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6

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62
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64response

65
66**Abstract:**

67The respiratory release of carbon dioxide (CO₂) 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 (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: β_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°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 β_1 and β_2 in Table 1), we also evaluated differences in the
177magnitude of respiration rates between treatments (denoted by the y-intercept, β_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 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 CO_2 from warmed plots compared to control plots at a given temperature
183(β_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

220were actually lower from warmed plots, despite experiencing higher soil temperatures (Fig. 3; see SI
221Appendix).
222
223*A Universal Decline in Temperature Sensitivity at Seasonally Elevated Temperatures*
224Our dataset of instantaneous soil respiration and temperature measurements allowed us to evaluate the
225temperature response function of soil respiration across biomes. We observed a similar Gaussian response
226pattern (expressed as a log-quadratic function, Eq. 1) in the soil respiration response across temperature
227gradients in most non-desert biomes, with respiration rates increasing with temperature up to ~25°C (23-
22834°C, depending on the biome), above which respiration rates level off and decrease (Table 1, Fig. 1, Fig.
229S4). This common functional form applies to all the non-desert biomes that reach temperatures above
23025°C (thus, excluding boreal forests and northern shrublands), despite variation in temperature response
231function parameters among biomes (Table 1, Fig. S4). Low soil moisture at high temperatures partially
232explains this decreasing sensitivity at elevated temperatures (Fig. S3). Nevertheless, respiration rates
233continue to reach a plateau or even slightly decrease at elevated soil temperatures, even under the wettest
234conditions in most biomes (Fig. S3, Table S4). In turn, we hypothesize that decreased autotrophic demand
235for ATP and enzyme capacity (27), in addition to microbial enzymatic activities reaching their
236physiological thermal limit (13, 28), play important roles in the reduced temperature sensitivity under
237warmer conditions. The desert was again unique among biomes in that control plots did not display
238decreased sensitivity at such high temperatures, and warmed plots displayed dramatically higher
239temperature threshold for reduced respiration (55°C) (Table 1, Fig. 1). The fundamentally different
240response of soil respiration to temperature in deserts could be due to several factors, namely higher
241respiration temperature optima and maxima of plant and microbial communities in the desert compared to
242other ecosystems (28), or the importance of abiotic (i.e., UV-driven) decomposition as a major component
243of 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 CO₂ 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 (α) 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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399References

400

4011. Schlesinger WH, Bernhardt E (2013) *Biogeochemistry, An Analysis of Global Change*. (Elsevier).
402 3rd Ed.
403
4042. Hashimoto S, et al. (2015) Global spatiotemporal distribution of soil respiration modeled using a
405 global database. *Biogeosciences* 12(13):4121-4132.
406
4073. Bond-Lamberty B, Thomson A (2010) Temperature-associated increases in the global soil
408 respiration record. *Nature* 464(7288):579–582.
409
4104. Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and
411 feedbacks to climate change. *Nature* 440(7081):165–73.
412
4135. Friedlingstein P, et al. (2006) Climate–Carbon Cycle Feedback Analysis: Results from the C 4 MIP
414 Model Intercomparison. *J Clim* 19(14):3337–3353.
415
4166. Rustad L, et al. (2001) A meta-analysis of the response of soil respiration, net nitrogen
417 mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*
418 126(4):543–562.
419

4207. Lu M, et al. (2013) Responses of ecosystem carbon cycle to experimental warming: a meta-
421 analysis. *Ecology* 94(3):726–738.
422
4238. Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems
424 to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob*
425 *Chang Biol* 17(2):927–942.
426
4279. Suseela V, Conant RT, Wallenstein MD, Dukes JS (2012) Effects of soil moisture on the
428 temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change
429 experiment. *Glob Chang Biol* 18(1):336–348.
430
43110. Reynolds LL, Johnson BR, Pfeifer-Meister L, Bridgham SD (2015) Soil respiration response to
432 climate change in Pacific Northwest prairies is mediated by a regional Mediterranean climate
433 gradient. *Glob Chang Biol* 21(1):487–500.
434
43511. Luo Y, Wan S, Hui D, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall
436 grass prairie. *Nature* 413(6856):622–625.
437
43812. Bradford MA, et al. (2008) Thermal adaptation of soil microbial respiration to elevated
439 temperature. *Ecol Lett* 11(12):1316–27.
440
44113. Crowther TW, Bradford MA (2013) Thermal acclimation in widespread heterotrophic soil
442 microbes. *Ecol Lett* 16(4):469–477.
443
44414. Melillo JM, et al. (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*
445 (80-) 298(5601):2173–2176.
446
44715. Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions
448 caused by acclimation or substrate loss? *Glob Chang Biol* 10(11):1870–1877.
449
45016. Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover
451 to warming. *Nature* 433(7023):298–301.
452
45317. Hartley IP, Heinmeyer A, Ineson P (2007) Effects of three years of soil warming and shading on
454 the rate of soil respiration: substrate availability and not thermal acclimation mediates observed
455 response. *Glob Chang Biol* 13(8):1761–1770.
456
45718. Vicca S, et al. (2009) No signs of thermal acclimation of heterotrophic respiration from peat soils
458 exposed to different water levels. *Soil Biol Biochem* 41(9): 2014-2016.
459
46019. Jing X, et al. (2014) No temperature acclimation of soil extracellular enzymes to experimental
461 warming in an alpine grassland ecosystem on the Tibetan Plateau. *Biogeochemistry* 117(1):39–54.
462
46320. Hartley IP, Hopkins DW, Garnett MH, Sommerkorn M, Wookey PA (2008) Soil microbial

- 464 respiration in arctic soil does not acclimate to temperature. *Ecol Lett* 11(10):1092–1100.
465
46621. Lloyd J, Taylor JA (1994) On the Temperature Dependence of Soil Respiration. *Funct Ecol*:315–
467 323.
468
46922. Tjoelker MG, Oleksyn J, Reich PB (2001) Modelling respiration of vegetation: evidence for a
470 general temperature-dependent Q₁₀. *Glob Chang Biol* 7(2):223–230.
471
47223. Exbrayat J-F, Pitman AJ, Zhang Q, Abramowitz G, Wang Y-P (2013) Examining soil carbon
473 uncertainty in a global model: response of microbial decomposition to temperature, moisture and
474 nutrient limitation. *Biogeosciences* 10(11):7095–7108.
475
47624. Crowther TW, et al. (2015) Biotic interactions mediate soil microbial feedbacks to climate change.
477 *Proc Natl Acad Sci* 112(22):7033–7038.
478
47925. Xu W, et al. (2013) A meta-analysis of the response of soil moisture to experimental warming.
480 *Environ Res Lett* 8(4):044027.
481
48226. Sierra CA, Trumbore SE, Davidson EA, Vicca S, Janssens I (2015) Sensitivity of decomposition
483 rates of soil organic matter with respect to simultaneous changes in temperature and moisture. *J*
484 *Adv Model Earth Syst* 7(1):335–356.
485
48627. Atkin OK, Edwards EJ, Loveys BR (2000) Response of root respiration to changes in temperature
487 and its relevance to global warming. *New Phytol* 147(1):141–154.
488
48928. Balsler TC, Wixon DL (2009) Investigating biological control over soil carbon temperature
490 sensitivity. *Glob Chang Biol* 15(12):2935–2949.
491
49229. Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by
493 photodegradation. *Nature* 442(7102):555–558.
494
49530. Tang J, Misson L, Gershenson A, Cheng W, Goldstein AH (2005) Continuous measurements of
496 soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada
497 Mountains. *Agric For Meteorol* 132(3):212–227.
498
49931. Melillo JM, et al. (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets.
500 *Proc Natl Acad Sci U S A* 108(23):9508–12.
501
50232. Serreze MC, Barry RG (2011) Processes and impacts of Arctic amplification: A research synthesis.
503 *Glob Planet Change* 77(1-2):85–96.
504
50533. Tarnocai C, et al. (2009) Soil organic carbon pools in the northern circumpolar permafrost region.
506 *Global Biogeochem Cycles* 23(2). doi:10.1029/2008GB003327.
507

50834. Lellei-Kovács E, et al. (2008) Experimental warming does not enhance soil respiration in a
509 semiarid temperate forest-steppe ecosystem. *Community Ecol* 9(1):29–37.
510
51135. Fox J, Monette G (1992) Generalized collinearity diagnostics. *JASA* 87:178–183.
512
51336. Cohen J (1988) *Statistical power analysis for the behavioral sciences (2nd ed.)* (Lawrence
514 Erlbaum, Hillsdale, NJ).
515
51637. Hedges L V., Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental
517 ecology. *Ecology* 80(4):1150–1156.
518
51938. Curtis PS, Wang X (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form,
520 and physiology. *Oecologia* 113(3):299–313.
521
52239. Viechtbauer W (2010) Conducting Meta-Analyses in R with the metafor Package. *J Stat Softw*
523 36(3):1–48.
524
52540. Flanagan LB, Sharp EJ, Letts MG (2013) Response of plant biomass and soil respiration to
526 experimental warming and precipitation manipulation in a Northern Great Plains grassland. *Agric*
527 *For Meteorol* 173:40–52.
528
52941. R Core Team (2015) R: A language and environment for statistical computing. Available at:
530 www.r-project.org.
531
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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 (ΔR) and temperature (ΔT) 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 (ΔT °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