Temperature response of soil respiration largely unaltered with experimental warming

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The respiratory release of carbon dioxide (CO_2) from soil is a major yet poorly understood flux in the global carbon cycle. Climatic warming is hypothesized to increase rates of soil respiration, potentially fueling further increases in global temperatures. However, despite considerable scientific attention in recent decades, the overall response of soil respiration to anticipated climatic warming remains unclear. We synthesize the largest global dataset to date of soil respiration, moisture, and temperature measurements, totaling >3,800 observations representing 27 temperature manipulation studies, spanning nine biomes and over 2 decades of warming. Our analysis reveals no significant differences in the temperature sensitivity of soil respiration between control and warmed plots in all biomes, with the exception of deserts and boreal forests. Thus, our data provide limited evidence of acclimation of soil respiration to experimental warming in several major biome types, contrary to the results from multiple single-site studies. Moreover, across all nondesert biomes, respiration rates with and without experimental warming follow a Gaussian response, increasing with soil temperature up to a threshold of ~25 °C, above which respiration rates decrease with further increases in temperature. This consistent decrease in temperature sensitivity at higher temperatures demonstrates that rising global temperatures may result in regionally variable responses in soil respiration, with colder climates being considerably more responsive to increased ambient temperatures compared with warmer regions. Our analysis adds a unique cross-biome perspective on the temperature response of soil respiration, information critical to improving our mechanistic understanding of how soil carbon dynamics change with climatic warming.

soil respiration | climate change | experimental warming | temperature sensitivity | biome

Compared with anthropogenic emissions, roughly nine times more carbon dioxide (CO_2) is released from soils to the atmosphere via soil respiration on an annual basis (1). Both plant root respiration and microbial respiration during the decomposition of organic matter contribute to this efflux of carbon (C) from soils, cumulatively

Significance

One of the greatest challenges in projecting future shifts in the global climate is understanding how soil respiration rates will change with warming. Multiple experimental warming studies have explored this response, but no consensus has been reached. Based on a global synthesis of 27 experimental warming studies spanning nine biomes, we find that although warming increases soil respiration rates, there is limited evidence for a shifting respiration response with experimental warming. We also note a universal decline in the temperature sensitivity of respiration at soil temperatures >25 °C. Together, our data indicate that future respiration rates are likely to follow the current temperature response function, but higher latitudes will be more responsive to warmer temperatures.

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estimated at ~90 Pg C·yr^{-1} (2). Rising temperatures are expected to stimulate soil respiration (3), both by accelerating rates of C cycling via autotrophic respiration and by providing a potentially powerful positive feedback to climatic warming via heterotrophic decomposition of organic matter. However, due to a suite of factors beyond temperature that control soil respiration rates (e.g., soil moisture, C substrate quality and quantity, and nutrient availability), the interaction between temperature and respiration remains uncertain (3–5). As such, soil respiration is a major and poorly understood flux in the global C cycle.

Experimental warming of soils is one approach used to understand the complex relationship between respiration and temperature because it allows scientists to separate the effects of warming from confounding environmental variation (e.g., soil type and plant species composition). Results of experimental studies reveal a range of responses of soil respiration to warming, with few unifying trends observed across biomes (6–8). Although warming has been shown to stimulate soil respiration within many sites, several studies show neutral or even negative responses to warming, often attributed to moisture limitation (9, 10), shifts in microbial physiological response or composition (11–13), or depletion of labile C pools (14–17). As such, multiple single-site analyses find evidence of acclimation (sometimes termed thermal adaptation) of soil respiration to experimental warming (10–14, 16, 17), although others report no evidence for such shifts in respiration response over time (18–20). Moreover, the response of soil respiration to temperature is not consistent across all temperature ranges, because the temperature sensitivity of respiration typically decreases under warmer conditions (21, 22). As a result, the interaction between soil respiration and climate warming remains one of the greatest sources of uncertainty in climate projections, despite being an important boundary condition in current Earth system models (ESMs) (4, 23, 24).

Current understanding of how soil respiration responds to experimental warming stems from single-site warming experiments or traditional metaanalyses based on average or cumulative soil respiration values in control versus warmed plots. To date, no cross-biome synthesis efforts of experimental warming have evaluated how temperature and moisture interact at high temporal frequencies to determine rates of soil respiration. Therefore, the goals of this study were to (*i*) synthesize the results of experimental warming studies to understand how the temperature response function of soil respiration changes with experimental warming treatments across biomes, with respect to both warming duration and seasonality; (*ii*) investigate the role of soil moisture in driving these responses; and (*iii*) examine whether a uniform model exists that can describe the response of soil respiration to temperature across all biomes. To do this, we generated an unprecedented global dataset of >3,800 observations of instantaneous soil respiration, soil temperature, and soil moisture based on data from 27 individual warming experiments spanning nine biomes and up to 22 y of experimental warming. Our analysis is unique among soil respiration synthesis efforts focused on warming experiments, in that we used instantaneous observations (i.e., plot-scale measurements of soil respiration averaged from individual sampling events) rather than annual or monthly averaged values to evaluate the temperature response function of soil respiration and the interaction with soil moisture at the global scale.

Table 1. Model parameters of soil respiration (natural log, in μmol C·m^{-2}·s^{-1}) (R) as a function of soil temperature (T) (°C), evaluating the interaction with warming treatment

Parameters for model: $\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$

Model	$\gamma_0 \pm$ SE	$\gamma_1 \pm$ SE	$\gamma_2 \pm$ SE	n	R^2	T at R max
All biomes except desert					0.39	
Control treatment	−1.292 ± 0.079	0.204 ± 0.011	−0.0042 ± 0.0003	1075		24.2
Warming treatment	−1.309 ± 0.119	0.205 ± 0.015	−0.0040 ± 0.0005	1268		25.3
Desert					0.42	
Control treatment	−2.571 ± 0.062	0.019 ± 0.008	0.0004 ± 0.0002	737		na
Warming treatment	−3.431 ± 0.088	0.072 ± 0.011	−0.0007 ± 0.0003	737		55.4
Boreal forest					0.84	
Control treatment	−0.063 ± 0.045	0.109 ± 0.0035	ns	160		na
Warming treatment	−0.010 ± 0.059	0.093 ± 0.0043	ns	306		na
Temperate forest					0.54	
Control treatment	−0.813 ± 0.166	0.160 ± 0.024	−0.0025 ± 0.0008	239		32.0
Warming treatment	−1.485 ± 0.349	0.197 ± 0.042	−0.0031 ± 0.0012	258		31.8
Northern shrubland					0.63	
Control treatment	−1.188 ± 0.081	0.142 ± 0.008	ns	172		na
Warming treatment	−1.153 ± 0.115	0.141 ± 0.012	ns	172		na
Southern shrubland					0.25	
Control treatment	−1.420 ± 0.421	0.157 ± 0.040	−0.0027 ± 0.0009	51		29.1
Warming treatment	−0.485 ± 0.642	0.066 ± 0.061	−0.0010 ± 0.0013	51		34.4
Grassland					0.51	
Control treatment	−1.517 ± 0.166	0.200 ± 0.024	−0.0036 ± 0.0006	269		27.8
Warming treatment	−1.558 ± 0.244	0.205 ± 0.030	−0.0036 ± 0.0008	297		28.7
Temperate agriculture					0.73	
Control treatment	−3.012 ± 0.173	0.305 ± 0.030	−0.0066 ± 0.0012	131		23.3
Warming treatment	−3.091 ± 0.291	0.313 ± 0.046	−0.0065 ± 0.0016	131		24.2

Models run with data from both treatments, with parameters for each treatment calculated using the model equation. Model equation: $\ln(R) \approx (\alpha_o + \alpha_1 T + \alpha_2 T^2) + (\beta_o + \beta_1 T + \beta_2 T^2)\, W$, with $\gamma_i = \alpha_i + \beta_i$. warming treatment ($W$ = 1) or control treatment (W = 0). n, sample size; na, not applicable; ns, not significant; R^2, correlation coefficient; and T at R max, soil temperature (°C) when $d\ln(R)/dT = 0$. Parameter units: γ_0, ln μmol C·m^{-2}·s^{-1}; γ_1, °C^{-1}; and γ_2, °C^{-2}. Bold biome names indicate significant interactions with treatment. All models are significant (P < 0.001). For comparison of model fits, see *SI Appendix*, Table S3. For model parameters including moisture, see *SI Appendix*, Table S2.

Results and Discussion

Evaluating Differences in Temperature Response Function with Experimental Warming. We first sought to determine whether respiration responses from experimentally warmed plots paralleled those of control plots over the seasonal range of temperature variation at the biome scale. After evaluating multiple functional forms, we used a log-quadratic temperature response function because this was the best supported model for most biomes (*SI Appendix*, Table S3):

$$\ln(R) = \gamma_0 + \gamma_1 T + \gamma_2 T^2, \qquad [1]$$

where R is soil respiration (μmol C·m^2·s^{-1}) and T is soil temperature (°C). Using this basic model, we included warming treatment as an interaction term to evaluate differences in the temperature response between warmed versus control plots (Table 1). We used this log-quadratic model for all biomes (model d in *SI Appendix*, Table S3), except the boreal forest and northern shrublands, where a log-linear model [$\ln(R) = \gamma_0 + \gamma_1 T$] was the better fit when including the warming treatment interaction term (model c in *SI Appendix*, Table S3). We evaluated two specific features of the temperature response function: (*i*) the temperature sensitivity (i.e., the shape of the curve denoted by the first derivative of Eq. **1**: $\equiv d\ln(R)/dT$; Table 1) and (*ii*) the magnitude of the respiration response when $T = 0$ (i.e., the *y* intercept of Eq. **1**: γ_0; Table 1).

Including data from all warming durations and seasons, we observed no significant differences in the temperature sensitivity of soil respiration between warmed or control treatments within each individual biome, with the exception of boreal forest and desert (Table 1 and Fig. 1). In the boreal forest and desert biomes, where significant differences in the temperature sensitivities between warmed versus control plots were observed, trends between treatments were not consistent; compared with control plots, warmed plots in the boreal forest had consistently lower temperature sensitivity, whereas in the desert, warmed plots had slightly higher temperature sensitivity at temperatures <24 °C but lower sensitivity at temperatures >24 °C (*SI Appendix*, Fig. S1, and Fig. 2).

The lack of difference in the temperature sensitivity of respiration between control and warmed plots in all biomes except the desert and boreal forests cannot be attributed to an insufficient magnitude of warming. Across our studies, the desert plots were subjected to a relatively small degree of warming (0.34 °C on average) but showed the largest differences in sensitivity between treatments. By contrast, grasslands experienced larger amounts of experimental warming (1.9 °C on average) (*SI Appendix*, Table S1) but did not display altered sensitivity between treatments.

In addition to evaluating changes in the temperature sensitivities with respiration (i.e., the shape of the temperature response function denoted by γ_1 and γ_2 in Table 1), we also evaluated differences in the magnitude of respiration rates between treatments (denoted by the *y* intercept, γ_0, in Table 1). The desert was the only biome to display a significantly different *y* intercept between warmed versus control plots, with warmed plots having a lower *y* intercept than control plots. Thus, compared with desert control plots, warmed plots emitted less CO_2 at a given temperature, despite being generally more sensitive to changes in soil temperature (Fig. 2*C*). Similar to the

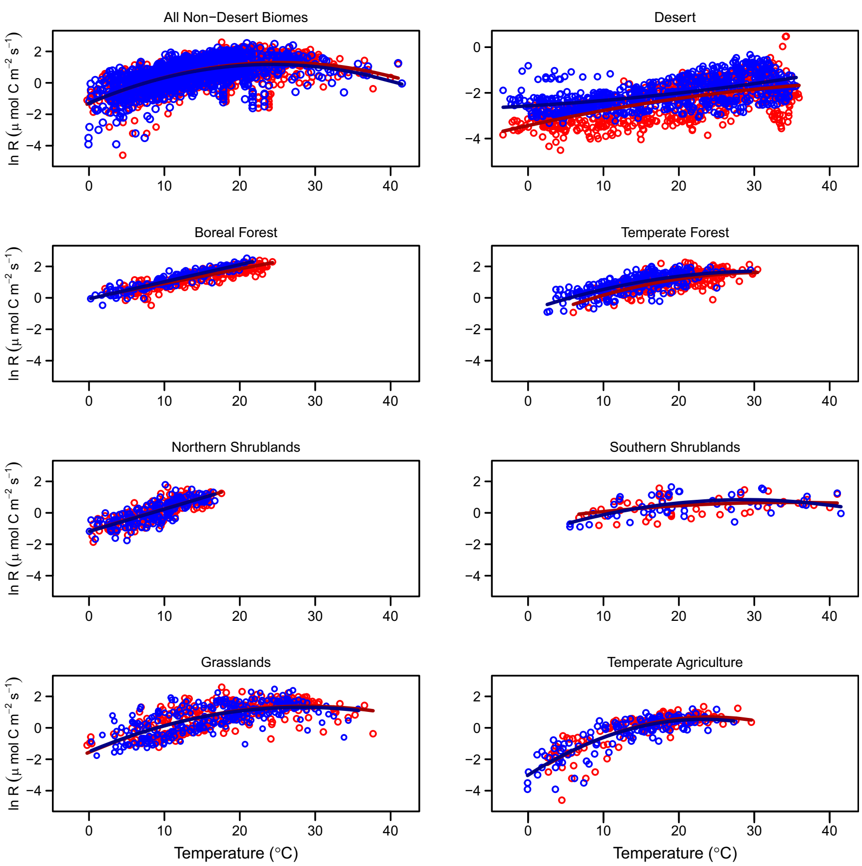

Fig. 1. Ln respiration (μmol C·m^{-2}·s^{-1}) as a function of soil temperature (°C) across biome types. Data are instantaneous measurements from control (blue circles) and warmed (red circles) treatments, with best fit regression lines fitted through control and warmed values (for coefficients, see Table 1). Temperature sensitivity in control versus warmed plots was not significantly different, except in desert and boreal forest biomes (Table 1). Note that *y* axis scales are all equal, except for desert, which had lower respiration rates compared with all other biomes (*SI Appendix*, Fig. S4). For partial regression plots of respiration on temperature and moisture, see *SI Appendix*, Fig. S7.

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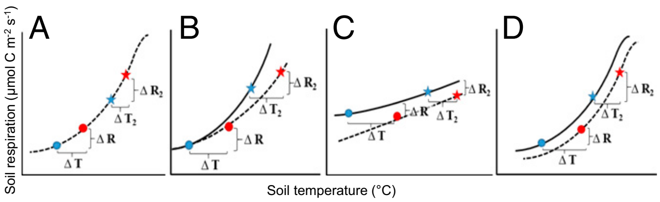

Fig. 2. Conceptual diagram of instantaneous delta respiration (ΔR) and temperature (ΔT) response between warmed (red symbols) and control (blue symbols) treatments on a given day of measurements at the lower end of the temperature range (<25 °C). Circles represent sampling date in spring, whereas stars represent sampling date in summer. (*A*) All nondesert biomes, except boreal forests. Despite the increase of respiration with warming on a given day of measurements, the temperature response function (the dashed line) across the different colors (the warming effect) is similar to that across the different symbols (the seasonal temperature variation). (*B*) Boreal forests. Warmed plots (dashed line) had lower sensitivity compared with control plots (solid line). However, no significant differences in the *y* intercept were observed. (*C*) Desert. Warmed plots (dashed line) had a lower *y* intercept but higher sensitivity compared with control plots (solid line). (*D*) Temperate forest. Despite displaying similar temperature sensitivities, *y* intercepts of warmed plots (dashed line) were marginally (P = 0.06) lower than control plots (solid line). Delta response was always calculated as warmed value minus control value.

desert, temperate forests showed a marginally significant (P = 0.06) trend of emitting less CO_2 from warmed plots compared with control plots at a given temperature (γ_0 in Table 1 and Fig. 2*D*). Therefore, although the shapes of the temperature response functions with and without experimental warming were similar in temperate forests, the magnitude of respiration from warmed plots was typically lower than from control plots. In turn, despite little difference in temperature sensitivities between treatments, the reduced fluxes from warmed plots provide evidence of acclimation to experimental warming in the temperate forest.

The lack of difference in temperature response between warmed and control plots in most biomes persists regardless of warming duration or season. For example, by partitioning the observations into categories of warming duration (<2, 2–5, 5–10, and >10 y) and season (growing, nongrowing, and shoulder) and running the model described by Eq. **1**, we continued to find no differences in the temperature response function between warmed and control plots, except in the boreal forest and desert. We then ran two additional multivariate regression models that added duration or season as predictors of soil respiration with interactions with warming treatment to our temperature response functions (*SI Appendix*, Table S3). Here we found similar outcomes, with significant interactions between season and warming treatment observed only in the boreal forest and desert. Significant interactions between duration and warming treatment were also observed in the boreal forest and desert, in addition to the temperate forest and northern shrubland. Thus, over time, respiration from warmed plots appears to respond differently to temperature compared with respiration from control plots in these four biomes (*SI Appendix*).

Together, our results show a similar temperature response of soil respiration from warmed and control plots across several major biome types, providing limited support of acclimation with experimental warming at the biome scale, across seasons and often independent of warming duration. However, the pronounced difference in the temperature response of respiration between treatments in the boreal forest and desert ecosystems suggests that acclimation of soil communities to warmer conditions is likely to have greater consequences for soil C dynamics in these biomes.

Changes in Soil Moisture with Experimental Warming. Reductions in soil moisture that accompany experimental warming can influence the soil respiration response to elevated temperatures (25, 26). Using log response ratios as our index of effect size, we found that soil moisture was significantly ($P < 0.05$) reduced in warmed plots across all sites, with the magnitude of this soil drying being weakly correlated to the amount of soil warming at each site (P = 0.08; r = –0.32; *SI Appendix*, Fig. S2*A*). In situations of severe soil drying, we found evidence that soil respiration becomes limited by moisture, which in turn changes the respiration–temperature relationship. For example, not only are the lowest moisture quartiles typically associated with a depressed temperature response function (*SI Appendix*, Fig. S3; γ_0, γ_1, and γ_2 in *SI Appendix*, Table S4), but the magnitude of the respiration response to warming decreased linearly with the degree of soil drying across our entire dataset ($P < 0.05$; Fig. 3). In fact, when moisture of warmed plots dropped by at least 30% relative to control plots, respiration rates were actually lower from warmed plots, despite experiencing higher soil temperatures (Fig. 3 and *SI Appendix*).

A Universal Decline in Temperature Sensitivity at Seasonally Elevated Temperatures. Our dataset of instantaneous soil respiration and temperature measurements allowed us to evaluate the temperature response function of soil respiration across biomes. We observed a similar Gaussian response pattern (expressed as a log-quadratic function; Eq. **1**) in the soil respiration response across temperature gradients in most nondesert biomes, with respiration rates increasing with temperature up to ∼25 °C (23–34 °C, depending on the biome), above which respiration rates level off and decrease (Table 1; Fig. 1; and *SI Appendix*, Fig. S4). This common functional form applies to all of the nondesert biomes that reach temperatures above 25 °C (thus excluding boreal forests and northern shrublands), despite variation in temperature response function parameters among biomes (Table 1 and *SI Appendix*, Fig. S4). Low soil moisture at high temperatures partially explains this decreasing sensitivity at elevated temperatures (*SI Appendix*, Fig. S3). Nevertheless, respiration rates continue to reach a plateau or even slightly decrease at elevated soil temperatures, even under the wettest conditions in most biomes (*SI Appendix*, Fig. S3 and Table S4). In turn, we hypothesize that decreased autotrophic demand for ATP and enzyme capacity (27), in addition to microbial enzymatic activities reaching their physiological thermal limit (13, 28), play important roles in the reduced temperature sensitivity under warmer conditions. The desert was again unique among biomes in that control plots did not display decreased sensitivity at such high temperatures, and warmed plots displayed dramatically higher temperature threshold for reduced respiration (55 °C) (Table 1 and Fig. 1). The fundamentally different response of soil respiration to temperature in deserts could be due to several

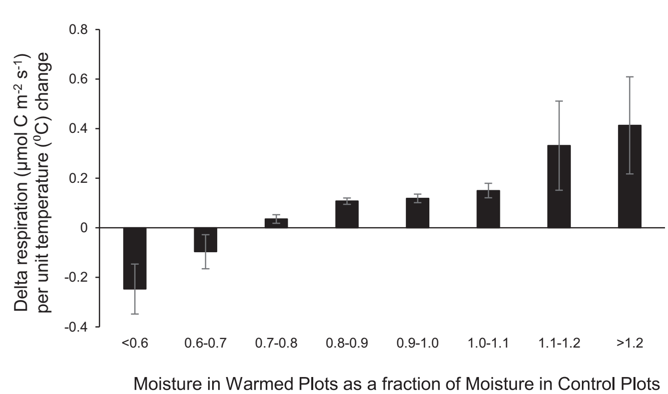

Fig. 3. Difference in respiration (μmol C·m^{-2}·s^{-1}) between warmed and control plots normalized by degree of warming (ΔT, °C), binned by amount of soil desiccation with warming (soil moisture content warmed plots divided by soil moisture content control plots) across the entire dataset. *x* axis values <1 indicate warmed plots have less moisture available than control plots. *y* axis values <0 indicate that respiration rates were lower from warmed plots, despite warmer soil temperatures. Respiration data were not log transformed. Delta respiration was always calculated as warmed values minus control values.

factors, namely, higher respiration temperature optima and maxima of plant and microbial communities in the desert compared with other ecosystems (28) or the importance of abiotic (i.e., UV-driven) decomposition as a major component of litter decomposition in deserts (29).

Regionally Variable Response to Global Change. The reversal in the direction of the temperature response at temperatures greater than ∼25 °C observed in most nondesert biomes suggests that warmer global temperatures will result in regionally variable responses in soil respiration rates because different regions occupy different positions on the shared temperature–response function. Compared with lower latitudes, higher-latitude sites more often experience soil temperatures <25 °C, where the relationship between soil respiration and temperature is nearly exponential. As such, our data indicate that higher-latitude sites will be more responsive to increased ambient temperatures compared with warmer regions that more frequently experience soil temperatures >25 °C. Our results also support the idea that models of soil respiration based on fixed parameters (e.g., fixed Q_{10} in an exponential function) are inadequate for describing the respiration response across the full temperature range (4, 21, 22). Without accounting for reduced temperature sensitivity at elevated temperatures, ESMs will likely overestimate soil respiration rates in response to climate warming, particularly from lower-latitude regions.

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

The lack of difference in the respiration temperature response functions that we observe between warmed versus control treatments within most biomes highlights a commonality among treatments often not observed in single-site studies (10–14, 16, 17). This finding suggests that in many regions of the globe, simply measuring ambient respiration rates across a seasonal temperature gradient within a site will yield a similar temperature response to measurements made in a soil warming experiment (Fig. 2*A*). That is, seasonally driven soil respiration–temperature response curves appear to be largely adequate at predicting how future warming will alter fluxes of CO_2 from soils to the atmosphere. Nevertheless, the relative roles of autotrophic versus heterotrophic soil respiration and how these processes change with warming remains poorly defined but critical to understanding the strength of soil respiration feedbacks to climate change (30). In addition, it is unclear if the lack of difference in respiration response between control versus warmed treatments that we observe here will persist over the long term because the majority of the extant experiments have a relatively short duration (<5 y). Considering that significant interactions between experiment duration and warming treatment were observed in several biome types, long-term studies are necessary to fully disentangle interactions between warming, soil respiration, and other ecosystem components (e.g., C substrate quality and quantity, nutrient and water availability, and shifts in microbial community) (31).

Our conclusions are based on the largest and highest-resolution global dataset of soil respiration response to experimental warming in existence, to our knowledge. The scale and magnitude of our dataset provide a unique opportunity to enhance our understanding of the sensitivity of global C stocks to warming. However, current understanding of how soil respiration will respond to warmer temperatures is restricted to the types of biomes where experimental warming studies occur, predominantly in North America and Europe. We stress the importance of expanding experimental warming studies to underrepresented regions, specifically the Arctic and the tropics. Northern latitudes are warming faster than other parts of the globe (32) and store extremely large amounts of C in soils (33). However, measurements of ecosystem respiration are far more common than those of soil respiration in the Arctic, making it challenging to tackle the roles of plant versus microbial responses to global change in these systems. Plant and microbial communities in tropical latitudes, where no experimental warming manipulations have been published, may be pushed past their physiological temperature optima with even slight warming. As we demonstrate here, major changes to the shape of the seasonal response curve at higher ambient temperatures are common but not well defined. Thus, exploring the biome-specific responses of soil respiration as temperatures shift beyond the historical range of variability is critical to understanding soil C dynamics in a warmer world.

Methods

Data for this study were obtained from a combination of unpublished data and published literature values (*SI Appendix*). Our synthesis generated a dataset that includes 3,817 observations, from control (n = 1,812), first-level (i.e., lowest-level or sole) warming (n = 1,812), second- (higher-) level warming (n = 179, four studies), and third-level warming (n = 14, one study) (*SI Appendix*, Table S1).

Evaluating Temperature Response Functions. Our models investigated the role of warming treatment, moisture, season, and warming duration in controlling the temperature response function of soil respiration across biomes (*SI Appendix*). Individual biomes represented by >100 data points were analyzed individually, which excluded montane meadow and tundra ecosystems from being analyzed in isolation. Different multivariate models (*SI Appendix*, Table S3) were used to investigate different questions (*SI Appendix*). To evaluate whether respiration responses from the warmed plots paralleled those from control plots, we used multiple linear regression to model respiration as a function of soil temperature, with temperature as a continuous variable and warming treatment as a binary categorical variable (Table 1) (models c and d in *SI Appendix*, Table S3). The categorical term was accompanied by an interaction with soil temperature, which allowed us to analyze the influence of warming treatment on soil respiration while taking into account the influence of temperature. Our criteria for the warming treatment interaction model selection (model c vs. d in *SI Appendix*, Table S3) were to (*i*) include only significant temperature terms and (*ii*) in models with significant temperature terms, use the Akaike information criterion (AIC) for model selection. We examined differences in the temperature sensitivity between warmed and control plots using the first derivative of Eq. **1** (Table 1). This model is equivalent to $R = \exp(\gamma_0 + \gamma_1 T + \gamma_2 T^2)$. However, for boreal forest and northern shrubland data, we used a log-linear model [i.e., $R = \exp(\gamma_0 + \gamma_1 T)$] because the second-order temperature term was not significant in models including the treatment interaction for these biomes (Fig. 1 and *SI Appendix*, Table S3). These two models nearly approximate one another when T is <25 °C, as in the cases of the boreal and northern shrubland. Thus, the better fit of the monotonic log-linear model in the boreal forest and northern shrubland biomes verifies our model choice of the log-quadratic function because the log-quadratic function shows a decreasing trend in soil respiration when temperature is higher than 25 °C. We calculated the temperature threshold of maximum respiration in each biome by setting the derivate of Eq. **1** equal to zero (Table 1). We also compared the AICs of model c or d with models excluding warming treatment as a predictor (model a or b) to further investigate whether warming treatments had an effect on the respiration response (*SI Appendix*, Table S3); lower AICs for models without the warming treatment term indicate that experimental warming does not alter the shape of the curve to a large degree. One southern shrubland site (Hungary; *SI Appendix*, Table S1) (34) contained limited data across its temperature gradient and therefore was not included in our analysis of southern shrubland temperature response functions, although the model results with and without inclusion of this site are included in *SI Appendix*, Table S3, for comparison. To test for a difference in sensitivity between biomes, we ran a multiple linear

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regression with biome type as a predictor and as an interaction term with temperature (model j in *SI Appendix*, Table S3).

Data Transformation and Model Diagnostics. Respiration data were transformed using natural log (which transforms exponential functions into linear functions) to meet assumptions of regression models and to minimize the role of outliers in altering the response functions. In turn, model outputs must be transformed to represent the actual values (i.e., *y* intercepts in Table 1 should be antilogged to represent the soil respiration flux at 0 °C). All model residuals fit the assumption of normal distributions, except the models of all nondesert biomes together and the temperate agriculture biome in isolation, where residuals were left-tail skewed. Because the desert had significantly lower respiration rates compared with all other biomes (*SI Appendix*, Fig. S4), models were never run with all data together, because combined residuals were distinctly bimodal. For all models included in our analysis, colinearity between soil moisture and soil temperature was evaluated by calculating variance inflation factors (35), which were always <1.5, indicating extremely limited colinearity. Power analysis (36) revealed power = 1 for all models, except multivariate regression of the southern shrubland warming interaction, where power = 0.95.

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

$$\mathrm{RR} = \ln(X_T/X_C) \quad [2]$$

and a random effect model (38). We used the standardized mean difference (raw mean difference divided by pooled SD) and random effect model to determine differences in temperature sensitivities between treatments across sites. All metaanalysis was done using the metafor package in R (39). Effect sizes with 95% confidence intervals overlapping zero indicate no significant effect of warming on the factor in question. Values greater than zero indicate that warming increased soil temperature, soil moisture, soil respiration, and/or temperature sensitivity, whereas values lower than zero indicate that warming decreased these values. In studies with multiple levels of warming treatment (four studies; *SI Appendix*, Table S1), data from the warmest treatment were used to compute effect sizes. Data from site ID 17 (40) were excluded from *SI Appendix*, Fig. S2, due to extremely high effect size (RR = 0.95) and small difference in temperature between treatments ($\Delta T = 0.5$). All tests of significance level used alpha (α) of 0.05. All analysis and statistics were done in R (version 3.2.0) (41).

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SI Appendix

Temperature response of soil respiration largely unaltered with experimental warming

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Supporting Methods

Dataset Generation and Description

A literature search was conducted on September 22, 2014 using Web of Science, which produced five studies presenting non-aggregated instantaneous data that were extractable (Table S1). Published datasets (16-17) and unpublished values make up the majority of the data in the dataset. We obtained unpublished data by first creating a list of all known experimental warming studies globally and asking the principal investigators to supply soil respiration data with corresponding soil temperature and moisture values. Because of widely variable experimental designs across studies, we averaged all plot-scale values for each sampling event to obtain one average (± SD) for each treatment for each sampling event ('sampling events' typically refer to a single day of sampling, although several studies complete full suites of sampling (i.e., 'sampling events') from all plots in both morning and afternoon). Only soil respiration values with corresponding soil moisture and soil temperature values from experimental warming studies were included in our analysis. Only observations from single-factor treatments (i.e., warming) were used, excluding values that combined warming with other treatments (e.g., precipitation or nitrogen manipulation). Four studies included more than one level of warming treatment (e.g., both 1.5 and 3°C warming treatments); in these cases, data from all levels of warming were used for our temperature response function analyses. All data were reported as instantaneous change in CO_2 efflux over a fixed area, with belowground (i.e., roots and rhizomes), but not aboveground vegetation, included. Thus, soil respiration values presented here include both heterotrophic and autotrophic soil respiration.

Experiment locations ranged from 33.5 to 68.4 °N latitude (Fig. S5) and the duration of warming at experiments ranged from <1 to 22 years (average 5.1 years) (Fig. S6). Depths of soil temperature (1-10 cm) and moisture measurements (5-30 cm) ranged across studies, but were always consistent between warmed and control plots within a particular study. The majority of the observations were taken between 5 and 10 years after warming commenced (n=1534), followed by 2-5 year duration (n=1109), less than 2 years (n=896) and >10 years (n=278). Each site was classified into a particular biome (grassland, northern shrubland (i.e., peatlands and heathlands), southern shrubland (i.e., Mediterranean or sub-tropical shrublands), tundra, desert, meadow, temperate agriculture, temperate forest and boreal forest) by the associated principal investigator. Tropical biomes are not represented in our analysis because no data from experimental warming studies in the tropics are yet available. However, the first known tropical warming experiment, Tropical Responses to Altered Climate Experiment (TRACE), is currently being set up in Luquillo Experimental Forest in Puerto Rico, with heating scheduled to commence during spring 2016.

Seasonality was defined by principal investigators contributing data as those months that fall into the following categories: growing (plants actively growing), non-growing (plants not actively growing), or shoulder (takes into account months of transition and intra-annual variability) season. Data from the growing season accounted for more than half of our observations (n=1840), followed by shoulder season (n=1112), and non-growing season (n=865). Absolute differences in soil temperature, moisture, and respiration across sites were always calculated as values from warmed plots minus values from control plots for each sampling event: e.g., $\Delta T = T_w - T_c$.

Evaluating role of Soil Moisture, Seasonality, and Warming Duration in Controlling Soil Respiration

We investigated the role of soil moisture in controlling the response of soil respiration in four ways. First, we evaluated the significance of soil moisture as a predictor of soil respiration by adding moisture as an additional continuous variable in a multiple linear regression model (Model e in Table S3, Table S2):

(3) $$\ln(R) = a_0 + a_1 T + a_2 T^2 + a_3 M$$

where R is soil respiration (μmol C m^2 s^{-1}), T is soil temperature (ºC), and M is soil moisture (cm^3 cm^{-3}). In cases where significant differences in the response functions of warmed vs. control treatments were observed (boreal and desert biomes), separate models that included moisture were run for each treatment (Table S2). Because respiration rates are often not linearly related to moisture content, we also conducted our analysis with an additional model (Eq. 4), which resulted in no differences in our conclusions (Table S6). Next, we created partial regression plots (i.e., added-variable plots) for both temperature and moisture (Fig. S7), allowing for visual inspection of the role of moisture compared to temperature in controlling the respiration response. Third, we examined how moisture alters the temperature sensitivity of respiration by running a separate model of respiration as a function of temperature with moisture as the interaction term (Model f in Table S3). To evaluate this response visually, we then partitioned the data into moisture quantiles and plotted the temperature sensitivities of respiration at these four different moisture levels (Fig. S3), reporting the coefficients in Table S4. Finally, we normalized each instantaneous difference in respiration between warmed and control plots (ΔR) by ΔT, and binned those values by amount of moisture available in warmed plots as a fraction of control plots (Fig. 3). Moisture bins containing less than 5% of total observations from each biome are not shown (not applicable in Fig. 3, where all bins represent at least 5% total data). This analysis allowed us to understand how differences in the magnitude of respiration between treatments change with moisture availability (Fig. S3).

We evaluated the influence of warming duration and seasonality on the respiration response between treatments in two ways: 1) by partitioning the observations into categories of warming duration (<2, 2-5, 5-10, and >10 years) and season (growing, non-growing, and shoulder) and running the multivariate regression model shown in Table 1 for each category separately, and 2) by running additional multivariate models (Models h and i in Table S3) that included duration or season as a fixed factor, with an interaction with warming treatment.

Supporting Results

Magnitudes of Temperature and Respiration Change with Experimental Warming

Experimental warming generally stimulated soil respiration, with a larger ΔT significantly correlated to a larger respiration effect size ($p<0.01$ and $r=0.66$; Fig. S2B, Table S1). Across all sites, experimental warming increased soil temperatures by 1.91 ^{0}C on average, although average soil warming by biome ranged from 0^{0}C in southern shrublands to 4.09 ^{0}C in temperate forests, with relatively large inter-biome differences (Table S1). On average, the magnitude of soil warming at many sites was too low (when ΔT <1.72 °C) to statistically increase respiration rates (Fig. S2B). In turn, the relatively low degree of average warming across many sites resulted in an insignificant grand mean effect size for soil respiration (RR= 0.05 [95% CI: -0.03-0.14], n=26), regardless of season and warming duration, with just five sites (Site IDs 2, 6, 7, 8, 27 Table S1) having a significantly positive response of respiration in the warmed plots. Methodological differences in warming methods resulted in a range of ΔT, and thus, ΔR across sites. In our dataset, experiments that warmed via electric cables observed the greatest average soil warming (ΔT =3.6 °C, n=5), compared to infrared (ΔT =2.3°C, n=11) and passive (ΔT = 0.4°C, n=11) warming methods. Electric cable was the dominant warming method in the temperate forest (4 out of 5 sites) and temperate agriculture (one site) biomes and in turn, these biomes were the only ones when analyzed individually to display a significant increase in respiration (ΔR) with warming using traditional meta-analysis (temperate forest: RR=0.18; 95% CI: 0.06-0.30, temperate agriculture: RR=0.21; 95% CI: 0.06-0.37).

Standardized Mean Difference of Temperature Sensitivity

Beyond investigating differences in the log-quadratic temperature response function (Eq. 1) between warming treatments, we also conducted a traditional meta-analysis on site-level temperature sensitivity parameters using the standardized mean difference (SMD) as our index of effect size, which normalizes raw mean differences by the pooled standard deviation. Examining data from across all sites, the grand mean effect size was not significantly different from zero (SMD= -0.29 [95% CI: -1.21, 0.64], n=27), demonstrating further evidence for the general lack of difference in temperature sensitivities between warmed and control plots with experimental warming (Fig. S8). Although the grand mean effect size was not significantly different from zero, 12 sites showed significantly higher SMDs of temperature sensitivity in warmed plots (Site IDs 5, 8, 9, 13, 14,16, 19, 21, 23, 26-28), while eight sites (Site ID 1, 2, 11, 12, 15, 20, 22, 24) demonstrated significantly lower SMD in warmed plots compared to control plots.

Role of Moisture in Controlling Respiration Rates

Meta-analysis of soil moisture data reveals that moisture was significantly reduced with warming (RR=-0.08, [95% CI:-0.12- -0.03]), with 7 out of 27 sites having significantly less soil moisture at the warmed compared to control plots. However, such decreases were only marginally significantly correlated with ΔT (r= -0.32, p=0.08) (Fig. S2A). Multivariate linear regression highlights that moisture typically explains a much smaller fraction (0-8%) of the total respiration response compared to temperature (34-82%), except in the case of southern shrublands, where moisture is a stronger predictor of respiration than soil temperature (R^2 model a or b versus Model e in Table S3, Fig. S7). We used partial regression plots (Fig. S7) to help visualize the effect of adding an additional variable (i.e., soil moisture) to a multiple regression model. Partial regression with temperature and moisture highlight the more important role of temperature in driving the soil respiration response compared to moisture (Fig. S7). This response is demonstrated by the lower slopes on the added-variable moisture plots (right hand panels). An exception to this is southern shrublands, where moisture added-variable plot has a much steeper slope compared to other biomes, aligning with the multivariate regression output showing moisture playing a more important role in predicting respiration compared to temperature in the southern shrublands.

Ambient soil moisture is a critical factor in mitigating the respiration-temperature relationship. For example, a negative $\Delta R/\Delta T$ response with soil drying is only apparent in the desert, grassland, and southern shrubland biomes (Fig. S9), likely because these biomes have the lowest ambient soil moisture content (Table S1) and thus, even minor desiccation with warming suppresses C fluxes. On the other hand, in the forest biomes where soil drying with warming was most severe (warmed plots have on average 84% and 87% of the moisture that was observed in control plots in the boreal and temperate forests, respectively), fluxes were still consistently higher from warmed plots despite drying (Fig. S9), due in part to relatively elevated ambient soil moisture conditions at these sites (Table S1).

Soil moisture often has a non-linear relationship with soil respiration. In order to determine if our multivariate linear model (Table S2) was a factor influencing our results, we re-ran our analysis using an additional function (Eq. 4, see below), which shows little difference in model fits (Table S6). Our study does not take into account differences in soil type between sites, as differences in soil type between warmed and control plots within a site should be minimal. In addition, soil moisture content largely reflects soil type across sites, as sandier soils hold less water than more clay-type soils. We see this in our data, as average soil moisture content in several biomes was negatively related to percent sand (r=0.98, 0.62, r=0.55 in northern shrublands, grasslands and forests, respectively). Our analyses of soil moisture are based on soil water content (SWC), otherwise known as soil moisture concentrations. However, soil matric potentials are a much better indicator of water availability in soils, as this metric takes into account soil texture and organic matter content, which can affect relative water availability at the site level (1, 2). Because both factors undoubtedly change across sites, soil matric potentials are likely a more sensitive metric to evaluate how differences in moisture availability influence soil respiration rates.

Role of Warming Duration and Seasonality on Soil Respiration Rates

Multivariate analysis of respiration that included warming duration as a predictor, with an interaction with warming treatment (Model h in Table S3) revealed a significant interaction between duration and warming treatment in four biomes: desert, boreal forest, temperate forest, and northern shrubland. Except for northern shrublands, the other three biomes displayed significantly depressed soil respiration rates with increasing warming duration. Considering that it is in these three biomes where we observed moderate (temperate forest) to strong (boreal forest and desert) evidence of altered temperature response functions to soil warming, it appears that duration of experimental warming is an important factor in driving these results. We also evaluated how duration of warming changes the temperature response function of respiration in warmed versus control treatments by re-running our analysis shown in Table 1 with data partitioned into the following groupings of years of warming duration (<2, 2-5, 5-10, and >10). This analysis continues to support prior conclusions, with no significant differences in the temperature response function in any biome regardless of warming duration, except the boreal forests and desert, and moderate ($p=0.06$) differences from 2-5 years of warming duration in temperature forest.

We investigated how season influenced soil respiration rates in a similar fashion to duration. First, we added season as a predictor to our multilinear regression model, with an interaction with warming treatment (Model i in Table S3). Here we found a significant interaction between season and warming treatment in the desert and boreal forest biomes only, indicating that in these two biomes respiration from warmed and control plots responds differently to temperature depending on the time of year. Next, we re-ran our analysis shown in Table 1 with data partitioned into season (non-growing, growing, shoulder) and found a similar result; for all biomes except the desert and boreal forests, no differences in temperature sensitivity were observed when analyzing any particular season in isolation. In the boreal forest, differences in temperature sensitivity were driven by growing season data, which make up the majority of the data (70%) for the boreal forest biome. On the other hand, the differences in sensitivity observed in the desert biome are driven by data from the non-growing season; this was the only season, when examined in isolation, where significant differences in the temperature sensitivity of respiration from warmed versus control plots are observed in the desert biome.

Model Choice

We used several different multivariate models (Table S3) to answer specific questions during our analysis. To address our first objective (i.e., determine whether respiration response from warmed plots paralleled that from control plots), we used a temperature-treatment interaction model (Models c or d in Table S3, depending on whether the 2nd-order temperature term was significant when including the treatment interaction term). We also compared the fits (specifically AICs) of Models c or d with models excluding warming treatment as a predictor (Models a or b) to determine if warming treatments had an effect on the respiration response (Table S3). Lower AICs in Models a or b (Table S3) compared to Models c or d (Table S3) provides further evidence that experimental warming does not alter the shape of the curve to a large degree in those biomes. Parameter values for Models a and b (Table S3) also shown in Table S5. Next, to evaluate our second objective (i.e., investigate the role of soil moisture in influencing how respiration responds to temperature across treatments), we included soil moisture as a predictor, with an interaction term with temperature in our multivariate models (Models e and f in Table S3). Finally, to determine how warming duration and seasonality were influencing our results, we ran three additional models with these terms as predictors (Model g in Table S3), with an interaction term with warming treatment (Models h and i in Table S3).

We did not use the traditional exponential model (the Q_{10} model) or the Arrhenius model to fit our data as these models cannot adequately reflect our findings that the temperature sensitivity decreased when temperature is above ~25°C. The inability of these models to represent varying temperature sensitivities across the temperature gradient has been discussed previously (3, 4). This study focused on understanding the temperature response of soil respiration with experimental warming, rather than modeling soil respiration. However, we also simulated our data using the following equation (5):

(4) $$R = e^{\alpha(T-T_o)}\left(\frac{T_m - T}{T_m - T_o}\right)^{\alpha(T_m - T_o)}\left(\frac{M}{k_m + M}\right)$$

With R = non-transformed soil respiration rate, T= soil temperature (°C), T_o = optimum soil temperature (°C), T_m = maximum soil temperature (°C), M = soil moisture concentration (cm^3 cm^{-3}). T_o, T_m, k_m, and α were solved individually for each biome. Irrespective of having a similar or better overall performance (R^2 in Table S6), we selected the log-linear or log-quadratic equations to fit our data (Table 1, Eq. 1, Models c and d in Table S3) because it facilitated use of the binary categorical variable to evaluate differences in temperature response functions with warming treatment.

Cross-Biome Differences

Temperature response functions of soil respiration were not equal across biomes; not only were the temperature sensitivities different (γ_1 and γ_2, Table 1), but the magnitudes of respiration (γ_o, Table 1) also differed, with highest fluxes from boreal forests and lowest fluxes from deserts (Fig. S4). Multivariate regression output highlights these across-biome differences, as adding 'biome' as a predictor to the larger multivariate regression of all non-desert data increased the predictive power of the model by 28% (Model j in Table S3).

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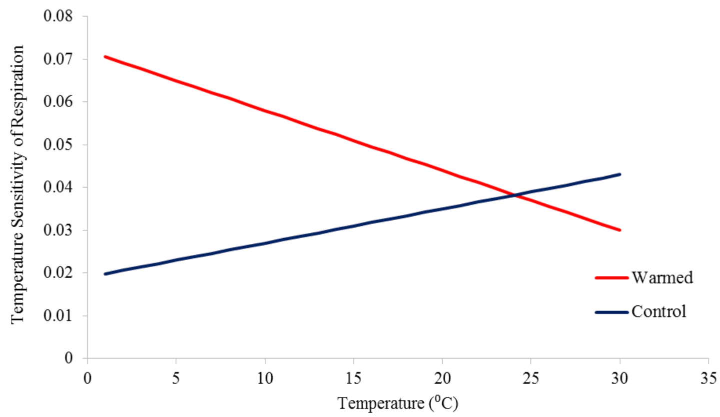
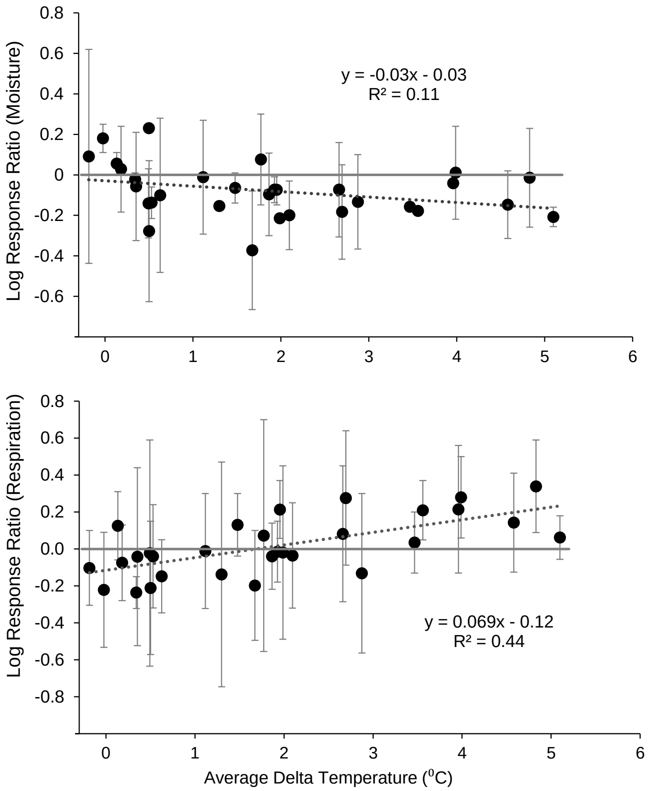
Fig. S1.



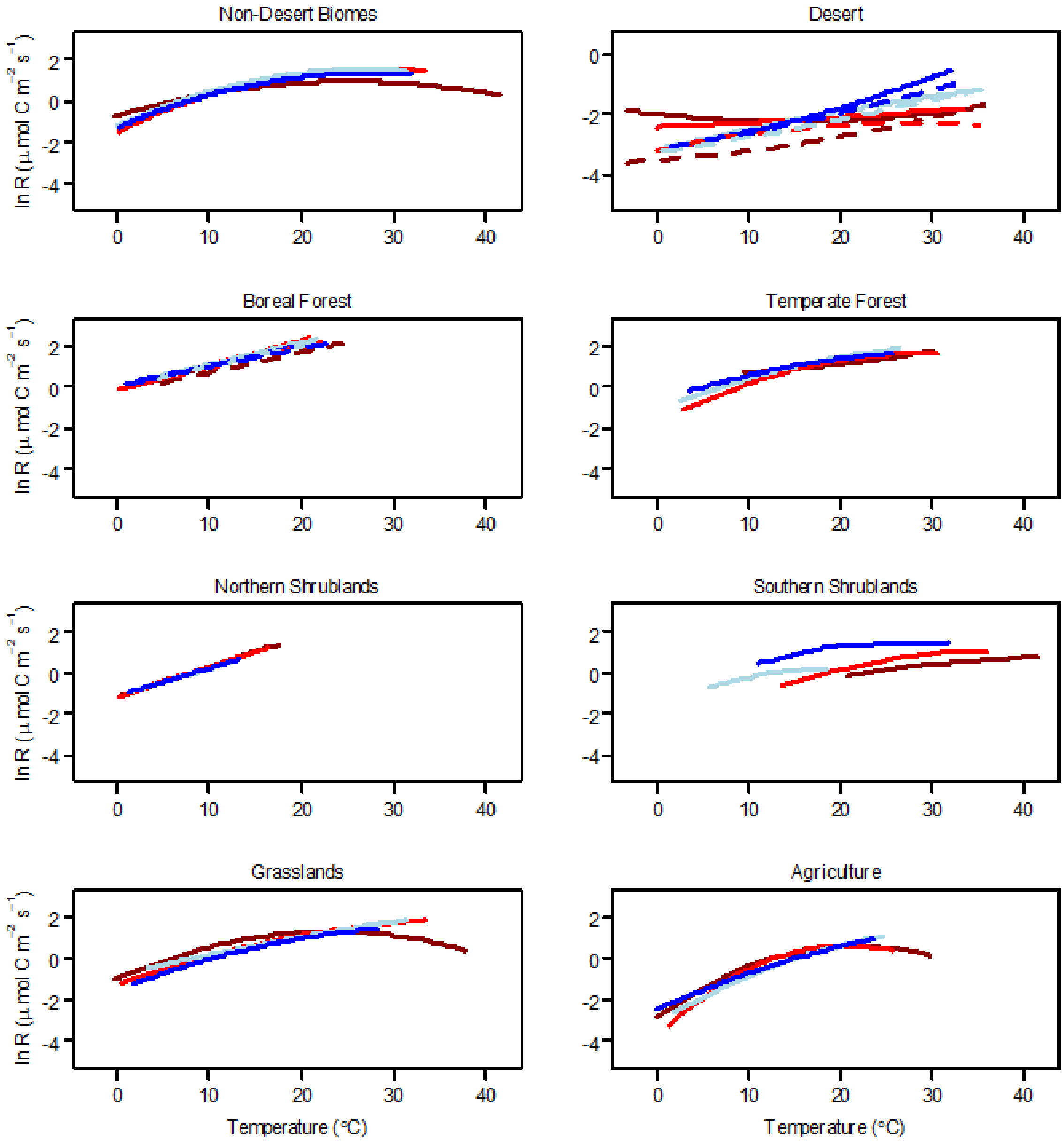
Temperature sensitivities for desert calculated as the linear functions describing the derivative of the log-quadratic fit of ln respiration as a function of soil temperatures: $\frac{\partial y}{\partial t} = -0.0014\, T + 0.072$ (warmed) and $\frac{\partial y}{\partial t} = 0.0008\, T + 0.019$ (control), where y refers to ln of respiration (µmol C m^{-2} s^{-1}) and T refers to temperature (°C).

Fig. S2.



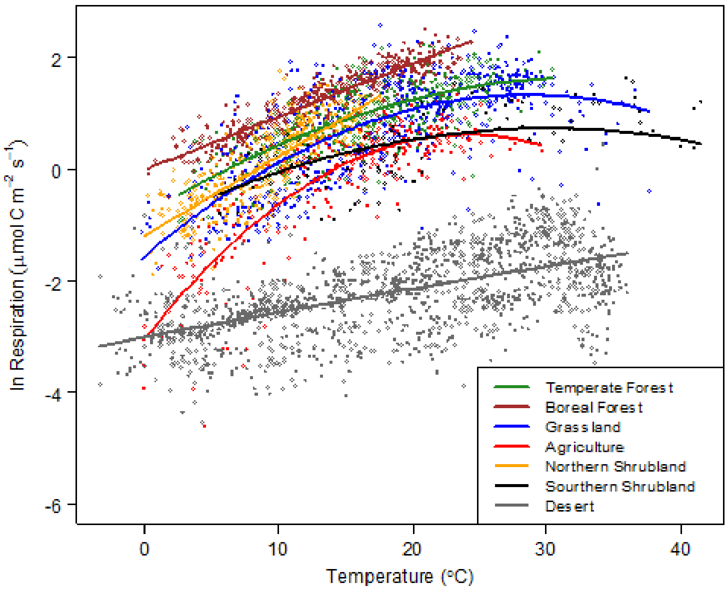
Effect size (log response ratio) as a function of degree of experimental warming (ΔT (°C)) for moisture (A) and respiration (B). Data from all biomes plotted here.

Fig. S3.



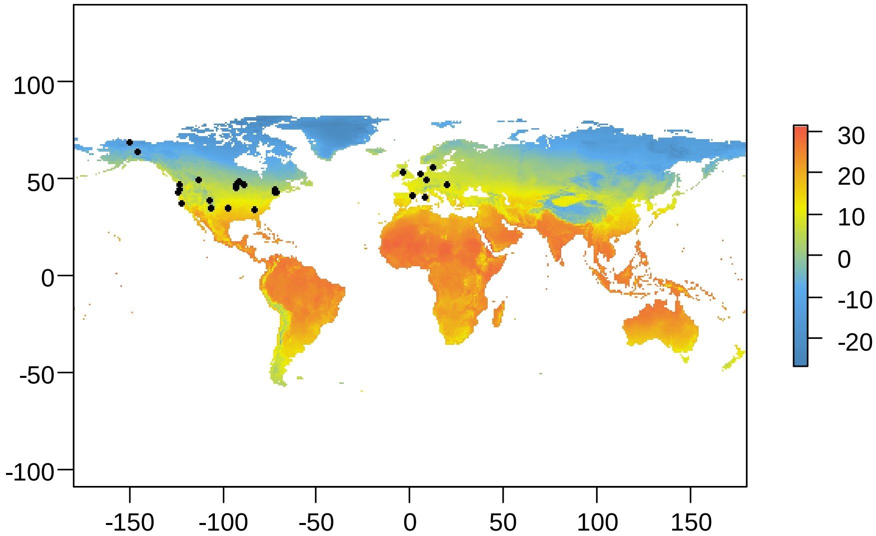
Best fit regression lines of natural log (ln) of respiration (µmol C m^{-2} s^{-1}) as a function of soil temperature (°C) across biome types, with data partitioned into moisture quantiles: dark red (1st (lowest) quartile), red (2nd quartile), light blue (3rd quartile), dark blue (4th (highest) quartile). For model parameters, see Table S3. Separate fits were calculated for control and warmed treatments where statistically different temperature sensitivities were observed (boreal forest and desert), with dashed lines for warmed data and solid lines for control data. Solid lines on all other plots represent both warmed and control data, as their fits were not statistically different from one another. Note the scale of Y-axis are all equal, except for desert, which had lower respiration rates compared to all other biomes.

Fig. S4.



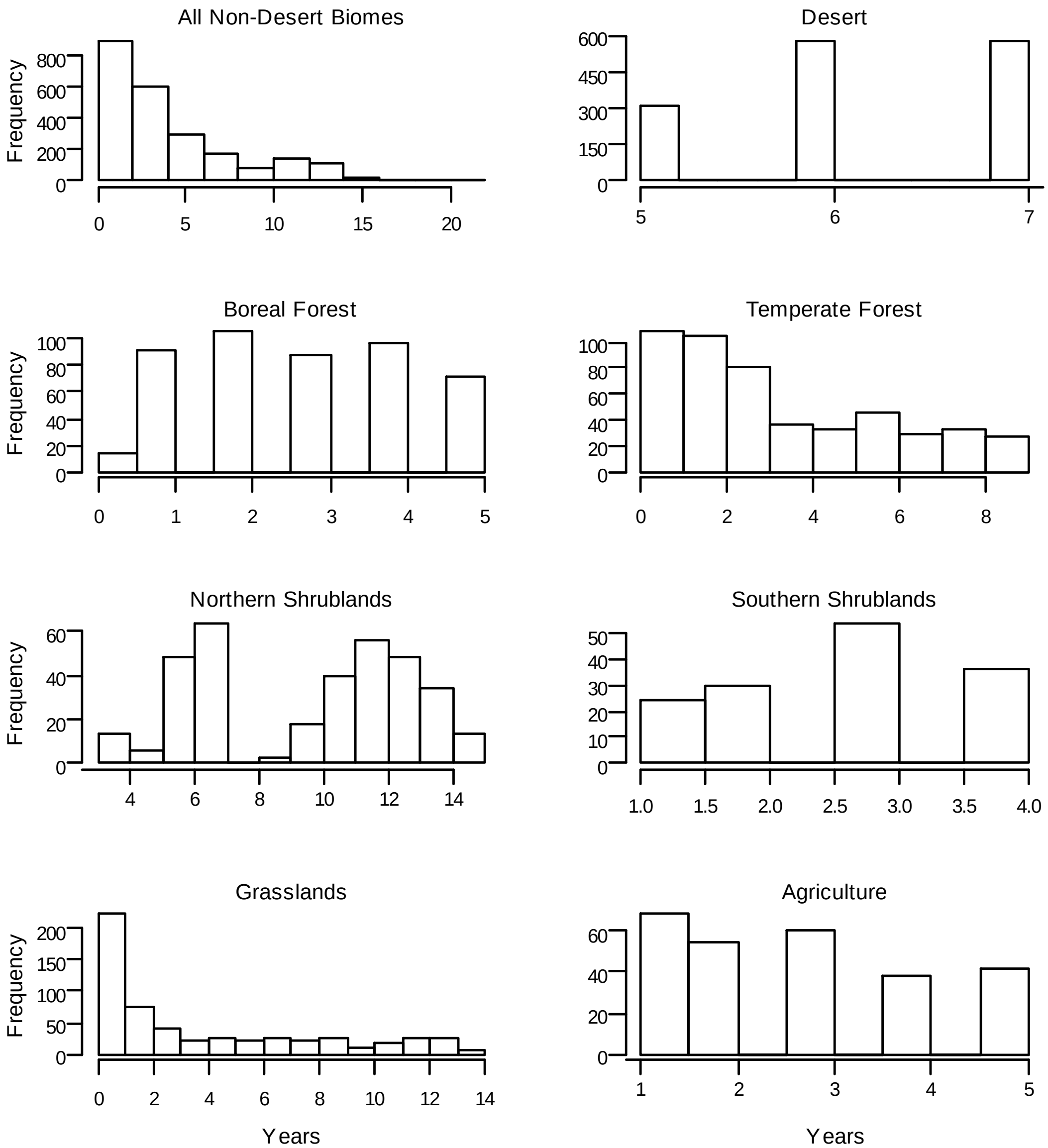
Ln respiration (μmol C m^{-2} s^{-1}) as a function of soil temperature (°C) for all data included in our study. Each dot represents an individual data point, including data from both control and warmed treatments (n=3817). Lines are best-fit regression lines using the log-quadratic temperature response functions for all biomes, except the boreal forest and northern shrublands, where log-linear functions were used (for coefficients, see Table S5).

Fig. S5.



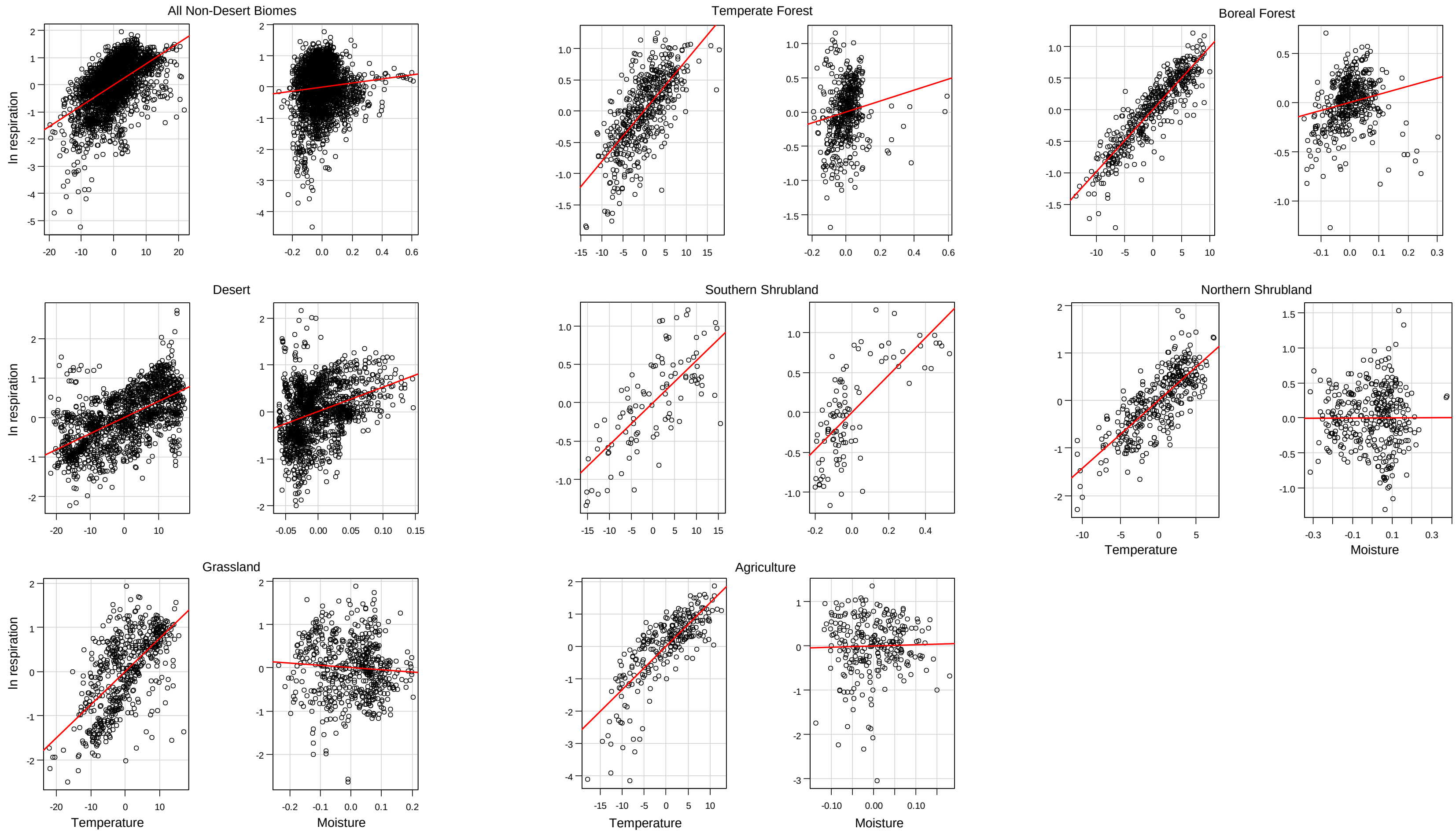
Map of study sites. Color refers to mean annual temperature (°C). Map created using ‘maps’, ‘mapdata’, and ‘raster’ packages in R.

Fig S6.



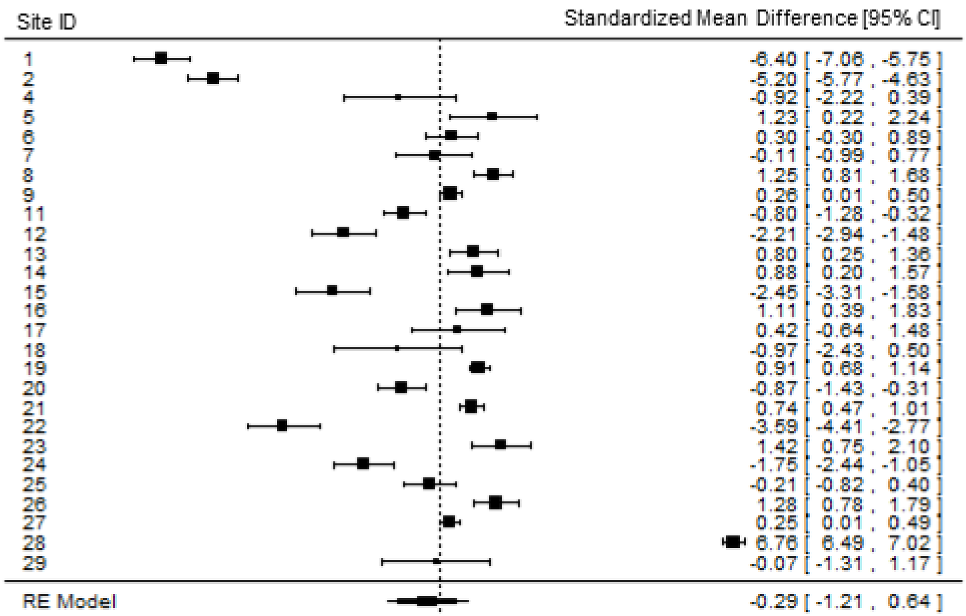
Histogram of duration of warming within each biome.

Fig. S7.



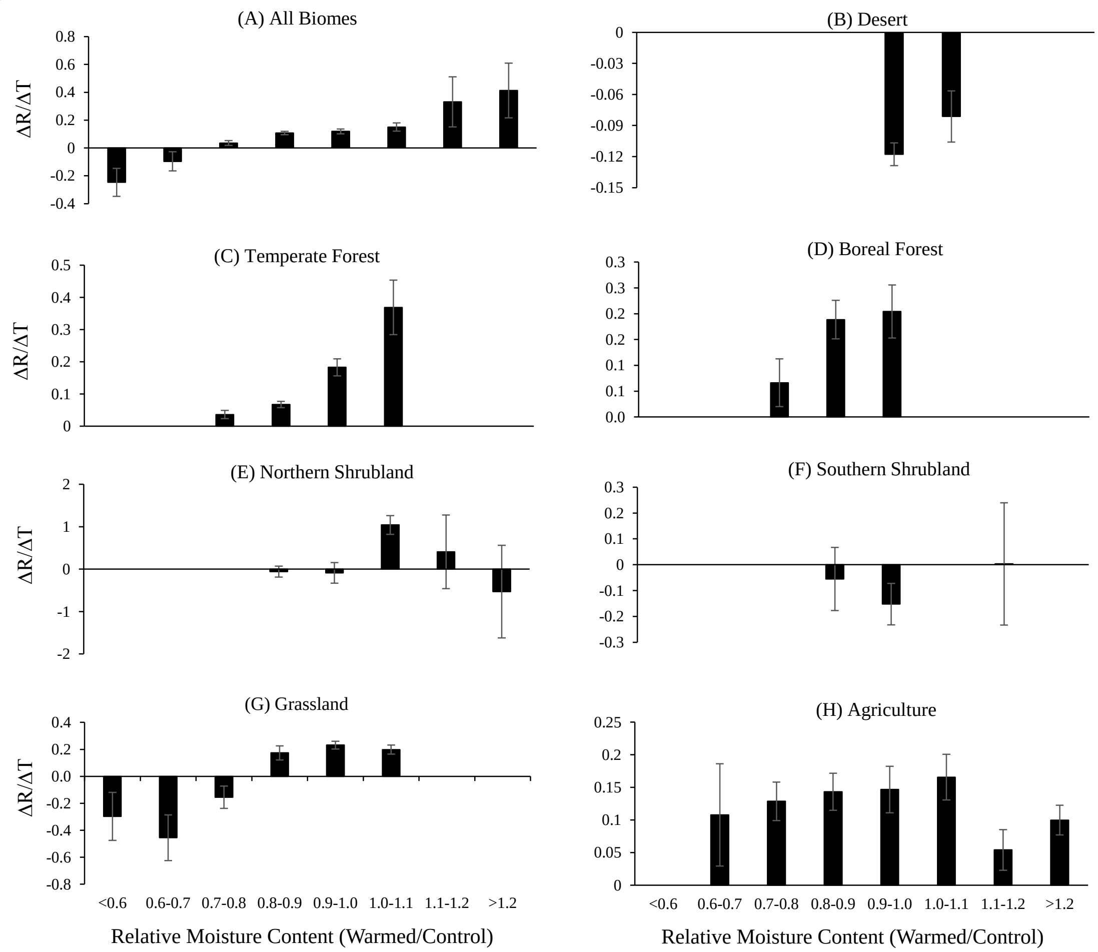
Partial regression plots of soil respiration as a function of temperature and moisture across all biomes. Plots created using the ‘car’ package and AvPlots function in R.

Fig. S8



Forest plot of first-order temperature sensitivities (γ_1 in Eq. 1) at each site. Size of filled squares indicates number of observations. Error bars represent 95% confidence intervals. Error bars that do not cross zero line indicate significant differences in temperature sensitivity between warmed and control plots. Values on right of zero line indicate higher sensitivity in warmed plots, while values on left of zero line indicate lower sensitivity of warmed plots.

Fig. S9.



Difference in respiration (μmol C m^{-2} s^{-1}) between warmed and control plots (ΔR) normalized by degree of warming (ΔT °C), binned by amount of soil desiccation with warming (soil moisture content in warmed plots divided by soil moisture content in control plots) for each individual biome. X axis values <1 indicate warmed plots have less moisture available than control plots. Y axis values <0 indicate that respiration rates were lower from warmed plots, despite warmer soil temperatures. Respiration data not log transformed. Note the scales of the Y-axes are different. For number of observations by biome see Table S3.

Supplementary Tables

Table S1.

						Control		Warmed Treatment (multiple levels)										
Site ID	Name	Ecosystem Type	Warming Method	n	Average Delta Temperature (^{0}C)	Average Respiration (µmol m^{-2} s^{-1})	SE	Average Respiration (µmol m^{-2} s^{-1})	SE	Average Ambient Moisture (cm^3 cm^{-3})	Average Delta Moisture (cm3 cm-3)	MAP (mm)	MAT (^{0}C)	Elevation (m)	Duration Range* *	%Sand	%Silt	%Clay
1	B4W_CFC	Boreal Forest	Infrared	75	1.87	4.38	0.29	4.21	0.25	0.213	0.020	752	4.23	413	5	60.9	30.5	8.6
1	B4W_CFC	Boreal Forest	Infrared	75	3.47			4.53	0.24		-0.031							
2	B4W_HWRC	Boreal Forest	Infrared	71	1.93	4.08	0.26	4.02	0.22	0.278	0.020	665	3.57	383	5	62.3	23.5	14.2
2	B4W_HWRC	Boreal Forest	Infrared	71	3.56			5.03	0.25		-0.045							
4	Tower_Burn	Boreal Forest	Passive	5	0.49	1.68	0.40	1.65	0.34	0.475	0.062	303	-2	457	2	31.6	56.8	11.8
5	Tower_Control	Boreal Forest	Passive	9	0.50	2.40	0.19	1.94	0.33	0.202	0.049	303	-2	499	2	34.1	53.5	12.4
6	Ford^	Temperate Forest	Infrared	22	4.58	2.89	0.28	3.33	0.31	0.240	0.033	879	4.9	402	5	62.1	29.0	9.0
7	HBEF	Temperate Forest	Electric Cable	10	4.83	5.18	0.52	7.28	0.61	0.144	0.002	1400	5.2	252	1	60.0	30.0	10.0
8	HF_Frey	Temperate Forest	Electric Cable	48	3.99	1.91	0.16	2.53	0.19	0.243	-0.003	1100	7	1026.5	8	62.0	22.0	15.0
9	HF_Melillo	Temperate Forest	Electric Cable	130	5.10	3.03	0.14	3.22	0.13	0.276	0.052	1080	7	1026.5	9	62.0	22.0	15.0
11	Whitehall	Temperate Forest	Electric Cable	29	2.10	3.10	0.34	3.00	0.29	0.171	0.031	99	17.6	207	4	63.9	18.0	18.1
11	Whitehall	Temperate Forest	Electric Cable	19	3.96			4.24	0.50		-0.007							
12	BACE^	Temperate Grassland	Infrared	14	0.35	3.22	0.59	3.09	0.51	0.225	0.013	1194	9.5	17	2	45.0	46.0	9.0
12	BACE^	Temperate Grassland	Infrared	14	1.99			3.16	0.49		-0.044							
12	BACE^	Temperate Grassland	Infrared	14	2.93			3.26	0.45		-0.070							
13	BioCON	Temperate Grassland	Infrared	27	1.67	5.30	0.59	4.35	0.46	0.079	0.025	660	6.7	282	2	94.4	0.0	2.5
14	COR	Temperate Grassland	Infrared	18	2.66	2.75	0.38	2.99	0.37	0.257	0.018	1134	11.4	164	2	36.5	49.0	14.5
15	SOR	Temperate Grassland	Infrared	18	2.88	2.92	0.47	2.56	0.38	0.234	0.029	1434	12.3	395	2	31.5	37.5	31.0
16	WA	Temperate Grassland	Infrared	17	2.70	2.18	0.29	2.87	0.37	0.162	0.027	1196	10.5	134	2	75.0	21.5	3.5
17	FluxnetCanada *	Temperate Grassland	Passive	7	0.50	3.27	0.70	8.44	0.98	0.220	-0.057	386	5.4	960	1	28.8	40.0	31.2
18	JasperRidge	Temperate Grassland	Infrared	4	1.77	4.87	1.53	5.23	0.35	0.076	-0.006	531	15.3	120	1	37.0	48.0	15.0
19	Kessler	Temperate Grassland	Infrared	164	1.48	2.20	0.13	2.51	0.15	0.255	0.016	914	16.3	335	13	36.0	55.0	10.0
20	MontainMeadow^	Meadow	Infrared	27	1.12	2.49	0.29	2.46	0.27	0.109	0.001	750		2920	20	na	na	na
21	Clocaenog	Northern Shrubland	Passive	114	0.13	1.23	0.09	1.40	0.09	0.421	-0.024	1289	8.2	490	13	40.2	50.0	9.8
22	Garraf	Southern Shrubland	Passive	30	0.18	1.11	0.09	1.03	0.07	0.185	-0.005	570	15.6	215	2	42.9	38.7	18.4
23	Hungary*	Southern Shrubland	Passive	21	0.63	0.42	0.03	0.37	0.03	0.051	0.005	505	10.4		3			
24	Oldbroek	Northern Shrubland	Passive	22	-0.02	1.39	0.16	1.11	0.12	0.215	-0.043	1072	10.1	25	3	93.5	6.0	0.5
25	PCCC^	Southern Shrubland	Passive	21	-0.18	3.08	0.22	2.78	0.20	0.328	-0.031	640	16.8	40	3	75.6	11.2	13.4
26	Brandbjerg	Northern Shrubland	Passive	36	0.53	1.73	0.17	1.66	0.17	0.178	0.023	757	8.7	9	2	91.0	7.0	2.0
27	HoCC	Temperate Agriculture	Electric Cable	131	1.95	1.07	0.06	1.32	0.07	0.210	0.015	679	8.7	395	5	9.0	69.0	22.0
28	Sevilleta	Desert	Passive	737	0.34	0.16	0.00	0.13	0.00	0.112	0.003	250	13.2	1525	3	68.0	22.0	10.0
29	Toolik	Wet Sedge Tundra	Passive	5	1.30	0.76	0.20	0.66	0.11	0.700	0.100	331	-8.5	717	1	na	na	na

*data from published literature only
^ data from both published and unpublished data
**Years of observations since warming started

Characteristics of each site included in study, including both published and unpublished sources (6–17).

Table S2

Parameters for models: $\ln(R) \sim \alpha_0 + \alpha_1 T + \alpha_2 T^2 + \alpha_3 M$						
Model	**$\alpha_0 \pm$ SE**	**$\alpha_1 \pm$ SE**	**$\alpha_2 \pm$ SE**	**$\alpha_3 \pm$ SE**	**n**	**R^2**
All Biomes Except Desert	-1.547 ± 0.078	0.210 ± 0.008	-0.004 ± 0.0022	0.692 ± 0.142	2343	0.39
Desert						
Control Treatment	-2.875 ± 0.069	0.009 ± 0.007	0.001 ± 0.0002	3.320 ± 0.474	737	0.38
Warming Treatment	-4.065 ± 0.078	0.005 ± 0.008	<0.0001 ± 0.0002	7.228 ± 0.549	737	0.53
Boreal Forest						
Control Treatment	0.020 ± 0.085	0.108 ± 0.003	na	-0.286 ± 0.256	160	0.88
Warming Treatment	-0.368 ± 0.074	0.098 ± 0.003	na	1.301 ± 0.231	306	0.82
Temperate Forest	-1.082 ± 0.157	0.152 ± 0.017	-0.002 ± 0.0005	0.817 ± 0.234	497	0.52
Northern Shrubland	-1.180 ± 0.106	0.142 ± 0.006	na	0.020 ± 0.187	344	0.63
Southern Shrubland	-1.825 ± 0.244	0.109 ± 0.022	-0.001 ± 0.0005	2.236 ± 0.234	102	0.6
Grassland	-1.338 ± 0.145	0.201 ± 0.015	-0.004 ± 0.0004	-0.708 ± 0.299	566	0.52
Temperate Agriculture	-3.076 ± 0.206	0.304 ± 0.022	-0.006 ± 0.0078	0.202 ± 0.597	262	0.72

Parameters for multivariate regression model of soil respiration (natural log, in µmol C m^{-2} s^{-1}) (R) as a function of soil temperature (°C) (T) and soil moisture (cm^3 cm^{-3}) (M). In biomes with significantly different temperature sensitivities between warming and control treatments (boreal and desert biomes), control and warmed data were run in model separately. n= number of observations, R^2 = coefficient of determination. Parameter units: α_0 = ln µmol C m^{-2} s^{-1}; α_1= °C^{-1}; α_2 = °C^{-2}, α_3 = cm^{-3} cm^3.

Table S3.

Model ID	Model Terms	Significant Interaction?	df	R^2	Δ AICc
All Biomes Except Desert (n=2343)					
a	R~**T**	NA	2341	0.30	1745
b	R~**T** + $\mathbf{T}^2$	NA	2340	0.39	1436
c	R~**T***W	No	2339	0.30	1744
d	R~**T***W + $\mathbf{T}^2$*W	No	2327	0.39	1437
e	R~**T** + $\mathbf{T}^2$ + **Moisture**	NA	2339	0.39	1415
f	R~**T***Moisture + $\mathbf{T}^2$*Moisture	No	2337	0.41	1359
g	R~**T** + $\mathbf{T}^2$ + **Moisture** + **Duration**	NA	2338	0.40	1393
h	R~**T** + $\mathbf{T}^2$ + **Duration***W	No	2337	0.39	1429
i	R~**T** + $\mathbf{T}^2$ + **Season***W	No	2335	0.44	1222
j	R~**T***Biome + $\mathbf{T}^2$*Biome + **Moisture**	Yes	2321	0.67	0
Desert (n=1474)					
a	R~**T**	NA	1472	0.34	318
b	R~**T** + T^2	NA	1471	0.34	320
c	R~**T*W**	Yes	1470	0.41	153
d	R~**T*W** + $\mathbf{T}^2$***W**	Yes	1468	0.42	144
e	R~**T** + $\mathbf{T}^2$ + **Moisture**	NA	1470	0.42	140
f	R~T***Moisture** + T^2*Moisture	Yes	1468	0.47	0
g	R~**T** + $\mathbf{T}^2$ + **Moisture** + Duration	NA	1469	0.42	139
h	R~**T** + T^2 + **Duration*W**	Yes	1468	0.42	143
i	R~**T** + $\mathbf{T}^2$ + **Season*W**	Yes	1466	0.44	76
Boreal Forest (n=466)					
a	R~**T**	NA	464	0.82	52
b	R~**T** + $\mathbf{T}^2$	NA	463	0.82	43
c	R~**T*W**	Yes	463	0.84	2
d	R~**T***W + T^2*W	No	460	0.84	0
e	R~**T** + **Moisture**	NA	463	0.82	34
f	R~**T***Moisture	Yes	462	0.83	21
g	R~**T** + **Moisture** + **Duration**	NA	462	0.83	29
h	R~**T** + **Duration*W**	Yes	461	0.83	8
i	R~**T** + $\mathbf{T}^2$ + **Season***W	Yes	459	0.83	12
Temperate Forest (n=497)					
a	R~**T**	NA	495	0.49	92
b	R~**T** + $\mathbf{T}^2$	NA	494	0.51	77
c	R~**T***W	No	493	0.52	62
d	R~**T***W + $\mathbf{T}^2$*W	No	491	0.54	46
e	R~**T** + $\mathbf{T}^2$ + **Moisture**	NA	493	0.52	67
f	R~**T***Moisture + T^2*Moisture	No	491	0.52	69
g	R~**T** + $\mathbf{T}^2$ + **Moisture** + Duration	NA	492	0.52	69
h	R~**T** + $\mathbf{T}^2$ + Duration***W**	Yes	491	0.54	45
i	R~**T** + $\mathbf{T}^2$ + **Season***W	No	489	0.58	0
Northern Shrubland (n=344)					
a	R~**T**	NA	342	0.63	60
b	R~**T** + T^2	NA	341	0.63	62
c	R~**T***W	No	340	0.63	64
d	R~**T***W + T^2*W	No	338	0.63	65
e	R~**T** + Moisture	NA	341	0.63	62
f	R~**T***Moisture	No	340	0.63	63
g	R~**T** + **Moisture** + **Duration**	NA	340	0.69	0
h	R~**T** + **Duration*W**	Yes	339	0.69	7
i	R~**T** + Season*W	No	337	0.63	66

Table S3 Continued.

Model ID	Model Terms	Significant Interaction?	df	R^2	Δ AICc
Southern Shrubland - no Hungary (n=102)					
a	R~**T**	NA	100	0.15	92
b	R~**T** + T^2	NA	99	0.23	85
c	R~**T***W	No	98	0.16	96
d	R~**T***W + **T**^{2}*W	No	96	0.25	88
e	R~**T** + **T**^{2} + **Moisture**	NA	98	0.60	19
f	R~**T***Moisture + T^2*Moisture	No	96	0.60	23
g	R~**T** + **T**^{2} + **Moisture** + **Duration**	NA	97	0.68	0
h	R~**T** + **T**^{2} + **Duration***W	No	96	0.47	46
i	R~**T** + **T**^{2} + Season*W	No	94	0.18	93
Southern Shrubland - with Hungary (n=144)					
a	R~T	NA	142	0.06	124
b	R~T + **T**^{2}	NA	141	0.09	120
c	R~**T***W	No	140	0.06	127
d	R~T*W + T^2*W	No	138	0.11	123
e	R~**T** + **T**^{2} + **Moisture**	NA	140	0.6	4
f	R~T*Moisture + **T**^{2}*Moisture	No	128	0.62	0
g	R~T + T^2 + **Moisture** + **Duration**	NA	139	0.62	1
Grassland (n=566)					
a	R~**T**	NA	564	0.45	151
b	R~**T** + **T**^{2}	NA	563	0.52	82
c	R~**T***W	No	562	0.45	154
d	R~**T***W + **T**^{2}*W	No	560	0.51	87
e	R~T + **T**^{2} + **Moisture**	NA	562	0.52	78
f	R~**T***Moisture + **T**^{2}*Moisture	Yes	560	0.54	51
g	R~**T** + **T**^{2} + Moisture + **Duration**	NA	561	0.56	24
h	R~**T** + **T**^{2} + **Duration***W	No	560	0.56	24
i	R~**T** + **T**^{2} + **Season***W	No	558	0.58	0
Temperate Agriculture (n=262)					
a	R~**T**	NA	260	0.66	73
b	R~**T** + **T**^{2}	NA	259	0.72	17
c	R~**T***W	No	258	0.66	75
d	R~**T***W + T^2*W	No	256	0.73	22
e	R~**T** + **T**^{2} + Moisture	NA	258	0.72	19
f	R~**T*Moisture** + **T**^{2}***Moisture**	Yes	256	0.74	9
g	R~**T** + **T**^{2} + Moisture + **Duration**	NA	257	0.73	16
h	R~**T** + **T**^{2} + Duration*W	No	256	0.73	18
i	R~**T** + **T**^{2} + **Season***W	No	254	0.74	0

Summary of various models and their fits of soil respiration as a function of multiple variables. R = soil respiration (natural log, in µmol C m^{-2} s^{-1}), T = soil temperature (°C), M= soil moisture content (cm^3 cm^{-3}), W = treatment (control or warmed), df=degrees of freedom, R^2= coefficient of determination, ΔAICc = delta Akaike information criterion, with zero as best and all other model values presented relative to zero. Bold indicates significant predictor of respiration. Asterisk indicates interaction term in model.

Table S4.

Parameters for models: $LnR \sim \alpha_o + \alpha_1 T + \alpha_2 T^2$					
Moisture Quartile ($cm^3\ cm^{-3}$)	α_o	α_1	α_2	n	R^2
Non-desert biomes					
First quartile (<0.163)	-0.897	0.147	-0.0029	585	0.13
Second quartile (0.163-0.228)	-1.410	0.211	-0.0038	580	0.49
Third quartile (0.228-0.29)	-1.224	0.201	-0.0036	559	0.42
Fourth quartile (>0.29)	-1.276	0.188	-0.0033	605	0.46
Desert - Control					
First quartile (<0.082)	-2.010	-0.032	0.0011	184	0.01
Second quartile (0.082-0.102)	-2.418	0.016	0.0002	185	0.23
Third quartile (0.102-0.139)	-3.200	0.074	-0.0005	183	0.59
Fourth quartile (>0.139)	-3.170	0.046	0.0012	185	0.88
Desert - Warmed					
First quartile (<0.082)	-3.544	0.023	0.0008	184	0.60
Second quartile (0.082-0.102)	-3.220	0.066	-0.0012	183	0.17
Third quartile (0.102-0.14)	-3.300	0.051	0.0002	184	0.46
Fourth quartile (>0.14)	-3.155	0.049	0.0054	186	0.76
Boreal Forest - Control					
First quartile (<0.21)	-0.147	0.110	na	40	0.90
Second quartile (0.21-0.245)	-0.150	0.120	na	40	0.94
Third quartile (0.245-0.284)	-0.014	0.108	na	40	0.94
Fourth quartile (>0.284)	0.026	0.100	na	40	0.72
Boreal Forest - Warmed					
First quartile (<0.186)	-0.308	0.099	na	77	0.85
Second quartile (0.186-0.226)	-0.069	0.100	na	77	0.82
Third quartile (0.226-0.263)	-0.067	0.103	na	76	0.90
Fourth quartile (>0.263)	0.106	0.087	na	76	0.75
Temperate Forest					
First quartile (<0.176)	0.530	0.002	0.0013	124	0.20
Second quartile (0.176-0.233)	-1.800	0.232	-0.0040	128	0.68
Third quartile (0.223-0.279)	-1.126	0.176	-0.0024	120	0.64
Fourth quartile (>0.279)	-0.672	0.140	-0.0019	125	0.54
Northern Shrubland					
First quartile (<0.2157)	-1.183	0.145	na	86	0.83
Second quartile (0.2157-0.389)	-1.167	0.144	na	86	0.57
Third quartile (0.389-0.458)	-1.106	0.128	na	86	0.37
Fourth quartile (>0.458)	-1.115	0.132	na	86	0.45
Southern Shrubland					
First quartile (<0.1128)	-1.990	0.114	-0.0012	26	0.31
Second quartile (0.1128-0.199)	-3.200	0.230	-0.0031	25	0.54
Third quartile (0.199-0.2898)	-1.505	0.167	-0.0040	25	0.37
Fourth quartile (>0.2898)	-1.560	0.228	-0.0042	26	0.55
Grassland					
First quartile (<0.141)	-0.990	0.195	-0.0040	141	0.29
Second quartile (0.141-0.23)	-1.240	0.156	-0.0020	142	0.68
Third quartile (0.23-0.29)	-0.827	0.104	0.0006	142	0.47
Fourth quartile (>0.291)	-1.570	0.175	-0.0020	141	0.52
Temperate Agriculture					
First quartile (<0.151)	-2.816	0.310	-0.0070	65	0.74
Second quartile (0.151-0.198)	-3.810	0.431	-0.0100	66	0.78
Third quartile (0.198-0.25)	-3.126	0.264	-0.0039	65	0.62
Fourth quartile (>0.25)	-2.530	0.207	-0.0026	66	0.76

Parameters for models of natural log (ln) respiration (μmol C $m^{-2}\ s^{-1}$) as a function of soil temperature (°C) by moisture quartile for each biome. Data also shown in Fig. S3.

Table S5

Model	$\gamma_0 \pm$ SE	$\gamma_1 \pm$ SE	$\gamma_2 \pm$ SE	n	R^2
All Biomes Except Desert					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-0.445 ± 0.038	0.072 ± 0.002	na	2343	0.30
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-1.302 ± 0.059	0.204 ± 0.008	-0.0041 ± 0.0002	2343	0.39
Desert					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-2.970 ± 0.032	0.042 ± 0.002	na	1474	0.34
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-2.993 ± 0.047	0.046 ± 0.006	-0.0001 ± 0.0002	1474	0.34
Boreal Forest					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	0.003 ± 0.031	0.095 ± 0.002	na	466	0.82
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-0.170 ± 0.060	0.127 ± 0.010	-0.0012 ± 0.0004	466	0.82
Temperate Forest					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-0.288 ± 0.061	0.076 ± 0.004	na	497	0.49
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-0.803 ± 0.136	0.146 ± 0.017	-0.0022 ± 0.0005	497	0.51
Northern Shrubland					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-1.171 ± 0.057	0.142 ± 0.006	na	344	0.63
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-1.176 ± 0.100	0.143 ± 0.024	-0.0001 ± 0.0013	344	0.63
Southern Shrubland					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-0.132 ± 0.145	0.026 ± 0.006	na	102	0.15
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-1.020 ± 0.317	0.118 ± 0.030	-0.0020 ± 0.0006	102	0.23
Grassland					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-0.654 ± 0.070	0.077 ± 0.004	na	566	0.45
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-1.531 ± 0.120	0.202 ± 0.015	-0.0035 ± 0.0004	566	0.51
Temperate Agriculture					
$\ln(R) \sim \gamma_0 + \gamma_1 T$	-2.166 ± 0.097	0.134 ± 0.006	na	262	0.66
$\ln(R) \sim \gamma_0 + \gamma_1 T + \gamma_2 T^2$	-3.025 ± 0.138	0.304 ± 0.022	-0.0063 ± 0.0008	262	0.72

Parameters for multivariate regression model of soil respiration (natural log, in µmol C m^{-2} s^{-1}) (*R*) as a function of soil temperature (°C) (*T*), including data from both control and warmed treatments (Models a and b in Table S3). Parameters shown for both the log-linear and log-quadratic temperature response functions. n = sample size, R^2= correlation coefficient. Parameter units: γ_0 = ln µmol C m^{-2} s^{-1}; γ_1 = °C^{-1}, γ_2 = °C^{-2}. All models significant ($p<0.001$). For comparison of model fits, see Table S3. For model parameters of control versus warmed plots, see Table 1.

Table S6.

Comparison of Model Fits (R^2)		
Biome Type	Eq. 3	Eq. 4
All non-desert	0.39	0.33
Desert	0.42	0.40
Boreal Forest	0.82	0.80
Temperate Forest	0.51	0.44
Northern Shrubland	0.63	0.53
Southern Shrubland (no Hungary)	0.60	0.13
Southern Shrubland (includes Hungary)	0.60	0.03
Grassland	0.52	0.39
Agriculture	0.72	0.63

Comparison of model fits (Eq. 3, Eq. 4) evaluating role of soil moisture in driving soil respiration.