LETTERS

Temperature-associated increases in the global soil respiration record

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Soil respiration, R_S, the flux of microbially and plant-respired carbon dioxide (CO_2) from the soil surface to the atmosphere, is the second-largest terrestrial carbon flux[1–3]. However, the dynamics of R_S are not well understood and the global flux remains poorly constrained[4,5]. Ecosystem warming experiments[6,7], modelling analyses[8,9] and fundamental biokinetics[10] all suggest that R_S should change with climate. This has been difficult to confirm observationally because of the high spatial variability of R_S, inaccessibility of the soil medium and the inability of remote-sensing instruments to measure R_S on large scales. Despite these constraints, it may be possible to discern climate-driven changes in regional or global R_S values in the extant four-decade record of R_S chamber measurements. Here we construct a database of world-wide R_S observations matched with high-resolution historical climate data and find a previously unknown temporal trend in the R_S record after accounting for mean annual climate, leaf area, nitrogen deposition and changes in CO_2 measurement technique. We find that the air temperature anomaly (the deviation from the 1961–1990 mean) is significantly and positively correlated with changes in R_S. We estimate that the global R_S in 2008 (that is, the flux integrated over the Earth's land surface over 2008) was 98 ± 12 Pg C and that it increased by 0.1 Pg C yr^{-1} between 1989 and 2008, implying a global R_S response to air temperature (Q_{10}) of 1.5. An increasing global R_S value does not necessarily constitute a positive feedback to the atmosphere, as it could be driven by higher carbon inputs to soil rather than by mobilization of stored older carbon. The available data are, however, consistent with an acceleration of the terrestrial carbon cycle in response to global climate change.

The high measured variability of R_S remains a significant problem in quantifying and predicting carbon fluxes on the scales of ecosystems to the whole Earth[11]. Although our poor understanding of the integrated effect of soil processes argues for a better appreciation of environmental constraints and the kinetic properties of soil organic compounds[12], a complementary way forward is to mine extant data for large-scale patterns and controls on carbon cycling[13,14]. This is particularly true for data on R_S, given the large but fragmented scientific literature on this topic and the lack of any recent meta-analysis or data synthesis[15].

We have assembled a database of all published studies that reported annual R_S data from non-agricultural ecosystems without experimental manipulation; these conditions were met by a total of 1,434 data points (data set S0) from 439 studies, three-quarters of which were published since the last major meta-analysis of R_S studies[15]. These data (Fig. 1) show a significant ($t_{1,425} = 7.357$, $P < 0.001$; Student's t-test with 1,425 degrees of freedom) positive temporal trend after accounting for the effects of climate (mean annual temperature and precipitation), measurement technique, leaf area index[16] (LAI) and nitrogen deposition[17], N_{dep}. The temporal trend remains when the data are limited to the years 1989–2008 (data set S1, 78% of S0; model A in Table 1). This period is roughly when most R_S studies standardized around the use of infrared gas analysers and gas chromatographic techniques[18]; these were the only techniques considered in further analyses of S1.

For the S1 data, temperature and precipitation anomalies (the deviations of these variables in a particular year from the 1961–1990 mean) were highly significant in explaining R_S changes after accounting for the effects listed above (model B in Table 1). Data from both temperate and tropical biomes showed a positive correlation with such anomalies, with in general no remaining temporal trend after climate anomalies had been accounted for. This correlation is not causation: it is possible that R_S is not changing with climate but rather that researchers are sampling higher-R_S points in a pattern that is correlated with, but not caused by, warmer temperatures and higher precipitation. For this reason, we tested LAI and N_{dep} for significance in explaining R_S variability. Remotely sensed LAI (model D) was highly significant ($t_{1,105} = 6.601$, $P < 0.001$) but added little explanatory power to the model, whereas site-specific LAI (that

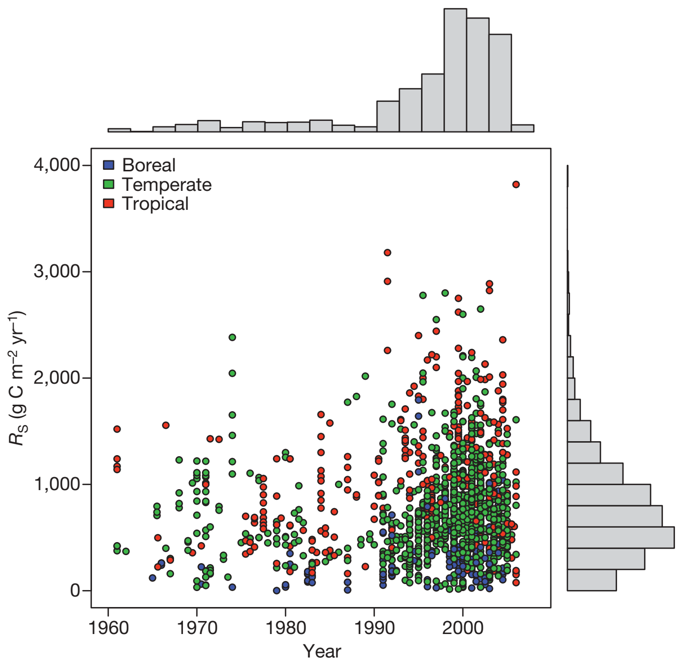

Figure 1 | Collected data on observed R_S, by biome. The 'boreal' biome includes Arctic and high-altitude studies. The histograms show the relative distributions of data along the axes.

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Table 1 | Summary of parameter significance and model diagnostics, by model type

Term*	Model A: no anomaly	Model B: anomaly	Model C: anomaly plus local LAI	Model D: anomaly plus remote LAI
T	4.167×10^{-1}†	3.910×10^{-1}†	4.903×10^{-1}†	4.583×10^{-1}†
P	5.887×10^{-3}†	8.137×10^{-3}†	5.339×10^{-3}†	5.407×10^{-3}†
T_{anom}	—	6.207×10^{-1}§	NS	NS
Boreal	—	−2.405†	ND	−2.405†
Temperate	—	2.420†	1.822†	1.105†
Tropical	—	4.764‡	ND	5.751†
P_{anom}	—	NS	NS	NS
Boreal	—	9.198×10^{-2}†	ND	9.198×10^{-2}†
Temperate	—	1.657×10^{-2}†	3.213×10^{-2}†	2.057×10^{-2}†
Tropical	—	0.006†	ND	1.726×10^{-2}†
L_1	—	—	7.104×10^{-1}†	—
L_2	—	—	—	1.397†
N_{dep}	NS	NS	1.198×10^{-3}‡	NS
Y	1.095×10^{-1}§	NS	NS	1.030×10^{-1}§
AIC	7,575	7,603	1,962	7,573
Adj. R^2	0.341	0.320	0.426	0.340
N	1,112	1,112	302	1,112

Values are regression coefficients for the intercepts shown. The final three rows show the Akaike information criterion (AIC); the adjusted coefficient of determination, R^2; and the number of observations, N. The dependent variable is the square root of annual soil respiration, R_S (g C m^{-2} yr^{-1}). The independent variables include mean annual temperature, T (°C), and precipitation, P (mm); temperature and precipitation anomaly (T_{anom} and P_{anom}, respectively); locally measured LAI, L_1 (unitless); remotely sensed LAI, L_2 (unitless); N_{dep} (kg N ha^{-1} yr^{-1}); and year of measurement, Y. The full model form is given in Methods. A blank cell indicates a term not tested in the corresponding model. ND, no data (<100 observations); NS, not significant.
* For clarity, interactive terms are not shown; †$P < 0.01$; ‡$P < 0.05$; §$P < 0.1$.

is, LAI measured as part of the study reporting R_S; model C in Table 1) improved the model fit but with the loss of three-quarters of the data points, as it is only sporadically reported in R_S studies[16]. Neither local nor remote LAI altered the significance of temperature and precipitation anomalies. In general, N_{dep} explained little R_S variability beyond that due to the effects of climate and LAI.

The number of available published R_S measurements has increased markedly over time (Fig. 1). Our analysis is based on climate anomalies and is thus robust to the fact that more high-flux sites have been measured in recent years, but it would be at least theoretically possible for the jump in measurements between 1989–1998 and 1999–2008, $N = 348$ and 773 respectively, to induce a trend. When the decades are analysed separately, temperate forests (which dominate the data) show a significant trend driven by temperature anomaly ($P = 0.004$ and $P = 0.010$ respectively); the full global data show a weak trend ($P = 0.09$) for 1989–1998, although not for 1999–2008. We thus conclude that the 1989–2008 trend is robust and real.

Although R_S was positively and unsurprisingly[8,15,16] correlated with mean annual temperature, there was a strong negative correlation ($t_{145} = -2.825$, $P = 0.002$) between temperature anomaly and R_S in boreal and Arctic ecosystems (Table 1). This was unexpected, as temperature is assumed to be one of the dominant factors constraining R_S generally[10] and high-latitude carbon cycling in particular[19,20], but the relationship was robust and not driven by, for example, a few influential outliers. Several possibilities could explain this result. First, these data could be correct, in the sense of not being a product of measurement error, sampling bias or some other sample deviation from the parent population. This would imply that warmer boreal temperatures are in fact associated with lower R_S values, for instance if water temperatures are inducing summer water stress in boreal trees[21], thus lowering carbon inputs to the soil and, hence, lowering R_S. Whether this is occurring on such large scales is an open question, but most high-latitude R_S studies have shown increases, not decreases, in climate-driven soil fluxes[22]. A second possibility is that this constitutes a type I (false-positive) error. The boreal data set is relatively small ($N = 145$), and deletion of as few as 10% of the data points makes the R_S/temperature anomaly relationship non-significant. A third, and unlikely, possibility is that there is some systematic error in the climate data used. For global modelling, we took the conservative approach of using a single model that incorporated all S1 data, that is, not fitting biome-specific models that could be compromised by small sample sizes. The resulting model (model B) explained the same amount of observational variability as a biome-specific model, without the questionable relationship between temperature anomaly and R_S at high latitudes.

The S1 data imply that R_S is responding to climate anomalies on the local scale. Climate is only one of many factors controlling decomposition and R_S (ref. 10), but this raises the question of the integrated global effect of these changes. We calculated R_S over the time period covered by these data by using the basic model (model B) to predict grid-cell R_S across the entire terrestrial land surface. We estimate that the annual global R_S in 2008 was 98 ± 12 Pg C, or 85 Pg C if agricultural areas are excluded, and is increasing at 0.1 Pg C yr^{-1} (~0.1% yr^{-1}; Fig. 2). The 0.1 Pg C yr^{-1} increase from 1989 to 2008 was significant ($t_{18} = 5.2$, $P < 0.001$), and a grid-cell-matched, two-sided t-test confirmed ($t_{60,843} = -129.0$, $P < 0.001$) that the computed 2008 global flux was significantly higher than that for 1989. This annual global R_S value is 20–30% higher than previous[3,8,15] estimates. It is, however, consistent with a previous global calculation of the heterotrophic soil flux[23], given the general heterotrophic contribution to R_S (ref. 24). The interannual variability of annual global R_S was 1.5 Pg C, similar to that found in an earlier modelling study[8].

We estimate that boreal, temperate and tropical ecosystems respectively contribute 13%, 20% and 67% to the total annual global flux (Fig. 3); boreal R_S increased by ~7% between 1989 and 2008, and temperate R_S and tropical R_S increased by ~2% and ~3%, respectively. This implies that although the largest absolute change over this time period occurred in tropical regions (1.8 Pg C), R_S in high-latitude ecosystems had the largest relative change, consistent with

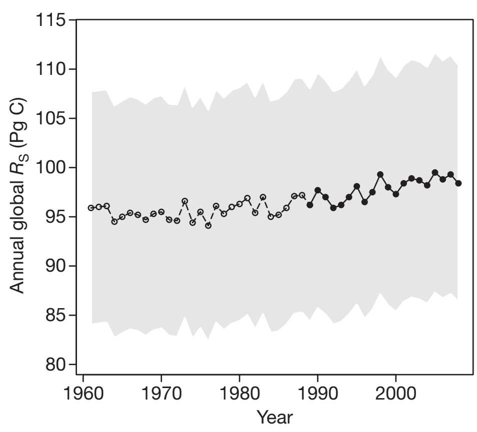

Figure 2 | Estimated annual global R_S. The dashed line indicates results outside the time period covered by main data set, S1 (1989–2008), but within the period covered by the entire R_S database, S0 (1961–2008), and should be considered speculative. The grey region shows the standard deviation of the Monte Carlo simulations ($N = 1{,}000$).

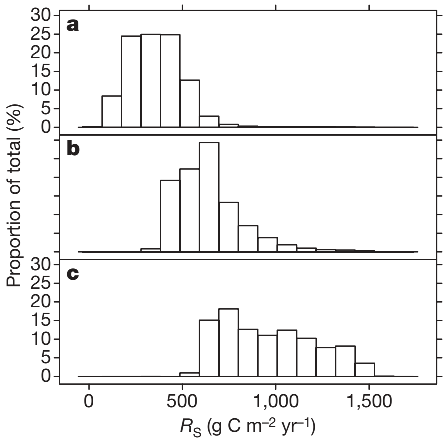

Figure 3 | Histograms of modelled R_S rates by grid cell. **a**, Boreal and high-latitude cells; **b**, temperate cells; **c**, tropical cells.

the large carbon stocks in, and greater degree of climate change being experienced by, these areas. We emphasize, however, that these results are based on the pooled global data set, which is emphatically not a random sample from the terrestrial surface, and that the high-latitude estimates in particular contradict the data collected so far.

These data suggest a moderate response of global R_S to temperature: a Q_{10} (rate of change of R_S with an increase in temperature of 10 °C) of 1.5. This value matches, within confidence limits, global Q_{10} values for R_S (2.1 ± 0.7 and 1.9 ± 0.4) constrained by the observed interannual variability in atmospheric CO_2 using the UK Met Office Hadley Centre coupled global model[11]. This Q_{10} value is based on air temperature (used here because of the availability and high accuracy of global air temperature data) instead of soil temperature; studies using soil temperatures typically report higher Q_{10} values. This positive global R_S response does not necessarily constitute a positive feedback loop between soil and the atmosphere; it could be driven by higher carbon inputs to soil rather than by mobilization of stored older carbon, as the temperature sensitivity[10,25,26] and priming potential[27] of recalcitrant carbon are uncertain. An interesting test is possible here, as a subset of studies using S1 estimated the source fluxes of R_S. In these partitioned R_S data ($N = 206$ measurements; Supplementary Information), the temperature anomaly is significant ($P < 0.05$) and has positive effects, of roughly equal magnitudes, on both the autotrophic and heterotrophic components of R_S. These data are limited and subject to larger errors because of the imprecision in the various methods used to partition R_S sources[24]; nonetheless, they suggest that both these R_S sources are responding to climate changes.

A meta-analysis of observational data cannot prove that the observed R_S trends are caused by climate changes, even if they are correlated with them. Several additional limitations of this study should be noted. The S1 data used here are dominated (86% of the data points) by measurements in well-drained upland sites, but the R_S of peatlands—which store an outsized fraction of global soil organic carbon—may increase more rapidly than a temperature-driven model would predict, driven by permafrost melting and increasing peat oxygenation in addition to temperature changes[22]. Also, measurements from agricultural systems were excluded, unlike in calculations of previous global estimates[3,8,15], because of the high variability in anthropogenic disturbance and fertilization in these systems. Finally, more detailed models that explicitly consider the seasonal R_S cycle[8,16] provide a better long-term framework for analysing R_S changes, although simple models such as those used here, based on annual R_S observations made across a wide range of space and time, provide a unique insight into R_S patterns and its changes with climate. These are all significant limitations of our analysis and the R_S data set on which it is based. Nonetheless, we submit that the trends in these observed R_S data strongly suggest that the global R_S is increasing in response to climate change.

METHODS SUMMARY

We collected all available studies in the scientific literature reporting annual ecosystem R_S measured in the field. A total of 1,434 data points drawn from 439 studies, performed between 1961 and 2008, met these conditions and constituted data set S0. A subset of these data (1,112 data points from 306 studies), spanning 1989–2008 and termed S1, formed the primary basis for study. Global climate, leaf area, cell area and nitrogen deposition data were downloaded from online sources and matched using a nearest-neighbour algorithm to the geographic coordinates of the collected R_S studies. We used linear models to examine the effects of climate (both mean annual climate and climate anomaly), biophysical variables and year of measurement. A square-root transformation was used to stabilize the variance in the observed data and ensure residual homoscedasticity, with observations weighted by the years of observed data reported for each R_S data point. Models were checked for influential outliers using a Cook's distance threshold and refitted, if necessary, after outlier removal. Global fluxes were estimated using the fitted model driven by the cell area, leaf area and climate data mentioned above. We used a Monte Carlo approach to propagate model errors to global estimates. All statistics and modelling were performed using the R statistical computing package[28] (version 2.9.1). Supplementary Information contains all code and data (or links to data sources) necessary to reproduce these results.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions B.B.-L. and A.T. designed the study. B.B.-L. collected studies and analysed data, and with A.T. wrote the manuscript.

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METHODS

We collected all available studies in the scientific literature reporting annual ecosystem R_S measured at unmanipulated field sites. To qualify for inclusion, a study had to report R_S (or allow for R_S to be calculated with few or no assumptions) as well as the dates, location and method of measurement. Additional data collected, when possible, included ecosystem LAI; mean annual temperature, T, and precipitation; heterotrophic and autotrophic contributions to R_S; and ecosystem state (managed, unmanaged or natural). A total of 1,434 data points drawn from 439 studies, performed between 1961 and 2008, met these conditions and constituted data set S0. A subset of these data (1,112 data points from 306 studies), spanning 1989–2008 and termed S1, formed the primary basis for study. In the S1 time period, R_S measurements have generally been standardized around the use of infrared gas analysers and gas chromatography[18], and we limited analysis to studies using these two techniques. The data were broadly categorized into 'tropical' ($T > 17\,^{\circ}\mathrm{C}$), 'boreal' and high-latitude or -altitude ($T < 2.0\,^{\circ}\mathrm{C}$), and 'temperate' (everything else).

Additional data sources. Global climate data sets ('Monthly Mean Air Temperature (Global 1900–2008)' and 'Monthly Total Precipitation (Global 1900–2008)') were downloaded from the Center for Climatic Research at the University of Delaware (http://climate.geog.udel.edu/~climate/); these data were used because of their high spatial resolution and currency (through 2008). The ECOCLIMAP global LAI data set[29] was downloaded and processed on a 5′′ scale (~10 km). A global N_{dep} data set (5°) from the Oak Ridge National Laboratory Distributed Active Archive Center (http://webmap.ornl.gov/wcsdown/wcsdown.jsp?dg_id=830_2) was also incorporated. Global grid area data (0.5°) were downloaded from the EOS-WEBSTER digital library at the University of New Hampshire (http://eos-webster.sr.unh.edu/). The non-agricultural land fraction was estimated using a global land-use database[30]. These data sets were matched using a nearest-neighbour algorithm to the geographic coordinates of the collected R_S studies. Climate anomalies were then computed for each R_S data point as the year-specific temperature or precipitation value minus the 1961–1990 mean value for that 0.5° grid cell; the computed anomalies are included in Supplementary Information.

Statistical procedures. We used linear models to examine the effects of climate (both mean annual climate and climate anomaly), biophysical variables and year of measurement. An automated process (the 'step' function in R; ref. 28) removed and added model terms, starting from a complete formula encompassing all independent variables and their interactions:

$$\sqrt{R_S} = T + T^2 + P + P^2 + T * P + T_{anom} + T * T_{anom} + P_{anom} + P * P_{anom} + L + N_{dep} + Y$$

where R_S is annual soil respiration, T is the mean annual temperature, P is the mean annual precipitation, T_{anom} and P_{anom} are the respective associated anomalies, L is the LAI, N_{dep} is the nitrogen deposition, Y is the year of measurement and '*' indicates a term interaction. (Further details on model formulation are given in Supplementary Information.) Term selection was based on Akaike information criterion. A square-root transformation was used to stabilize the variance in the observed data and ensure residual homoscedasticity. Observations were weighted by the years of observed data reported for each R_S data point, to account for studies that reported multi-year R_S means. Models were checked for influential outliers using a Cook's distance threshold of 0.5 and refitted, if necessary, after outlier removal. Data from the years 1989–2008 formed the basic analytical set, because older measurement methods were used before this.

Global fluxes were estimated using the fitted model(s) driven by the cell area, leaf area and climate data from the sources listed above. We used a Monte Carlo approach to propagate model errors to global estimates. For each trial ($N = 1{,}000$ in total), a new, random, model was generated on the basis of the estimate and standard error for each parameter in the original fitted model, and used to compute the annual global R_S for each year in the period 1961–2008. Means and 95% confidence intervals were then computed from the final data set generated by all random models. A global Q_{10} response was calculated using two linear models fitted respectively to the 1989–2008 annual global R_S and mean global air temperature. The Q_{10} calculation was based on the fitted end-point values in 1989 and 2008. All statistics and modelling were performed using the R statistical computing package[28] (version 2.9.1). Supplementary Information contains all code and data (or links to data sources) necessary to reproduce these results.

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