be more responsive to increased  
252ambient temperatures compared to warmer regions that more frequently experience soil temperatures  
253 $> 25^{\circ}\text{C}$ . Our results also support the idea that models of soil respiration based on fixed parameters (e.g.,  
254fixed  $Q_{10}$  in an exponential function) are inadequate for describing the respiration response across the full  
255temperature range (4, 21, 22). Without accounting for reduced temperature sensitivity at elevated  
256temperatures, ESMs will likely over-estimate soil respiration rates in response to climate warming,  
257particularly from lower latitude regions.

258

#### 259*Limited Evidence of Acclimation of Soil Respiration to Experimental Warming*

260Acclimation of soil respiration to soil warming can manifest itself in different ways, both via changing the  
261shape of the temperature response curve (i.e., temperature sensitivity) and position of the curve on the y-  
262axis (i.e., y-intercept). Our analyses addressed both of these factors, finding evidence of shifting  
263sensitivities only in the desert and boreal forest biomes, and lower fluxes at a given temperature (i.e., y-  
264intercepts) from warmed plots in the desert ( $p < 0.01$ ) and temperate forest ( $p = 0.06$ ) biomes. Such reduced  
265fluxes from warmed plots in the desert and temperate forests could be a consequence of soil drying, as  
266desert and temperate forest warmed plots had less soil moisture than control plots (3% and 13%  
267difference in soil moisture between warmed and control plots in desert and temperate forests,  
268respectively). However, reduced C substrate supply (14) and microbial acclimation (11, 13) could be  
269factors contributing to reduced fluxes at a given temperature in these biomes.

270

271The lack of difference in the respiration temperature response functions that we observe between warmed  
272versus control treatments within most biomes highlights a commonality among treatments often not  
273observed in single-site studies (10–14, 16, 17). This finding suggests that, in many regions of the globe,

274 simply measuring ambient respiration rates across a seasonal temperature gradient within a site will yield  
275 a similar temperature response to measurements made in a soil warming experiment (Fig. 2A). That is,  
276 seasonally-driven soil respiration-temperature response curves appear to be largely adequate at predicting  
277 how future warming will alter fluxes of CO<sub>2</sub> from soils to the atmosphere. Nevertheless, the relative roles  
278 of autotrophic versus heterotrophic soil respiration and how these processes change with warming  
279 remains poorly defined, but critical to understanding the strength of soil respiration feedbacks to climate  
280 change (30). In addition, it is unclear if the lack of difference in respiration response between control  
281 versus warmed treatments that we observe here will persist over the long-term, as the majority of the  
282 extant experiments have a relatively short duration (<5 years). Considering that significant interactions  
283 between experiment duration and warming treatment were observed in several biome types, long-term  
284 studies are necessary to fully disentangle interactions between warming, soil respiration and other  
285 ecosystem components (e.g., C substrate quality and quantity, nutrient and water availability, shifts in  
286 microbial community) (31).

287

288 Our conclusions are based on the largest and highest resolution global dataset of soil respiration response  
289 to experimental warming in existence, to our knowledge. The scale and magnitude of our dataset provide  
290 a unique opportunity to enhance our understanding of the sensitivity of global C stocks to warming.  
291 However, current understanding of how soil respiration will respond to warmer temperatures is restricted  
292 to the types of biomes where experimental warming studies occur, predominantly in North America and  
293 Europe. We stress the importance of expanding experimental warming studies to underrepresented  
294 regions, specifically the Arctic and the tropics. Northern latitudes are warming faster than other parts of  
295 the globe (32) and store extremely large amounts of C in soils (33). However, measurements of ecosystem  
296 respiration are far more common than those of soil respiration in the Arctic, making it challenging to  
297 tackle the roles of plant versus microbial responses to global change in these systems. Plant and microbial  
298 communities in tropical latitudes, where no experimental warming manipulations have been published,

299may be pushed past their physiological temperature optima with even slight warming. As we demonstrate  
300here, major changes to the shape of the seasonal response curve at higher ambient temperatures are  
301common, but not well defined. Thus, exploring the biome-specific responses of soil respiration as  
302temperatures shift beyond the historical range of variability is critical to understanding soil C dynamics in  
303a warmer world.

304

### 305**Methods**

306Data for this study were obtained from a combination of unpublished data and published literature values  
307(SI Appendix). Our synthesis generated a dataset that includes 3817 observations, from control (n=1812),  
308first (i.e., lowest or sole) level warming (n=1812), second (higher) level warming (n=179, four studies),  
309and third-level warming (n=14, one study) (Table S1).

310

#### 311*Evaluating Temperature Response Functions*

312Our models investigated the role of warming treatment, moisture, season, and warming duration in  
313controlling the temperature response function of soil respiration across biomes (SI Appendix). Individual  
314biomes represented by >100 data points were analyzed individually, which excluded montane meadow  
315and tundra ecosystems from being analyzed in isolation. Different multivariate models (Table S3) were  
316used to investigate different questions (SI Appendix). To evaluate whether respiration responses from the  
317warmed plots paralleled those from control plots, we used multiple linear regression to model respiration  
318as a function of soil temperature, with temperature as a continuous variable and warming treatment as a  
319binary categorical variable (warming (“W=1”) or control (“W”=0) treatment) (Table 1) (Model c and d,  
320Table S3). The categorical term was accompanied by an interaction with soil temperature, which allowed  
321us to analyze the influence of warming treatment on soil respiration while taking into account the  
322influence of temperature. Our criteria for the warming treatment interaction model selection (Model c vs d  
323in Table S3) were to 1) include only significant temperature terms, and 2) in models with significant  
324temperature terms, use Akaike information criterion (AIC) for model selection. We examined differences  
325in the temperature sensitivity between warmed and control plots using the first derivative of Eq. 1 (Table  
3261). This model is equivalent to  $R = \exp(\beta_0 + \beta_1 T + \beta_2 T^2)$ . However, for boreal forest and northern

327shrubland data, we used a log-linear model (i.e.,  $R = \exp(\beta_0 + \beta_1 T)$ ), because the second order temperature  
328term was not significant in models including the treatment interaction for these biomes (Fig. 1, Table S3).  
329These two models nearly approximate one another when  $T$  is  $<25$  °C, as in the cases of the boreal and  
330northern shrubland. Thus, the better fit of the monotonic log-linear model in the boreal forest and northern  
331shrubland biomes verifies our model choice of the log-quadratic function, as the log-quadratic function  
332shows a decreasing trend in soil respiration when temperature is higher than 25 °C. We calculated the  
333temperature threshold of maximum respiration in each biome by setting the derivate of Eq. 1 equal to zero  
334(Table 1). We also compared the AICs of Models c or d with models excluding warming treatment as a  
335predictor (Models a or b) to further investigate whether warming treatments had an effect on the  
336respiration response (Table S3); lower AICs for models without the warming treatment term indicate that  
337experimental warming does not alter the shape of the curve to a large degree. One southern shrubland site  
338(“Hungary”, Table S1) (34) contained limited data across its temperature gradient and therefore was not  
339included in our analysis of temperature response functions, although the model results with and without  
340inclusion of this site are included in Table S3 for comparison. To test for a difference in sensitivity  
341between biomes, we ran a multiple linear regression with biome type as a predictor and as an interaction  
342term with temperature (Model j in Table S3).

343

#### 344*Data Transformation and Model Diagnostics*

345Respiration data were transformed using natural log (which transforms exponential functions into linear  
346functions) in order to meet assumptions of regression models and to minimize the role of outliers in  
347altering the response functions. In turn, model outputs must be transformed to represent the actual values  
348(i.e., y-intercepts in Table 1 should be anti-logged to represent the soil respiration flux at 0°C). All model  
349residuals fit the assumption of normal distributions, except the models of all non-desert biomes together  
350and the temperate agriculture biome in isolation, where residuals were left-tail skewed. Because the desert  
351had significantly lower respiration rates compared to all other biomes (Fig. S4), models were never run  
352with all data together, as combined residuals were distinctly bi-modal. For all models included in our  
353analysis, co-linearity between soil moisture and soil temperature was evaluated by calculating variance

354inflation factors (VIF) (35), which were always <1.5, indicating extremely limited co-linearity. Power  
355analysis (36) revealed power = 1 for all models, except multivariate regression of the southern shrubland  
356warming interaction, where power=0.95.

357

### 358*Meta-Analysis*

359We used meta-analysis to quantify 1) how warming altered the magnitude of soil respiration and moisture  
360across sites (SI Appendix, Fig. S2) and 2) whether first-order temperature sensitivities were different  
361between warmed and control plots at the site level (SI Appendix, Fig. S8). We used the log response ratio  
362(RR) as our index of effect size (37) in determining how warming altered the magnitudes of temperature,  
363respiration, and moisture, which was calculated as the natural log proportional change in the means of the  
364treatment ( $X_T$ ) and the control ( $X_C$ ) groups:

365

$$366(3) \quad RR = \ln(X_T/X_C)$$

367

368and a random effect model (38). We used the standardized mean difference (raw mean difference divided  
369by pooled standard deviation) and random effect model to determine differences in temperature  
370sensitivities between treatments across sites. All meta-analysis was done using the metafor package in R  
371(39). Effect sizes with 95% confidence intervals overlapping zero indicate no significant effect of  
372warming on the factor in question. Values greater than zero indicate that warming increased soil  
373temperature, soil moisture, soil respiration, and/or temperature sensitivity, while values lower than zero  
374indicate that warming decreased these values. In studies with multiple levels of warming treatment (4  
375studies, Table S1), data from the warmest treatment were used to compute effect sizes. Data from Site ID  
37617(40) were excluded from Fig. S2 due to extremely high effect size (RR=0.95) and small difference in  
377temperature between treatments ( $\Delta T = 0.5$ ). All tests of significance level used alpha ( $\alpha$ ) of 0.05. All  
378analysis and statistics were done in R (version 3.2.0) (41).

379

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391

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398

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531  
532

### 533Figure Legends

534Fig. 1. Ln respiration ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) as a function of soil temperature ( $^{\circ}\text{C}$ ) across biome types. Data are  
535instantaneous measurements from control (blue circles) and warmed (red circles) treatments, with best fit  
536regression lines fitted through control and warmed values (for coefficients, see Table 1). Temperature  
537sensitivity in control versus warmed plots was not significantly different, except in desert and boreal  
538forest biomes (Table 1). Note, Y-axis scales are all equal, except for desert, which had lower respiration  
539rates compared to all other biomes (Fig. S4). For partial regression plots of respiration on temperature and  
540moisture, see Fig. S7.

541  
542Fig. 2. Conceptual diagram of instantaneous delta respiration ( $\Delta R$ ) and temperature ( $\Delta T$ ) response  
543between warmed (red symbols) and control (blue symbols) treatments on a given day of measurements at  
544the lower end of the temperature range ( $<25^{\circ}\text{C}$ ). Circles represent sampling date in spring, while stars  
545represent sampling date in summer. A) All non-desert biomes, except boreal forests: Despite the increase

546of respiration with warming on a given day of measurements, the temperature response function (the  
547dotted line) across the different colors (the warming effect) is similar to that across the different symbols  
548(the seasonal temperature variation). B) Boreal forests: Warmed plots (dashed line) had lower sensitivity  
549compared to control plots (solid line). However, no significant differences in the y-intercept were  
550observed c) Desert: Warmed plots (dashed line) had a lower y-intercept, but higher sensitivity compared  
551to control plots (solid line). D) Temperate forest: Despite displaying similar temperature sensitivities, y-  
552intercepts of warmed plots (dashed line) were marginally ( $p=0.06$ ) lower than control plots (solid line).  
553Delta response was always calculated as warmed value minus control value.

554

555Fig. 3. Difference in respiration ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) between warmed and control plots normalized by degree  
556of warming ( $\Delta T$  °C), binned by amount of soil desiccation with warming (soil moisture content warmed  
557plots divided by soil moisture content control plots) across the entire dataset. X axis values  $<1$  indicate  
558warmed plots have less moisture available than control plots. Y axis values  $<0$  indicate that respiration  
559rates were lower from warmed plots, despite warmer soil temperatures. Respiration data were not log  
560transformed. Delta respiration was always calculated as warmed values minus control values.  
561