The influence of soil communities on the temperature sensitivity of soil respiration

Article

Accepted Version

Johnston, A. S. A. and Sibly, R. M. ORCID: https://orcid.org/0000-0001-6828-3543 (2018) The influence of soil communities on the temperature sensitivity of soil respiration. Nature Ecology & Evolution, 2. pp. 1597-1602. ISSN 2397-334X doi: 10.1038/s41559-018-0648-6 Available at https://centaur.reading.ac.uk/78849/

To link to this article DOI: http://dx.doi.org/10.1038/s41559-018-0648-6

Publisher: Nature

The influence of soil communities on the temperature sensitivity of soil respiration

Alice S.A. Johnston[1*], Richard M. Sibly[1]

[1] School of Biological Sciences, University of Reading, UK.
* Corresponding Author:
alice.johnston@reading.ac.uk; +44 (0)118 378 6439
School of Biological Sciences, University of Reading, Reading, RG6 6AH

Soil respiration represents a major carbon flux between terrestrial ecosystems and the atmosphere, and is expected to accelerate under climate warming. Despite its importance in climate change forecasts, however, our understanding of the effects of temperature on soil respiration (R_S) is incomplete. Using a metabolic ecology approach we link soil biota metabolism, community composition and heterotrophic activity, to predict R_S rates across five biomes. We find that accounting for the ecological mechanisms underpinning decomposition processes predicts climatological R_S variations observed in an independent dataset (n = 312). The importance of community composition is evident because without it R_S is substantially underestimated. With increasing temperature, we predict a latitudinal increase in R_S temperature sensitivity, with Q_{10} values ranging between 2.33 ±0.01 in tropical forests to 2.72 ±0.03 in tundra. This global trend has been widely observed, but has not previously been linked to soil communities.

Soils store the majority of Earth's terrestrial carbon, and so play a crucial role in the direction and magnitude of future climate changes[1]. However, the influence of ongoing climate change on the soil carbon sink is a major area of uncertainty[2-4]. Temperature-associated increases in the global soil CO_2 flux (soil respiration, R_S) has led to the supposition that global warming will drive a positive soil-climate feedback[5,6]. Of particular concern is the potential long-term vulnerability of large soil C stocks at high latitudes[7]. However, our incomplete understanding of the temperature – R_S relationship limits constrained forecasts of terrestrial carbon fluxes in the future[8].

The temperature sensitivity of R_S across ecosystems is a key determinant of the soil-climate feedback, but it is difficult to quantify due to the many confounding factors that affect soil metabolic rates[2,9]. For instance, Q_{10} values (the proportional increase in R_S with a 10 °C increase in temperature) are highly variable across different vegetation types and climates[2,10]. Nevertheless, Earth system models (ESMs) typically assume a globally constant temperature sensitivity by incorporating fixed Q_{10} values of around 2 (that is, R_S rates double with an increase in temperature of 10 °C)[11,12]. Thus, while there is a growing consensus that future warming will enhance R_S rates, how the response will vary across climatic regions and soil characteristics is not well established[13,14]. Here, we propose that a better understanding of R_S temperature sensitivity can be gained by accounting for the various organisms that live in the soil.

Soil respiration is the biotic conversion of organic C to CO_2 by all of the organisms (heterotrophs: soil microbes and fauna, and autotrophs: plant roots and their mycorrhizal symbionts) that live in the soil. Thus, R_S rates are the product of the body sizes, metabolic rates, abundances and community composition of soil-inhabiting organisms[15-18]. Because individual metabolic rates exhibit varying temperature sensitivities[19], we would also expect R_S responses to increasing temperatures to fluctuate according to soil community composition. However, empirical quantification of soil biota contributions to R_S at large spatio-temporal scales is complicated by the vast biodiversity and complexity of soil systems[20].

In this study, we use a model derived from metabolic theory[21] to integrate soil biota metabolism, community composition and heterotrophic activity in R_S estimates across biomes. The model accounts for the way in which metabolic rates vary with temperature and body size between soil community groups. We then extrapolate to heterotrophic respiration (R_H) rates by accounting for the abundance of soil biota across tundra, boreal forest, temperate forest, temperate grassland and tropical forest soils. By quantifying the contribution of R_H to R_S, using an R_H fraction (H_F) which accounts for autotrophs (plant roots and their symbiotic mycorrhizae) not modelled here, we predict R_S across biomes and mean annual temperature (MAT) ranges. To test the hypothesis that soil community traits strongly influence R_S temperature sensitivities, we compare models that do or do not account for metabolic variation of soil biota. To test how predictive our approach is, we make a further comparison with a classical linear regression fitted to the R_S data. Finally, we increase study-specific MAT’s by 10 °C to compare Q_{10} estimates with available data across the five biomes, and discuss how these compare to those Q_{10}’s used in ESMs and observed in long-term field experiments.

Results

Metabolic ecology of soil communities

Metabolism underpins fundamental mechanisms of organism-environment interactions, and sets the basis for linking individual to ecosystem processes[22]. To investigate the temperature sensitivities of metabolism for diverse soil communities, we compiled a metabolic dataset for fourteen soil biota groups (bacteria, protozoa, nematode, collembola, enchytraeidae, acari, ant, beetle, isopod, centipede, spider, termite, millipede, earthworm). The dataset (n = 3768) covers nearly 15 orders of magnitude in body mass (M) and temperatures (T) between -2 and 40 °C. In the first instance, the metabolic dataset was fitted to the linear form of the metabolic scaling equation without accounting for variations in metabolic parameters between soil biota (termed the 'general' model herein):

$$\ln(B) = \ln(B_0) + a \ln(M) - E/kT \qquad (1)$$

where B is standard metabolic rate (J hr^{-1}), B_0 is a taxon-specific normalisation constant, a represents the allometric scaling exponent which usually takes a value close to ¾, E is the activation energy (eV), k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) and T is experimental temperature (K)[21]. General model (Equation (1)) regression analysis yields an allometric exponent, a, of 0.81 (±0.002) and activation energy, E, of 0.67 (±0.01) (Supplementary Table 1). Both metabolic parameters are within the range predicted by the metabolic theory of ecology (MTE), a: 0.67 – 1 and E: 0.6 – 0.7 eV[23,24]. Yet, while the general model predicts metabolic rates with individual body mass well, it does not capture the apparent high variation in soil biota temperature sensitivities (Supplementary Figure 1), indicating the need to account for metabolic traits between soil community groups.

Soil biota were classified into community groups according to their body size distribution as microbes (< 0.0001 mg FM), mesofauna (0.0001 – 8 mg FM) or macrofauna (> 8 mg FM). Microbes include bacteria, mesofauna include protozoa, nematode, acari, collembola and enchytraeidae groups, and macrofauna include ant, spider, isopod, centipede, beetle, termite, millipede and earthworm groups. Although protozoa and nematodes are technically classified as microfauna rather than mesofauna, the metabolic data for these groups were collected at a single experimental temperature. Thus, regression analysis by soil biota groupings was not possible. The community group (CG) model includes two-way interaction terms between CG – body mass and CG – temperature to yield community-specific metabolic parameters (B_0, a & E):

$$\ln(B_{\mathrm{CG}}) = \ln(B_{0\mathrm{CG}}) + a_{\mathrm{CG}} \ln(\mathrm{M}) - E_{\mathrm{CG}}(1/kT) \qquad (2)$$

CG model (Equation (2)) analysis yields ranges in a from 0.66 to 0.87 and E from 0.64 to 0.74 eV (Figs. 1a & b, Supplementary Table 1). Interestingly, analysis of the CG model reveals that the temperature sensitivity of metabolism (E) increases with decreasing body size, from 0.64 (±0.01) for macrofauna to 0.74 (±0.19) for microbes (Supplementary Table 1). That is, smaller sized soil community groups exhibit a greater proportional increase in their metabolic rates with a given increase in temperature, than individuals belonging to larger size community groups. This suggests a higher contribution of soil microbes (in particular, as mass-specific metabolic rates in mesofauna are lower) to R_S rates at increasing temperatures, if resources are available to fulfil higher energy requirements. The distribution of the CG model residuals against the independent variables (body mass and temperature, Figs. 1c & d) and fitted lowess line, further indicate an absence of systematic errors, which are much greater for the general model (Supplementary Figure 1).

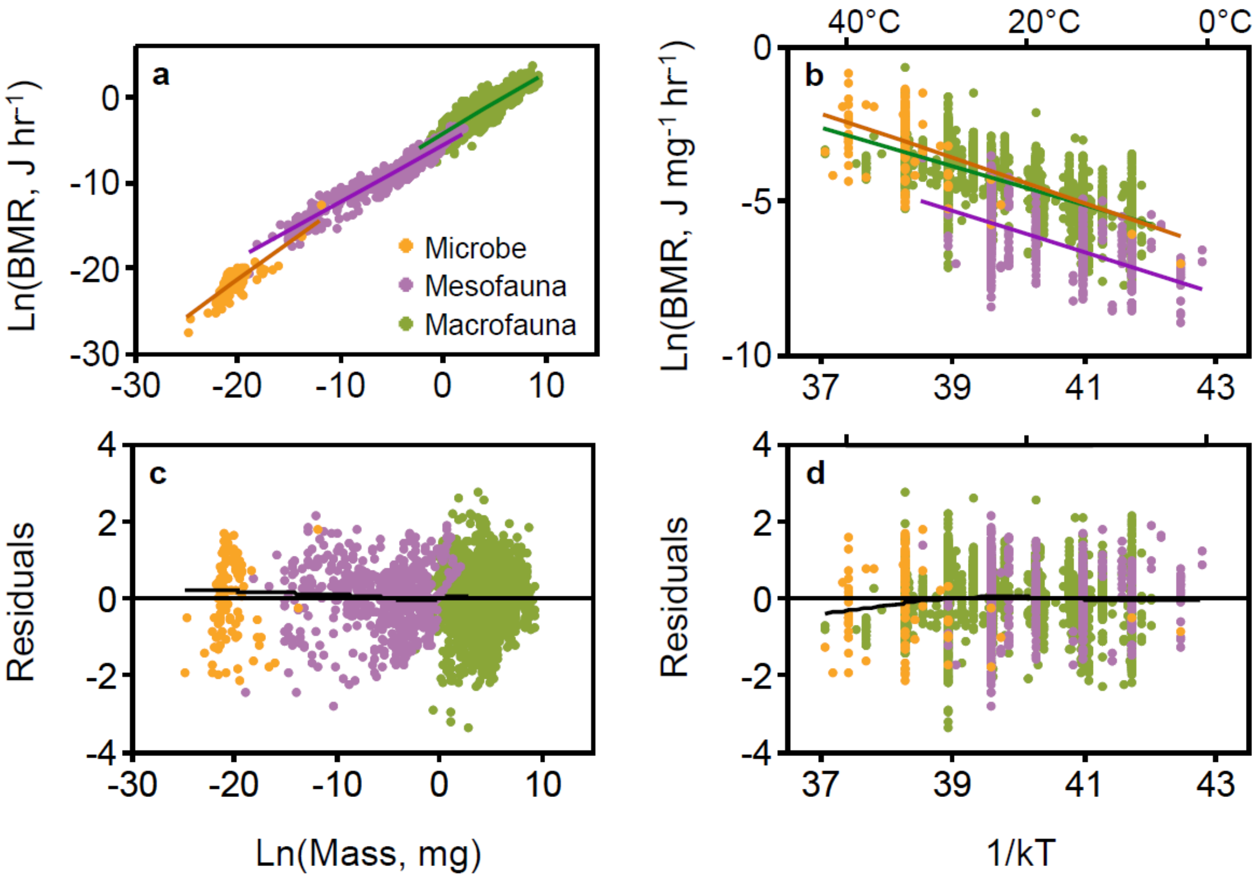

Figure 1. Metabolic scaling relationships in soil communities. Left-hand plots (a & c) show individual metabolic rates (*B*), corrected to a temperature of 20 °C using equation (2), plotted against individual body mass (*M*, mg FM). Right-hand plots (b & d) show *B*, corrected to a body mass of 1 mg using equation (2), plotted against temperature in an Arrhenius plot. Top plots (a & b) show community group (CG) model predictions of metabolic rates with individual body mass and temperature, and bottom plots (c & d) show distributions of the CG model residuals, with deviations of the data from model predictions characterised by lowess fits (black curves). Microbes (orange) include bacteria, mesofauna (purple) include protozoa, nematodes, acari, collembola and enchytraeidae, and macrofauna (green) include ant, spider, isopod, centipede, beetle, termite, millipede and earthworm groups (n = 3768). Metabolic parameter values are provided in Supplementary Table 1.

Linking soil metabolism to biome-specific R_S rates

Linking the individual metabolic rates of soil biota to biome-specific R_S (g C m^{-2} year^{-1}) requires quantification of soil biota population abundances (*A,* no. m^{-2}) and R_H fractions (H_F, which measure the proportion of R_S contributed by heterotrophs and so also accounts for autotrophs) across biomes. First, individual-level metabolic rates (*B*, as in equation (2)) for each soil biota group (*i*) were calculated for an individual of average body mass *(M)* at a given MAT (*T*). *B* is then converted to respiration rate units (g C yr^{-1}) by using the conversion factors 37490 J gC^{-1} = 20100 J LO$_2^{-1}$ × (1 / 0.5363 g C LO$_2^{-1}$) [25,26] and 8760 hr yr^{-1}. The heterotrophic respiration rate (R_H) is the soil community's respiration rate, which is calculated according to individual-level respiration rates (r_i) and population abundance (A_i) as: $R_H = \sum_i r_i A_i$, where the summation is over the soil biota groups in the biome. Our R_H predictions are compared to independent data in Supplementary Figures 2 & 3. Finally, accounting for H_F's reported in the Bond-Lamberty and Thomson [27] dataset (Supplementary Figure 4, n = 66) gives: $R_S = \frac{1}{H_F}\sum_i r_i A_i$. R_S was calculated at MAT for each of the R_S studies used to evaluate our approaches predictions (n = 312), using metabolic parameters, individual body masses and soil biota population abundances in Supplementary Tables 2, 3 & 4 respectively.

Soil community composition across biomes

Population biomass (g FM m^{-2}) and abundance (number m^{-2}) measurements for the fourteen soil biota groups for which metabolic data is available were collected across tundra, boreal forest, temperate forest, temperate grassland and tropical forest soils (n = 2187). Community group biomasses across the five biomes investigated here were significantly different ($p = 0.000$, Supplementary Table 5). In general, high latitude (tundra and boreal) soils harbour more soil microbes and mesofauna by biomass than temperate and tropical soils. Soil macrofauna follow an inverse trend, increasing in biomass from tundra to temperate grasslands and tropical forests (Fig. 2). Given the higher temperature sensitivity of smaller sized soil biota (Fig. 1), we would expect higher abundances of soil microbes and mesofauna in tundra and boreal soils to be linked to higher R_S temperature sensitivities at high latitudes.

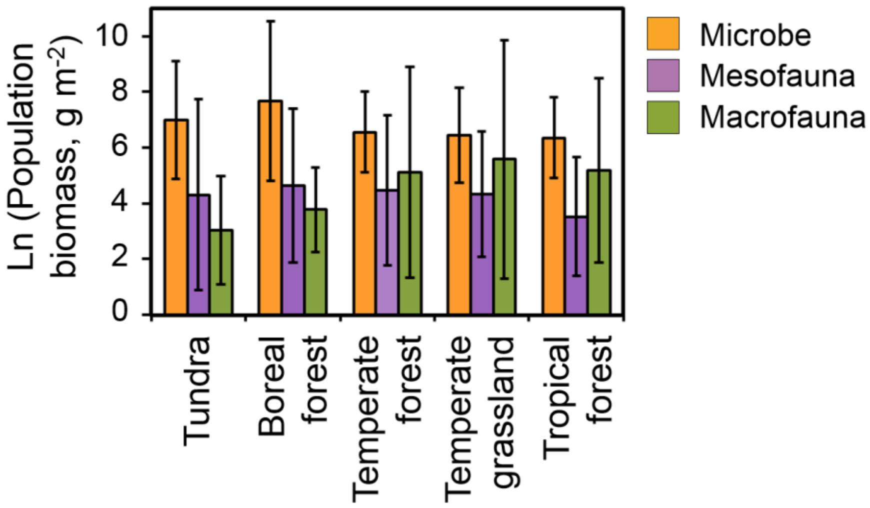

Figure 2. Soil community composition across biomes. Soil community groups are classified by body size distribution (microbe, mesofauna and macrofauna). Biomass (g fresh mass m^{-2}) measurements incorporate the sum of soil biota population biomasses for each community group. Average biome-specific soil microbial biomasses were taken from the study of Xu et al. [28], while soil mesofauna and macrofauna data were compiled in this study (n = 2187, Supplementary Figure). Presented values are means ± reported standard errors for microbes, while error bars for mesofauna and macrofauna were calculated as the square root of the summed variances for soil biota group population biomasses. Differences in community group biomass are significantly different across biomes (*p* = 0.000, Supplementary Table 5).

***The influence of soil communities on R_S* across biomes**

Comparison of our R_S predictions (lines) with independent R_S data (symbols) in Fig. 3a demonstrates good prediction of R_S rates across biomes and MAT's (R^2 = 0.66, n = 312, no *p*-value can be reported as predictions are independent of the data). Temperature sensitivity differences across biomes emerge from the approach by integrating variation in the metabolic ecology and community composition of soils. However, high variability in the R_S data likely points to site-specific interactions between individual, population and community-level dynamics with other environmental factors (e.g. resource quantity and quality), as well as temperature (Fig. 3b).

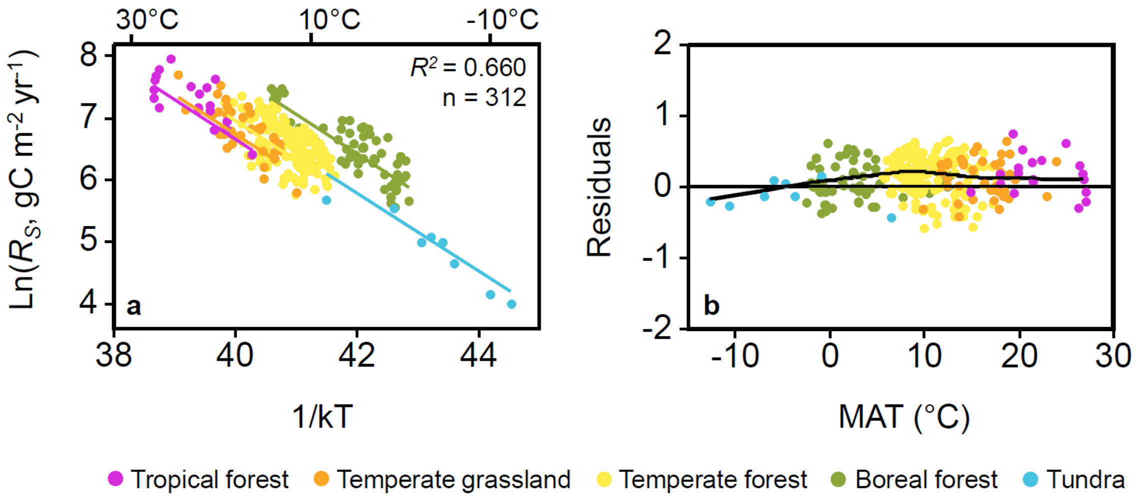

Figure 3. Temperature sensitivity of soil respiration (R_S) across biomes and MAT's. Plots show a) independent R_S data (symbols: n = 312) and predicted R_S from the community group (CG) model presented here (lines) and b) CG model residual distributions against MAT (°C) with fitted lowess line (solid black line).

To test whether incorporating the varying temperature sensitivities of soil biota was important in achieving good R_S predictions (Fig. 3 and 4a), we compare the CG model presented here to R_S predictions using the general model (Fig. 4b) and a linear regression between R_S and MAT fitted to the data (Fig. 4c). Not accounting for metabolic variation between soil community groups in the general model significantly reduces the accuracy of the metabolic approach (Fig. 4b). This result indicates that soil community body size distribution and metabolic ecology strongly influence the temperature sensitivity of R_S across the five biomes investigated here. Comparison of the CG model with the linear regression ($\mathrm{Ln}(R_S) = 22.54 - 0.388\ (1/kT)$, Fig. 4c) and AIC values, further indicates that accounting for soil ecology enables better R_S predictions. Improved prediction of R_S rates are particularly evident in boreal and tundra soils of the CG model, where the data indicate higher R_S temperature sensitivity (Fig. 3a). Weak temperature control in the linear regression presented here and ESMs which implement fixed Q_{10} values are unable to capture these climatological differences in R_S temperature sensitivities[7], with serious consequences for future climate change projections.

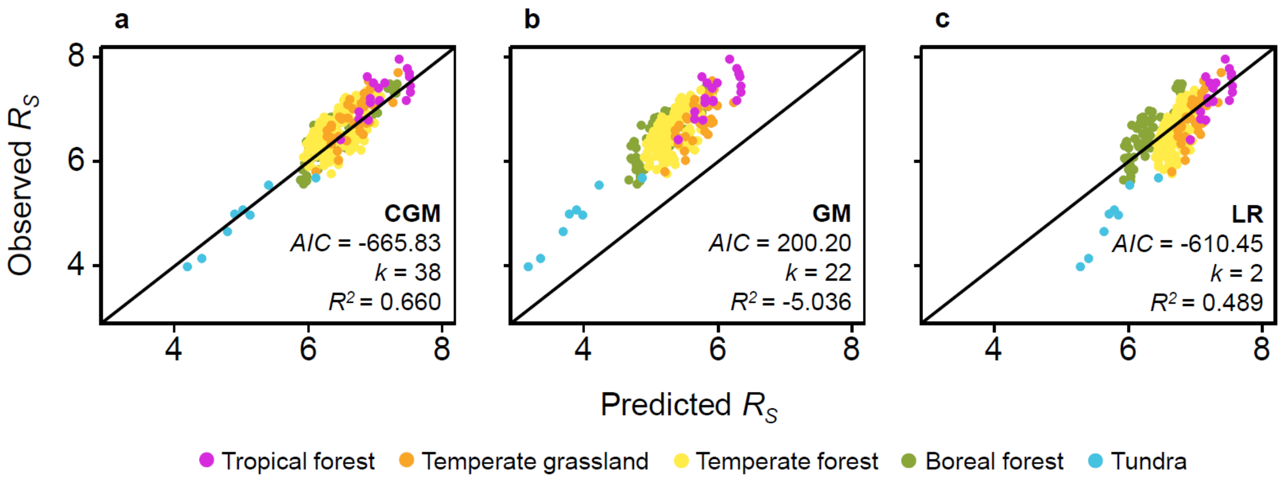

Figure 4. Model comparisons and goodness of fits with independent soil respiration (R_S, gC m^{-2} $year^{-1}$) data. The community group model (CGM) (a) is compared to the general metabolic model (GM) (b) which does not account for metabolic variation in soil communities, and an empirical fitted linear regression (LR) to the R_S data ($\mathrm{Ln}(R_S) = 22.54 - 0.388\,(1/kT)$, $r^2 = 0.489$, $p < 0.0001$) (c). p-values cannot be calculated for a & b as predictions are independent of the data. Solid black lines are 1:1 lines which would demonstrate perfect prediction and lower AIC values indicate a better goodness of fit to the data while accounting for model complexity (k: number of parameters). Note that the r^2 value for the general model (b) is negative because the residual sum of squares from the model is higher than the total sum of squares from the data.

Biome-specific Q_{10}’s were calculated, using the CG model, by taking R_S rates for study-specific MAT’s (MAT_0, n = 119) and for an increase in temperature of 10 °C (MAT_{+10}), to give $Q_{10} = R_S(MAT_{+10}) / R_S(MAT_0)$. We compare our median Q_{10} values (symbols) to those reported in the Bond-Lamberty and Thomson [27] dataset (boxes) in Fig. 5. With increasing temperature, the metabolic approach indicates that R_S in tundra and boreal soils is more temperature sensitive than temperate and tropical soils, with mean Q_{10} values increasing from 2.33 ±0.001 in tropical forests to 2.72 ±0.03 in tundra. Many studies have reported similar climatological responses, in which R_S in colder high latitude climates increase more rapidly with increasing temperature[7,8,10,27,29-33], but none have yet linked variations in R_S temperature sensitivity to the mechanisms driving decomposition processes by soil communities. However, our estimates also assume static biome-specific soil communities, and that greater metabolic rates at higher temperatures are met with sufficient food resources.

Temperature, soil water and resource availability interact to affect the provision of food resources to soil communities[34], and the inclusion of these environment-community feedbacks would likely result in lower R_S sensitivity predictions in warm climates as the soil biota become food limited[15]. Conversely, freeze-thaw cycles in tundra soils lead to deviation of R_S temperature dependence from thermodynamic laws [7], increasing below 0 °C as the decomposition of structurally complex molecules by arctic microbes exhibit a higher temperature sensitivity of metabolism[35]. Our Q_{10}

estimates thus overestimate tropical soil and underestimate tundra and boreal soil responses to increasing temperatures (Fig. 5), in line with long-term field Q_{10}'s of 5.2 ±2.4 for tundra and boreal, 2.7 ±1.7 for temperate and 2.2 ±0.9 for tropical climates[36]. Exploring alternative thermodynamic hypotheses, such as non-linear temperature curves and acclimatisation mechanisms, could explain more of the variability in the Q_{10} data and Q_{10}'s under long-term warming. On the other hand, our approach estimates much higher Q_{10} values than the static value of 2 used in many ESMs, which are often parameterised with short-term observations based on eddy covariance fluxes and soil incubations[2,37]. This divergence between short- and long-term Q_{10} values has been suggested as evidence for the inclusion of emergent behaviour over long timescales[7], which in this study includes the metabolic response of soil communities and shifts in soil community composition across biomes.

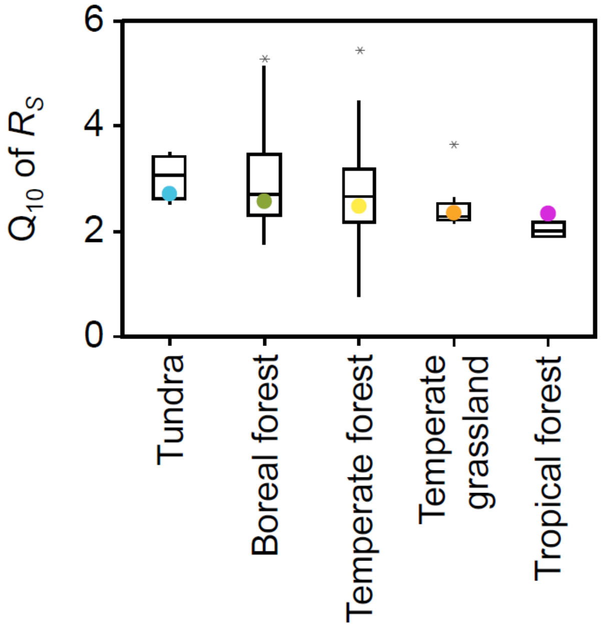

Figure 5. Observed and predicted Q_{10} values for R_S across biomes. Q_{10} data from the Bond-Lamberty and Thomson [27] dataset (n = 119) presented as boxes with the median and first and third quartiles shown. CG predictions of Q_{10} values across biomes are given by coloured symbols, showing median predicted values, with imperceptible first and third quartile whiskers.

Discussion

We use a metabolic ecology approach to better understand the relationships between soil biota metabolism, community composition and R_S rates. We find that accounting for the metabolic ecology of soils (Fig. 1) together with soil community composition (Fig. 2) reveals variations in R_S with MAT across five biomes (Fig. 3). Important in achieving good R_S predictions was incorporating the varying temperature sensitivities of soil community groups. In comparison, assuming all soil biota exhibit identical temperature sensitivities resulted in substantial under-estimation of R_S rates (Fig. 4b). The metabolic ecology and body size distribution of soil communities thus strongly influence the temperature sensitivity of R_S across biomes. With increasing temperature, our approach suggests that R_S would be most strongly enhanced in colder climatic regions (Fig. 5), because of the higher temperature sensitivity of soil biota inhabiting these soils.

Soil community composition will also be influenced by multiple global drivers (e.g. warming, CO_2 fertilisation, N deposition) in the future, which will alter the direction and magnitude of R_S responses. Thus, to better anticipate the effects of global environmental changes on R_S requires a better understanding of the ecological mechanisms underpinning macroecological patterns in soil communities. Yet, fundamental knowledge gaps in soil ecology need to be addressed to understand the primary drivers of soil community composition across a broad spectrum of environmental variables. Unravelling these complex interactions would allow us to represent the mechanistic links between the belowground and aboveground components of terrestrial ecosystems, develop more predictive models of soil systems and improve forecasts of future climate changes on numerous ecosystem functions, including R_S. Our study stresses the importance of considering the soil organisms which facilitate ecosystem functions, and demonstrates the utility of fundamental ecological principles in describing complex soil systems.

Methods

Metabolic ecology of soil biota. Metabolic data for a wide range of soil biota was compiled from the dataset of Ehnes, et al. [19], which includes data from the meta-analyses of Meehan [38] and Chown, et al. [39] together with their own measurements for acari, collembola, enchytraeidae, centipedes, millipedes, isopods, spiders, ants, beetles, termites and earthworms (n = 3399). In addition, we compiled data for bacteria from Makarieva, et al. [40] (n = 56), protozoa from Laybourn and Finlay [41] and Fenchel and Finlay [42] (n = 143), nematodes from Klekowski, et al. [43] and Ferris, et al. [44] (n = 105) and enchytraeidae from Nielsen [45] (n = 58). Detailed differences at the species-level are avoided in order to explore the collective metabolism of soil community groups across biomes. All measurements were converted to wet weight (mg) and standard metabolic rate per hour ($J\ hr^{-1}$), using a dry to fresh mass ratio of 0.2:1[19], 1 mL O_2 = 20.1 J[26] and 1 mL O_2 = 0.5363 mg C[25].

Soil biota populations and community composition. Linking individual to population-level metabolism requires estimation of the population abundances of different soil biota across biomes. Here, we extend the dataset of Fierer, et al. [46], who collected population biomass data for acari, collembola, enchytraeidae, nematodes and earthworms in tundra, boreal forest, temperate forest, temperate grassland and tropical forest soils (n = 799). We compiled additional data for all of the soil biota groups and biomes of Fierer, et al. [46], and for ants, beetles, centipedes, isopods, millipedes, protozoa, spiders and termites in biomes for which data was available (n = 1382). Average biome-specific microbial biomass values were taken from the extensive review of Xu, et al.

[28], which compiles 1182 measurements across the biomes investigated here (Supplementary Table 4).

Population biomass measurements required conversion to population abundance by estimates of mean individual body masses (*M*) for the fourteen different soil biota groups. We assume that *M* for different soil biota groups are constant across biomes. Although this assumption likely introduces error due to variations in individual life histories across climates, not enough information exists to apply more detailed individual-level relationships. To minimise error we collated data from a number of sources reporting *M* for the different soil biota groups (Supplementary Table 3). Average *M* (mg dry mass) used in this study were: protozoa (6.55×10^{6}), nematodes (0.0020), acari (0.0096), collembola (0.055), enchytraeidae (0.055), ants (2.23), beetles (4.35), isopods (4.47), centipedes (6.59), spiders (7.42), termites (9.90), millipedes (17.06) and earthworms (52.37). All population biomass measurements are expressed here as fresh mass (g FM/m^{2}) using the conversion to fresh mass of five times dry mass[19]. Using a single dry to fresh mass conversion factor for all soil biota groups will also introduce some error, as variations likely exist across soil biota groups and biomes[47]. Measurements given in the dataset of Fierer et al. [46] (g C m^{-2}) were further corrected by accounting for a 50 % carbon content. We do not make additional extrapolations to specific soil depths, as this is highly variable between soil biota groups and soil types, and often not reported in field studies. If population measurements were expressed on per mass of dry soil basis, appropriate bulk density values were used to convert these measurements to density (per m^{2}) for the soil type reported.

Heterotrophic respiration (R_H) . Using our metabolic approach, R_H rates were estimated by summing the metabolic rates of soil communities at MAT in a given biome. Community-level metabolic rates were calculated by taking metabolic parameters (B_0, *a* and *E*; Supplementary Table 1) for each soil community group, individual body masses (*M*, mg fresh mass) for each soil biota group (Supplementary Table 3) and their population abundance (*A*, number m^{-2}) in different biomes (Supplementary Table 4). Metabolic rates were then transformed to respiration rates (g C) by using the conversion factors 37490 J gC^{-1} = 20100 J LO$_2^{-1}$ × (1 / 0.5363 g C LO$_2^{-1}$) [25,26] and 8760 hr yr^{-1}. To investigate whether our model predicts R_H rates across biomes and MAT’s, prior to extrapolating to R_S as detailed below, we compared our predictions with available R_H data in the Bond-Lamberty and Thomson [27] dataset (n = 66). R_H data were compiled for un-manipulated field studies reporting annual R_H and R_S rates, and were averaged for single study years and/or locations where applicable. Measurements were also excluded if reported R_H rates were equal to or higher than reported R_S rates. If MAT’s were not reported, or the same MAT was given for multiple years in the same study, NOAA weather stations were used to collect MAT measurements based on the study sites latitude and longitude (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation). The CG model’s predictions of R_H rates were then evaluated ($r^2 = 0.757$, Supplementary Figure 2), in comparison to the general metabolic model ($r^2 = -2.261$) and a linear regression approach ($r^2 = 0.529$) (Supplementary Figure 3). Accounting for model complexity in *AIC* calculations indicates that the CG model does not perform better than the linear regression given its large number of parameters, but this may be a result of the limited size of the data set. To test whether the CG approach performs better given more data we used the R_H data to calculate an R_H fraction (H_F) for each biome to account for the contribution of heterotrophs to R_S. This allowed us to use the larger R_S data set (n = 312) to evaluate the CG model with greater precision as reported in Fig. 4.

R_H fraction (H_F)

R_H fractions (H_F) were calculated as R_H / R_S for studies reporting both annual R_H and R_S rates (g C m^{-2} $year^{-1}$, n = 66) and assuming $R_S = R_H + R_A$[48]. By using R_H values, rather than R_A, we avoid some of the issues in separating heterotrophic and autotrophic contributions to R_S, as R_H is typically measured directly whereas R_A is typically derived by calculating the difference between R_S and other ecosystem fluxes[48]. Mean H_F ±SE across the five biomes investigated here were 0.39 ±0.10, 0.63 ±0.02, 0.58 ±0.03, 0.63 ±0.04 and 0.77 ±0.07 for tundra, boreal forest, temperate forest, temperate grassland and tropical forest soils, respectively. Variability in H_F within biomes is likely linked to the experimental difficulties associated with separating the autotrophic and heterotrophic components of soils and the methodology used to do so in the field[48-50]. To explain some of this variability, and to account for the temperature sensitivity of R_A, we performed a regression analysis between H_F and MAT, which revealed a weak but significant positive correlation ($H_F = 0.54 + 0.0069$ MAT; $r^2 = 0.104$, $p = 0.008$, Supplementary Figure 4). This linear relationship is incorporated in our calculations to extrapolate from R_H to R_S rates across biomes and MAT’s.

Soil respiration (R_S)

To compare our R_S estimates with independent data, annual R_S rates (g C m^{-2} yr^{-1}) were compiled from the global soil respiration datasets of Bond-Lamberty and Thomson [27] and Carey, et al. [51] for tundra, boreal forest, temperate forest, temperate grassland and tropical forest soils (n = 312). Data were included from un-manipulated field studies reporting average annual R_S and MAT, and measurements from both datasets were averaged for single study years and/or locations where applicable. R_S measurements compiled from the Bond-Lamberty and Thomson [27] dataset included 119 Q_{10} values, which were used to evaluate predicted Q_{10}’s across biomes using our CG model.

Data availability. The datasets generated and analysed during the current study are available on Dryad (https://doi.org/10.5061/dryad.416kv03).

References

1 Hicks Pries, C. E., Castanha, C., Porras, R. C. & Torn, M. S. The whole-soil carbon flux in response to warming. *Science* **355**, 1420-1423, doi:10.1126/science.aal1319 (2017).

2 Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165-173 (2006).

3 Crowther, T. W. *et al.* Quantifying global soil carbon losses in response to warming. *Nature* **540**, 104-108 (2016).

4 Bradford, M. A. *et al.* Managing uncertainty in soil carbon feedbacks to climate change. *Nature Climate Change* **6**, 751-758 (2016).

5 Bond-Lamberty, B. & Thomson, A. Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579-582 (2010).

6 Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184-187 (2000).

7 Koven, C. D., Hugelius, G., Lawrence, D. M. & Wieder, W. R. Higher climatological temperature sensitivity of soil carbon in cold than warm climates. *Nature Climate Change* **7**, 817-822 (2017).

8 Giardina, C. P., Litton, C. M., Crow, S. E. & Asner, G. P. Warming-related increases in soil CO2 efflux are explained by increased below-ground carbon flux. *Nature Climate Change* **4**, 822-827 (2014).

9 Reichstein, M. *et al.* On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology* **11**, 1424-1439 (2005).

10 Raich, J. W. & Schlesinger, W. H. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* **44**, 81-99 (1992).

11 Exbrayat, J. F., Pitman, A. J., Zhang, Q., Abramowitz, G. & Wang, Y. P. Examining soil carbon uncertainty in a global model: response of microbial decomposition to temperature, moisture and nutrient limitation. *Biogeosciences* **10**, 7095-7108 (2013).

12 Yang, J. *et al.* The role of satellite remote sensing in climate change studies. *Nature Climate Change* **3**, 875-883 (2013).

13 Rustad, L. E. *et al.* A Meta-Analysis of the Response of Soil Respiration, Net Nitrogen Mineralization, and Aboveground Plant Growth to Experimental Ecosystem Warming. *Oecologia* **126**, 543-562 (2001).

14 Balser, T. C. & Wixon, D. L. Investigating biological control over soil carbon temperature sensitivity. *Global Change Biology* **15**, 2935-2949 (2009).

15 Thakur, M. P. *et al.* Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nature Climate Change* **8**, 75-78 (2018).

16 Eisenhauer, N., Cesarz, S., Koller, R., Worm, K. & Reich, P. B. Global change belowground: impacts of elevated CO2, nitrogen, and summer drought on soil food webs and biodiversity. *Global Change Biology* **18**, 435-447 (2012).

17 Suttle, K. B., Thomsen, M. A. & Power, M. E. Species Interactions Reverse Grassland Responses to Changing Climate. *Science* **315**, 640-642 (2007).

18 Yvon-Durocher, G. *et al.* Reconciling the temperature dependence of respiration across timescales and ecosystem types. *Nature* **487**, 472-476 (2012).

19 Ehnes, R. B., Rall, B. C. & Brose, U. Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters* **14**, 993-1000 (2011).

20 Briones, M. J. I., Ostle, N. J., McNamara, N. P. & Poskitt, J. Functional shifts of grassland soil communities in response to soil warming. *Soil Biology and Biochemistry* **41**, 315-322 (2009).

21 Sibly, R. M., Brown, J. H. & Kodric-Brown, A. *Metabolic Ecology: A Scaling Approach* (Wiley-Blackwell, Oxford, 2012).

22 Brown, J. H. & Sibly, R. M. *Metabolic Ecology* Ch. 2 (Wiley-Blackwell, Oxford, 2012).

23 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789 (2004).

24 Kozłowski, J., Konarzewski, M. & Gawelczyk, A. T. Cell size as a link between noncoding DNA and metabolic rate scaling. *Proceedings of the National Academy of Sciences* **100**, 14080-14085 (2003).

25 Lampert, W. The measurement of respiration. *A manual on methods for the assessment of secondary productivity in fresh waters* **17**, 413-468 (1984).

26 Peters, R. H. *The ecological implications of body size*. Vol. 2 (Cambridge University Press, 1983).

27 Bond-Lamberty, B. & Thomson, A. A global database of soil respiration data. *Biogeosciences* **7**, 1915-1926 (2010).

28 Xu, X., Thornton, P. E. & Post, W. M. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography* **22**, 737-749 (2013).

29 Karhu, K. *et al.* Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* **513**, 81-84 (2014).

30 Clein, J. S. & Schimel, J. P. Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biology and Biochemistry* **27**, 1231-1234 (1995).

31 Dorrepaal, E. *et al.* Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* **460**, 616-619 (2009).

32 Nie, M. *et al.* Positive climate feedbacks of soil microbial communities in a semi-arid grassland. *Ecology Letters* **16**, 234-241 (2013).

33 Aerts, R. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* **94**, 713-724 (2006).

34 Davidson, E. A., Janssens, I. A. & Luo, Y. On the variability of respiration in terrestrial ecosystems: moving beyond Q10. *Global Change Biology* **12**, 154-164 (2006).

35 Mikan, C. J., Schimel, J. P. & Doyle, A. P. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology and Biochemistry* **34**, 1785-1795 (2002).

36 Chen, H. & Tian, H. Q. Does a General Temperature-Dependent Q10 Model of Soil Respiration Exist at Biome and Global Scale? *Journal of Integrative Plant Biology* **47**, 1288-1302 (2005).

37 Mahecha, M. D. *et al.* Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level. *Science* **329**, 838-840 (2010).

38 Meehan, T. D. Mass and temperature dependence of metabolic rate in litter and soil invertebrates. *Physiological and biochemical zoology* **79**, 878-884 (2006).

39 Chown, S. L. *et al.* Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Functional Ecology* **21**, 282-290 (2007).

40 Makarieva, A. M., Gorshkov, V. G. & Li, B.-L. Energetics of the smallest: do bacteria breathe at the same rate as whales? *Proceedings of the Royal Society B: Biological Sciences* **272**, 2219-2224 (2005).

41 Laybourn, J. & Finlay, B. J. Respiratory energy losses related to cell weight and temperature in ciliated protozoa. *Oecologia* **24**, 349-355 (1976).

42 Fenchel, T. & Finlay, B. J. Respiration Rates in Heterotrophic, Free-Living Protozoa. *Microbial Ecology* **9**, 99-122 (1983).

43 Klekowski, R., Wasilewska, L. & Paplinska, E. Oxygen consumption by soil-inhabiting nematodes. *Nematologica* **18**, 391-403 (1972).

44 Ferris, H., Lau, S. & Venette, R. Population energetics of bacterial-feeding nematodes: respiration and metabolic rates based on CO2 production. *Soil Biology and Biochemistry* **27**, 319-330 (1995).

45 Nielsen, C. O. Respiratory metabolism of some populations of enchytraeid worms and freeliving nematodes. *Oikos* **12**, 17-35 (1961).

46 Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A. & Cleveland, C. C. Global patterns in belowground communities. *Ecology letters* **12**, 1238-1249 (2009).

47 Petersen, H. & Luxton, M. A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. *Oikos* **39**, 288-388 (1982).

48 Subke, J. A., Inglima, I. & Francesca Cotrufo, M. Trends and methodological impacts in soil CO2 efflux partitioning: a metaanalytical review. *Global Change Biology* **12**, 921-943 (2006).

49 Bond-Lamberty, B., Wang, C. & Gower, S. T. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* **10**, 1756-1766 (2004).

50 Hogberg, P., Nordgren, A., Buchmann, N. & Taylor, A. F. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **411**, 789 (2001).

51 Carey, J. C. *et al.* Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences* **113**, 13797-13802 (2016).

Acknowledgements

This research has been financially supported by a NERC Soil Security Programme fellowship (NE/N019504/1). We thank Chris Venditti, James Brown, Gabriel Yvon-Durocher, Charles Hall and four anonymous reviewers for their feedback and suggestions on the manuscript.

Author contributions

AJ conceived the idea and compiled and analysed the data; AJ and RS developed the methodology and wrote the manuscript.

Competing interests

The authors declare no competing financial interests.