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

Article

Accepted Version

It is advisable to refer to the publisher's version if you intend to cite from the work. See Guidance on citing.

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

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

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

3

4 [1] School of Biological Sciences, University of Reading, UK.

5 * Corresponding Author:

6 alice.johnston@reading.ac.uk; +44 (0)118 378 6439

7 School of Biological Sciences, University of Reading, Reading, RG6 6AH

8

9 **Soil respiration represents a major carbon flux between terrestrial ecosystems and the**

10 **atmosphere, and is expected to accelerate under climate warming. Despite its importance in**

11 **climate change forecasts, however, our understanding of the effects of temperature on soil**

12 **respiration (R_S) is incomplete. Using a metabolic ecology approach we link soil biota**

13 **metabolism, community composition and heterotrophic activity, to predict R_S rates across**

14 **five biomes. We find that accounting for the ecological mechanisms underpinning**

15 **decomposition processes predicts climatological R_S variations observed in an independent**

16 **dataset (n = 312). The importance of community composition is evident because without it R_S**

17 **is substantially underestimated. With increasing temperature, we predict a latitudinal**

18 **increase in R_S temperature sensitivity, with Q_{10} values ranging between 2.33 ±0.01 in tropical**

19 **forests to 2.72 ±0.03 in tundra. This global trend has been widely observed, but has not**

20 **previously been linked to soil communities.**

21

22 Soils store the majority of Earth's terrestrial carbon, and so play a crucial role in the direction and

23 magnitude of future climate changes[1]. However, the influence of ongoing climate change on the soil

24 carbon sink is a major area of uncertainty[2-4]. Temperature-associated increases in the global soil

25 CO_2 flux (soil respiration, R_S) has led to the supposition that global warming will drive a positive soil-

26 climate feedback[5,6]. Of particular concern is the potential long-term vulnerability of large soil C

27 stocks at high latitudes[7]. However, our incomplete understanding of the temperature – R_S

28 relationship limits constrained forecasts of terrestrial carbon fluxes in the future[8].

29

30 The temperature sensitivity of R_S across ecosystems is a key determinant of the soil-climate

31 feedback, but it is difficult to quantify due to the many confounding factors that affect soil metabolic

32 rates[2,9]. For instance, Q_{10} values (the proportional increase in R_S with a 10 °C increase in

33 temperature) are highly variable across different vegetation types and climates[2,10]. Nevertheless,

34 Earth system models (ESMs) typically assume a globally constant temperature sensitivity by

35 incorporating fixed Q_{10} values of around 2 (that is, R_S rates double with an increase in temperature

36 of 10 °C)[11,12]. Thus, while there is a growing consensus that future warming will enhance R_S rates,

37 how the response will vary across climatic regions and soil characteristics is not well

38   established[13,14]. Here, we propose that a better understanding of R_S temperature sensitivity can be

39   gained by accounting for the various organisms that live in the soil.

40

41   Soil respiration is the biotic conversion of organic C to CO_2 by all of the organisms (heterotrophs:

42   soil microbes and fauna, and autotrophs: plant roots and their mycorrhizal symbionts) that live in the

43   soil. Thus, R_S rates are the product of the body sizes, metabolic rates, abundances and community

44   composition of soil-inhabiting organisms[15-18]. Because individual metabolic rates exhibit varying

45   temperature sensitivities[19], we would also expect R_S responses to increasing temperatures to

46   fluctuate according to soil community composition. However, empirical quantification of soil biota

47   contributions to R_S at large spatio-temporal scales is complicated by the vast biodiversity and

48   complexity of soil systems[20].

49

50   In this study, we use a model derived from metabolic theory[21] to integrate soil biota metabolism,

51   community composition and heterotrophic activity in R_S estimates across biomes. The model

52   accounts for the way in which metabolic rates vary with temperature and body size between soil

53   community groups. We then extrapolate to heterotrophic respiration (R_H) rates by accounting for the

54   abundance of soil biota across tundra, boreal forest, temperate forest, temperate grassland and

55   tropical forest soils. By quantifying the contribution of R_H to R_S, using an R_H fraction (H_F) which

56   accounts for autotrophs (plant roots and their symbiotic mycorrhizae) not modelled here, we predict

57   R_S across biomes and mean annual temperature (MAT) ranges. To test the hypothesis that soil

58   community traits strongly influence R_S temperature sensitivities, we compare models that do or do

59   not account for metabolic variation of soil biota. To test how predictive our approach is, we make a

60   further comparison with a classical linear regression fitted to the R_S data. Finally, we increase study-

61   specific MAT's by 10 °C to compare Q_{10} estimates with available data across the five biomes, and

62   discuss how these compare to those Q_{10}'s used in ESMs and observed in long-term field

63   experiments.

64

65   **Results**

66

67   ***Metabolic ecology of soil communities***

68   Metabolism underpins fundamental mechanisms of organism-environment interactions, and sets the

69   basis for linking individual to ecosystem processes[22]. To investigate the temperature sensitivities of

70   metabolism for diverse soil communities, we compiled a metabolic dataset for fourteen soil biota

71   groups (bacteria, protozoa, nematode, collembola, enchytraeidae, acari, ant, beetle, isopod,

72   centipede, spider, termite, millipede, earthworm). The dataset (n = 3768) covers nearly 15 orders of

73   magnitude in body mass (*M*) and temperatures (*T*) between -2 and 40 °C. In the first instance, the

74   metabolic dataset was fitted to the linear form of the metabolic scaling equation without accounting

75   for variations in metabolic parameters between soil biota (termed the 'general' model herein):

76

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

78

79   where B is standard metabolic rate (J hr^{-1}), B_0 is a taxon-specific normalisation constant, a

80   represents the allometric scaling exponent which usually takes a value close to ¾, E is the

81   activation energy (eV), k is Boltzmann's constant (8.62 × 10^{-5} eV K^{-1}) and T is experimental

82   temperature (K)[21]. General model (Equation (1)) regression analysis yields an allometric exponent,

83   a, of 0.81 (±0.002) and activation energy, E, of 0.67 (±0.01) (Supplementary Table 1). Both

84   metabolic parameters are within the range predicted by the metabolic theory of ecology (MTE), a:

85   0.67 – 1 and E: 0.6 – 0.7 eV[23,24]. Yet, while the general model predicts metabolic rates with

86   individual body mass well, it does not capture the apparent high variation in soil biota temperature

87   sensitivities (Supplementary Figure 1), indicating the need to account for metabolic traits between

88   soil community groups.

89

90   Soil biota were classified into community groups according to their body size distribution as

91   microbes (< 0.0001 mg FM), mesofauna (0.0001 – 8 mg FM) or macrofauna (> 8 mg FM). Microbes

92   include bacteria, mesofauna include protozoa, nematode, acari, collembola and enchytraeidae

93   groups, and macrofauna include ant, spider, isopod, centipede, beetle, termite, millipede and

94   earthworm groups. Although protozoa and nematodes are technically classified as microfauna

95   rather than mesofauna, the metabolic data for these groups were collected at a single experimental

96   temperature. Thus, regression analysis by soil biota groupings was not possible. The community

97   group (CG) model includes two-way interaction terms between CG – body mass and CG –

98   temperature to yield community-specific metabolic parameters (B_0, a & E):

99

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

101

102   CG model (Equation (2)) analysis yields ranges in a from 0.66 to 0.87 and E from 0.64 to 0.74 eV

103   (Figs. 1a & b, Supplementary Table 1). Interestingly, analysis of the CG model reveals that the

104   temperature sensitivity of metabolism (E) increases with decreasing body size, from 0.64 (±0.01) for

105   macrofauna to 0.74 (±0.19) for microbes (Supplementary Table 1). That is, smaller sized soil

106   community groups exhibit a greater proportional increase in their metabolic rates with a given

107   increase in temperature, than individuals belonging to larger size community groups. This suggests

108   a higher contribution of soil microbes (in particular, as mass-specific metabolic rates in mesofauna

109   are lower) to R_S rates at increasing temperatures, if resources are available to fulfil higher energy

110   requirements. The distribution of the CG model residuals against the independent variables (body

111   mass and temperature, Figs. 1c & d) and fitted lowess line, further indicate an absence of

112   systematic errors, which are much greater for the general model (Supplementary Figure 1).

113

114
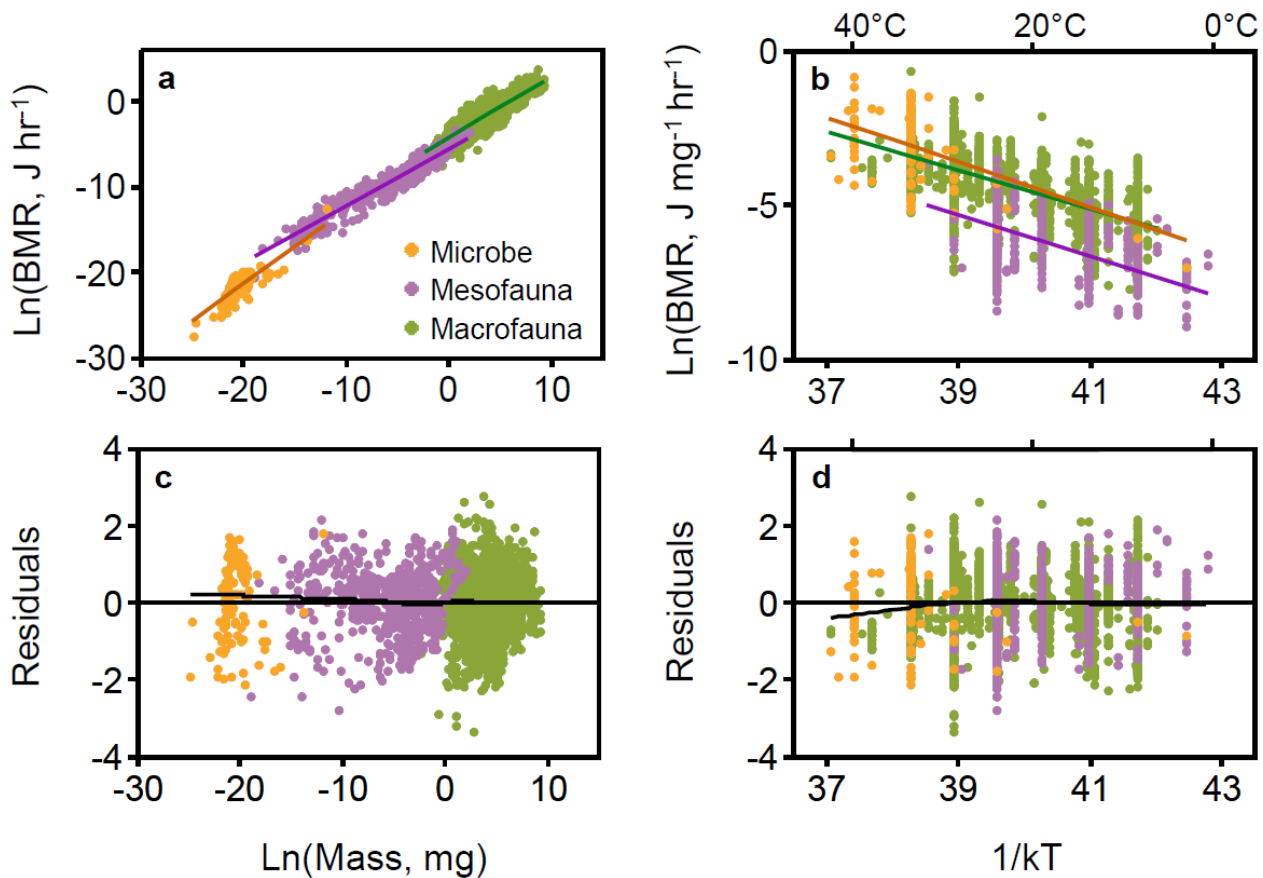
Figure 1. Metabolic scaling relationships in soil communities. Left-hand plots (a & c) show individual metabolic rates
(*B*), corrected to a temperature of 20 °C using equation (2), plotted against individual body mass (*M*, mg FM). Right-hand
plots (b & d) show *B*, corrected to a body mass of 1 mg 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

133   community's respiration rate, which is calculated according to individual-level respiration rates (r_i)

134   and population abundance (A_i) as: $R_H = \sum_i r_i A_i$, where the summation is over the soil biota groups

135   in the biome. Our R_H predictions are compared to independent data in Supplementary Figures 2 &

136   3. Finally, accounting for H_F's reported in the Bond-Lamberty and Thomson [27] dataset

137   (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

138   R_S studies used to evaluate our approaches predictions (n = 312), using metabolic parameters,

139   individual body masses and soil biota population abundances in Supplementary Tables 2, 3 & 4

140   respectively.

141

142   ***Soil community composition across biomes***

143   Population biomass (g FM m^{-2}) and abundance (number m^{-2}) measurements for the fourteen soil

144   biota groups for which metabolic data is available were collected across tundra, boreal forest,

145   temperate forest, temperate grassland and tropical forest soils (n = 2187). Community group

146   biomasses across the five biomes investigated here were significantly different ($p = 0.000$,

147   Supplementary Table 5). In general, high latitude (tundra and boreal) soils harbour more soil

148   microbes and mesofauna by biomass than temperate and tropical soils. Soil macrofauna follow an

149   inverse trend, increasing in biomass from tundra to temperate grasslands and tropical forests (Fig.

150   2). Given the higher temperature sensitivity of smaller sized soil biota (Fig. 1), we would expect

151   higher abundances of soil microbes and mesofauna in tundra and boreal soils to be linked to higher

152 R_S temperature sensitivities at high latitudes.

153
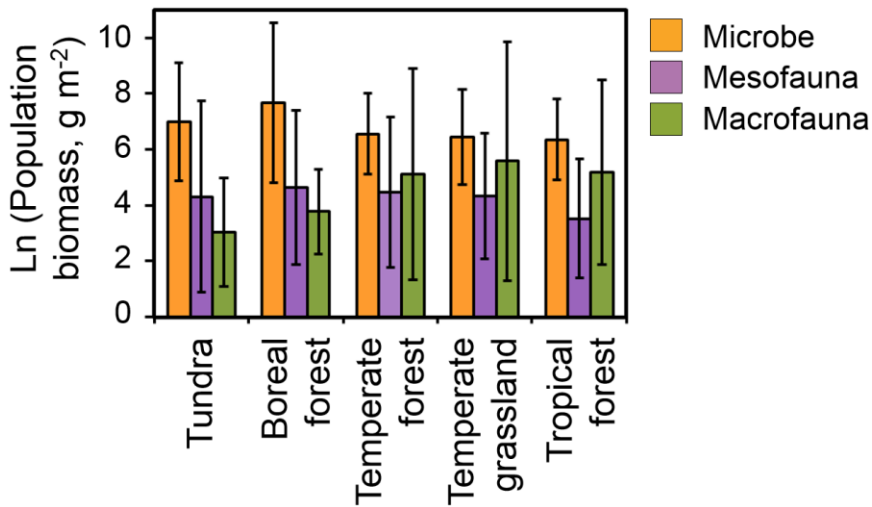
154

155 **Figure 2. Soil community composition across biomes.** Soil community groups are classified by body size distribution

156 (microbe, mesofauna and macrofauna). Biomass (g fresh mass m^{-2}) measurements incorporate the sum of soil biota

157 population biomasses for each community group. Average biome-specific soil microbial biomasses were taken from the

158 study of Xu et al. [28], while soil mesofauna and macrofauna data were compiled in this study (n = 2187, Supplementary

159 Figure). Presented values are means ± reported standard errors for microbes, while error bars for mesofauna and

160 macrofauna were calculated as the square root of the summed variances for soil biota group population biomasses.

161 Differences in community group biomass are significantly different across biomes (p = 0.000, Supplementary Table 5).

162

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

164 Comparison of our R_S predictions (lines) with independent R_S data (symbols) in Fig. 3a

165 demonstrates good prediction of R_S rates across biomes and MAT's (R^2 = 0.66, n = 312, no p-value

166 can be reported as predictions are independent of the data). Temperature sensitivity differences

167 across biomes emerge from the approach by integrating variation in the metabolic ecology and

168 community composition of soils. However, high variability in the R_S data likely points to site-specific

169 interactions between individual, population and community-level dynamics with other environmental

170 factors (e.g. resource quantity and quality), as well as temperature (Fig. 3b).

171
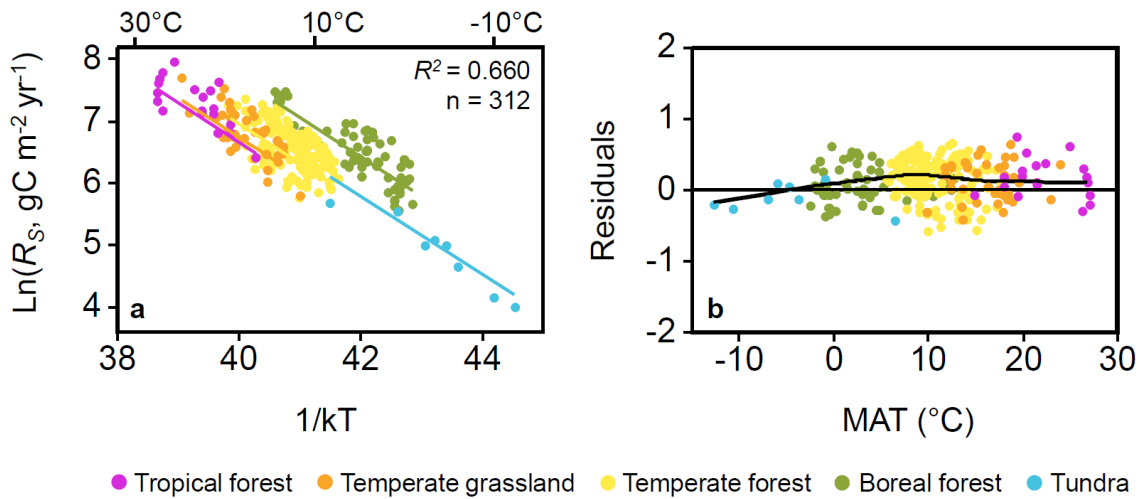
Figure 3. Temperature sensitivity of soil respiration (R_S) across biomes and MAT's. Plots show a) independent R_S data (symbols: n = 312) and predicted R_S from the community group (CG) model presented here (lines) and b) CG model residual distributions against MAT (°C) with fitted lowess line (solid 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 (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.
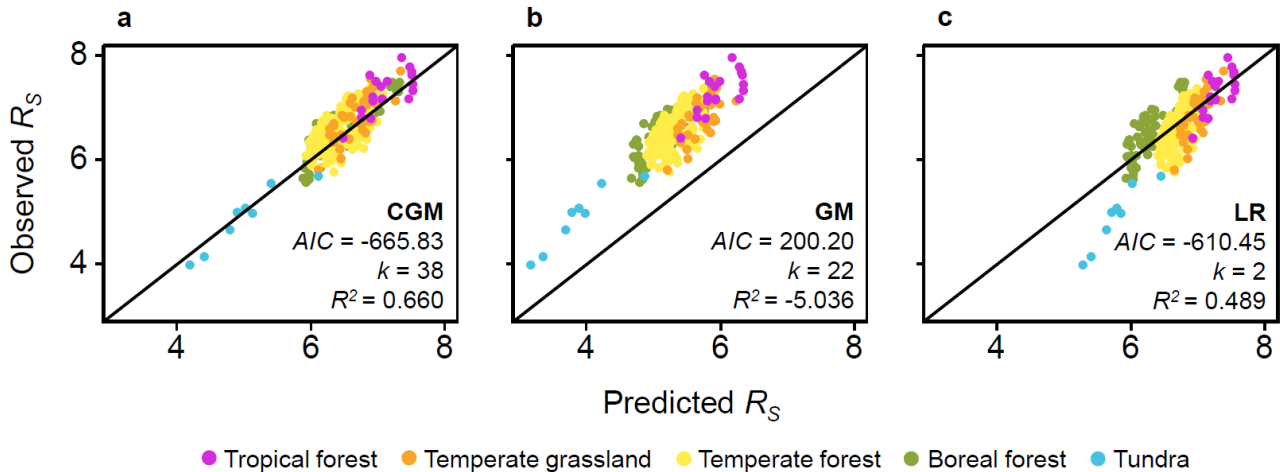
Figure 4. Model comparisons and goodness of fits with independent soil respiration (R_S, gC m^{-2} year^{-1}) data. The community group model (CGM) (a) is compared to the general metabolic model (GM) (b) which does not account for metabolic variation in soil communities, and an empirical fitted linear regression (LR) to the R_S data (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}

219   estimates thus overestimate tropical soil and underestimate tundra and boreal soil responses to

220   increasing temperatures (Fig. 5), in line with long-term field Q_{10}'s of 5.2 ±2.4 for tundra and boreal,

221   2.7 ±1.7 for temperate and 2.2 ±0.9 for tropical climates[36]. Exploring alternative thermodynamic

222   hypotheses, such as non-linear temperature curves and acclimatisation mechanisms, could explain

223   more of the variability in the Q_{10} data and Q_{10}'s under long-term warming. On the other hand, our

224   approach estimates much higher Q_{10} values than the static value of 2 used in many ESMs, which

225   are often parameterised with short-term observations based on eddy covariance fluxes and soil

226   incubations[2,37]. This divergence between short- and long-term Q_{10} values has been suggested as

227   evidence for the inclusion of emergent behaviour over long timescales[7], which in this study includes

228   the metabolic response of soil communities and shifts in soil community composition across biomes.

229
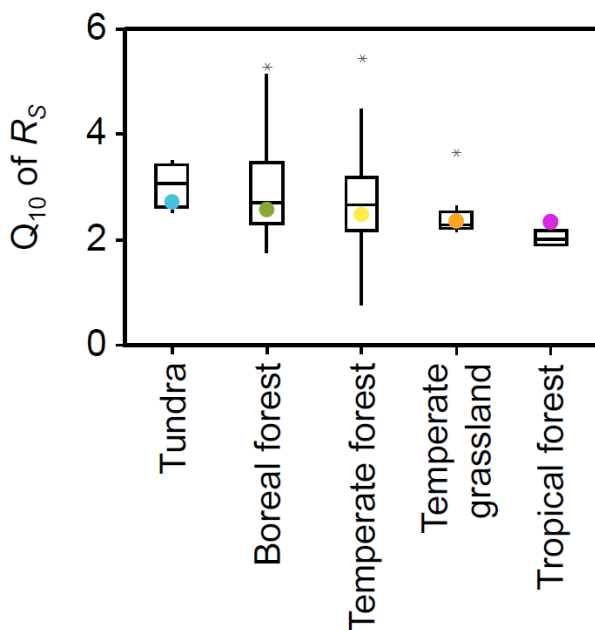
230

231   **Figure 5. Observed and predicted Q_{10} values for R_S across biomes.** Q_{10} data from the Bond-Lamberty and Thomson

232   [27] dataset (n = 119) presented as boxes with the median and first and third quartiles shown. CG predictions of Q_{10} values

233   across biomes are given by coloured symbols, showing median predicted values, with imperceptible first and third quartile

234   whiskers.

235

Discussion

237   We use a metabolic ecology approach to better understand the relationships between soil biota

238   metabolism, community composition and R_S rates. We find that accounting for the metabolic

239   ecology of soils (Fig. 1) together with soil community composition (Fig. 2) reveals variations in R_S

240   with MAT across five biomes (Fig. 3). Important in achieving good R_S predictions was incorporating

241   the varying temperature sensitivities of soil community groups. In comparison, assuming all soil

242   biota exhibit identical temperature sensitivities resulted in substantial under-estimation of R_S rates

243   (Fig. 4b). The metabolic ecology and body size distribution of soil communities thus strongly

244 influence the temperature sensitivity of R_S across biomes. With increasing temperature, our

245 approach suggests that R_S would be most strongly enhanced in colder climatic regions (Fig. 5),

246 because of the higher temperature sensitivity of soil biota inhabiting these soils.

247

248 Soil community composition will also be influenced by multiple global drivers (e.g. warming, CO_2

249 fertilisation, N deposition) in the future, which will alter the direction and magnitude of R_S responses.

250 Thus, to better anticipate the effects of global environmental changes on R_S requires a better

251 understanding of the ecological mechanisms underpinning macroecological patterns in soil

252 communities. Yet, fundamental knowledge gaps in soil ecology need to be addressed to understand

253 the primary drivers of soil community composition across a broad spectrum of environmental

254 variables. Unravelling these complex interactions would allow us to represent the mechanistic links

255 between the belowground and aboveground components of terrestrial ecosystems, develop more

256 predictive models of soil systems and improve forecasts of future climate changes on numerous

257 ecosystem functions, including R_S. Our study stresses the importance of considering the soil

258 organisms which facilitate ecosystem functions, and demonstrates the utility of fundamental

259 ecological principles in describing complex soil systems.

260

261 **Methods**

262 *Metabolic ecology of soil biota.* Metabolic data for a wide range of soil biota was compiled from

263 the dataset of Ehnes, et al. [19], which includes data from the meta-analyses of Meehan [38] and

264 Chown, et al. [39] together with their own measurements for acari, collembola, enchytraeidae,

265 centipedes, millipedes, isopods, spiders, ants, beetles, termites and earthworms (n = 3399). In

266 addition, we compiled data for bacteria from Makarieva, et al. [40] (n = 56), protozoa from Laybourn

267 and Finlay [41] and Fenchel and Finlay [42] (n = 143), nematodes from Klekowski, et al. [43] and Ferris, et

268 al. [44] (n = 105) and enchytraeidae from Nielsen [45] (n = 58). Detailed differences at the species-level

269 are avoided in order to explore the collective metabolism of soil community groups across biomes.

270 All measurements were converted to wet weight (mg) and standard metabolic rate per hour (J hr^{-1}),

271 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].

272

273 *Soil biota populations and community composition.* Linking individual to population-level

274 metabolism requires estimation of the population abundances of different soil biota across biomes.

275 Here, we extend the dataset of Fierer, et al. [46], who collected population biomass data for acari,

276 collembola, enchytraeidae, nematodes and earthworms in tundra, boreal forest, temperate forest,

277 temperate grassland and tropical forest soils (n = 799). We compiled additional data for all of the

278 soil biota groups and biomes of Fierer, et al. [46], and for ants, beetles, centipedes, isopods,

279 millipedes, protozoa, spiders and termites in biomes for which data was available (n = 1382).

280 Average biome-specific microbial biomass values were taken from the extensive review of Xu, et al.

281 [28], which compiles 1182 measurements across the biomes investigated here (Supplementary Table

282 4).

283

284 Population biomass measurements required conversion to population abundance by estimates of

285 mean individual body masses (M) for the fourteen different soil biota groups. We assume that M for

286 different soil biota groups are constant across biomes. Although this assumption likely introduces

287 error due to variations in individual life histories across climates, not enough information exists to

288 apply more detailed individual-level relationships. To minimise error we collated data from a number

289 of sources reporting M for the different soil biota groups (Supplementary Table 3). Average M (mg

290 dry mass) used in this study were: protozoa (6.55×10^6), nematodes (0.0020), acari (0.0096),

291 collembola (0.055), enchytraeidae (0.055), ants (2.23), beetles (4.35), isopods (4.47), centipedes

292 (6.59), spiders (7.42), termites (9.90), millipedes (17.06) and earthworms (52.37). All population

293 biomass measurements are expressed here as fresh mass (g FM/m^2) using the conversion to fresh

294 mass of five times dry mass[19]. Using a single dry to fresh mass conversion factor for all soil biota

295 groups will also introduce some error, as variations likely exist across soil biota groups and

296 biomes[47]. Measurements given in the dataset of Fierer et al. [46] (g C m^{-2}) were further corrected by

297 accounting for a 50 % carbon content. We do not make additional extrapolations to specific soil

298 depths, as this is highly variable between soil biota groups and soil types, and often not reported in

299 field studies. If population measurements were expressed on per mass of dry soil basis, appropriate

300 bulk density values were used to convert these measurements to density (per m^2) for the soil type

301 reported.

302

303 ***Heterotrophic respiration (R_H) .*** Using our metabolic approach, R_H rates were estimated by

304 summing the metabolic rates of soil communities at MAT in a given biome. Community-level

305 metabolic rates were calculated by taking metabolic parameters (B_0, a and E; Supplementary Table

306 1) for each soil community group, individual body masses (M, mg fresh mass) for each soil biota

307 group (Supplementary Table 3) and their population abundance (A, number m^{-2}) in different biomes

308 (Supplementary Table 4). Metabolic rates were then transformed to respiration rates (g C) by using

309 the conversion factors 37490 J gC^{-1} = 20100 J LO$_2$$^{-1}$ $\times$ (1 / 0.5363 g C LO$_2$$^{-1}$) [25,26] and 8760 hr yr^{-1}.

310 To investigate whether our model predicts R_H rates across biomes and MAT's, prior to extrapolating

311 to R_S as detailed below, we compared our predictions with available R_H data in the Bond-Lamberty

312 and Thomson [27] dataset (n = 66). R_H data were compiled for un-manipulated field studies reporting

313 annual R_H and R_S rates, and were averaged for single study years and/or locations where

314 applicable. Measurements were also excluded if reported R_H rates were equal to or higher than

315 reported R_S rates. If MAT's were not reported, or the same MAT was given for multiple years in the

316 same study, NOAA weather stations were used to collect MAT measurements based on the study

317 sites latitude and longitude (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation). The CG

318   model's predictions of R_H rates were then evaluated (r^2 = 0.757, Supplementary Figure 2), in

319   comparison to the general metabolic model (r^2 = -2.261) and a linear regression approach (r^2 =

320   0.529) (Supplementary Figure 3). Accounting for model complexity in *AIC* calculations indicates that

321   the CG model does not perform better than the linear regression given its large number of

322   parameters, but this may be a result of the limited size of the data set. To test whether the CG

323   approach performs better given more data we used the R_H data to calculate an R_H fraction (H_F) for

324   each biome to account for the contribution of heterotrophs to R_S. This allowed us to use the larger

325   R_S data set (n = 312) to evaluate the CG model with greater precision as reported in Fig. 4.

326

327   ***R_H fraction (H_F)***

328   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

329   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

330   of the issues in separating heterotrophic and autotrophic contributions to R_S, as R_H is typically

331   measured directly whereas R_A is typically derived by calculating the difference between R_S and

332   other ecosystem fluxes[48]. Mean H_F ±SE across the five biomes investigated here were 0.39 ±0.10,

333   0.63 ±0.02, 0.58 ±0.03, 0.63 ±0.04 and 0.77 ±0.07 for tundra, boreal forest, temperate forest,

334   temperate grassland and tropical forest soils, respectively. Variability in H_F within biomes is likely

335   linked to the experimental difficulties associated with separating the autotrophic and heterotrophic

336   components of soils and the methodology used to do so in the field[48-50]. To explain some of this

337   variability, and to account for the temperature sensitivity of R_A, we performed a regression analysis

338   between H_F and MAT, which revealed a weak but significant positive correlation (H_F = 0.54 + 0.0069

339   MAT; r^2 = 0.104, p = 0.008, Supplementary Figure 4). This linear relationship is incorporated in our

340   calculations to extrapolate from R_H to R_S rates across biomes and MAT's.

341

342   ***Soil respiration (R_S)***

343   To compare our R_S estimates with independent data, annual R_S rates (g C m^{-2} yr^{-1}) were compiled

344   from the global soil respiration datasets of Bond-Lamberty and Thomson [27] and Carey, et al. [51] for

345   tundra, boreal forest, temperate forest, temperate grassland and tropical forest soils (n = 312). Data

346   were included from un-manipulated field studies reporting average annual R_S and MAT, and

347   measurements from both datasets were averaged for single study years and/or locations where

348   applicable. R_S measurements compiled from the Bond-Lamberty and Thomson [27] dataset included

349   119 Q_{10} values, which were used to evaluate predicted Q_{10}'s across biomes using our CG model.

350

351   **Data availability.** The datasets generated and analysed during the current study are available on

352   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 CO_2 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 CO_2, 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).

408 24 Kozłowski, J., Konarzewski, M. & Gawelczyk, A. T. Cell size as a link between noncoding
409   DNA and metabolic rate scaling. *Proceedings of the National Academy of Sciences* **100**,
410   14080-14085 (2003).
411 25 Lampert, W. The measurement of respiration. *A manual on methods for the assessment of*
412   *secondary productivity in fresh waters* **17**, 413-468 (1984).
413 26 Peters, R. H. *The ecological implications of body size*. Vol. 2 (Cambridge University Press,
414   1983).
415 27 Bond-Lamberty, B. & Thomson, A. A global database of soil respiration data.
416   *Biogeosciences* **7**, 1915-1926 (2010).
417 28 Xu, X., Thornton, P. E. & Post, W. M. A global analysis of soil microbial biomass carbon,
418   nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography* **22**,
419   737-749 (2013).
420 29 Karhu, K. *et al.* Temperature sensitivity of soil respiration rates enhanced by microbial
421   community response. *Nature* **513**, 81-84 (2014).
422 30 Clein, J. S. & Schimel, J. P. Microbial activity of tundra and taiga soils at sub-zero
423   temperatures. *Soil Biology and Biochemistry* **27**, 1231-1234 (1995).
424 31 Dorrepaal, E. *et al.* Carbon respiration from subsurface peat accelerated by climate warming
425   in the subarctic. *Nature* **460**, 616-619 (2009).
426 32 Nie, M. *et al.* Positive climate feedbacks of soil microbial communities in a semi-arid
427   grassland. *Ecology Letters* **16**, 234-241 (2013).
428 33 Aerts, R. The freezer defrosting: global warming and litter decomposition rates in cold
429   biomes. *Journal of Ecology* **94**, 713-724 (2006).
430 34 Davidson, E. A., Janssens, I. A. & Luo, Y. On the variability of respiration in terrestrial
431   ecosystems: moving beyond Q10. *Global Change Biology* **12**, 154-164 (2006).
432 35 Mikan, C. J., Schimel, J. P. & Doyle, A. P. Temperature controls of microbial respiration in
433   arctic tundra soils above and below freezing. *Soil Biology and Biochemistry* **34**, 1785-1795
434   (2002).
435 36 Chen, H. & Tian, H. Q. Does a General Temperature-Dependent Q10 Model of Soil
436   Respiration Exist at Biome and Global Scale? *Journal of Integrative Plant Biology* **47**, 1288-
437   1302 (2005).
438 37 Mahecha, M. D. *et al.* Global Convergence in the Temperature Sensitivity of Respiration at
439   Ecosystem Level. *Science* **329**, 838-840 (2010).
440 38 Meehan, T. D. Mass and temperature dependence of metabolic rate in litter and soil
441   invertebrates. *Physiological and biochemical zoology* **79**, 878-884 (2006).
442 39 Chown, S. L. *et al.* Scaling of insect metabolic rate is inconsistent with the nutrient supply
443   network model. *Functional Ecology* **21**, 282-290 (2007).
444 40 Makarieva, A. M., Gorshkov, V. G. & Li, B.-L. Energetics of the smallest: do bacteria breathe
445   at the same rate as whales? *Proceedings of the Royal Society B: Biological Sciences* **272**,
446   2219-2224 (2005).
447 41 Laybourn, J. & Finlay, B. J. Respiratory energy losses related to cell weight and temperature
448   in ciliated protozoa. *Oecologia* **24**, 349-355 (1976).
449 42 Fenchel, T. & Finlay, B. J. Respiration Rates in Heterotrophic, Free-Living Protozoa.
450   *Microbial Ecology* **9**, 99-122 (1983).
451 43 Klekowski, R., Wasilewska, L. & Paplinska, E. Oxygen consumption by soil-inhabiting
452   nematodes. *Nematologica* **18**, 391-403 (1972).
453 44 Ferris, H., Lau, S. & Venette, R. Population energetics of bacterial-feeding nematodes:
454   respiration and metabolic rates based on CO2 production. *Soil Biology and Biochemistry* **27**,
455   319-330 (1995).
456 45 Nielsen, C. O. Respiratory metabolism of some populations of enchytraeid worms and
457   freeliving nematodes. *Oikos* **12**, 17-35 (1961).
458 46 Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A. & Cleveland, C. C. Global patterns in
459   belowground communities. *Ecology letters* **12**, 1238-1249 (2009).
460 47 Petersen, H. & Luxton, M. A Comparative Analysis of Soil Fauna Populations and Their Role
461   in Decomposition Processes. *Oikos* **39**, 288-388 (1982).

462   48   Subke, J. A., Inglima, I. & Francesca Cotrufo, M. Trends and methodological impacts in soil
463   CO2 efflux partitioning: a metaanalytical review. *Global Change Biology* **12**, 921-943 (2006).
464   49   Bond-Lamberty, B., Wang, C. & Gower, S. T. A global relationship between the heterotrophic
465   and autotrophic components of soil respiration? *Global Change Biology* **10**, 1756-1766
466   (2004).
467   50   Hogberg, P., Nordgren, A., Buchmann, N. & Taylor, A. F. Large-scale forest girdling shows
468   that current photosynthesis drives soil respiration. *Nature* **411**, 789 (2001).
469   51   Carey, J. C. *et al.* Temperature response of soil respiration largely unaltered with
470   experimental warming. *Proceedings of the National Academy of Sciences* **113**, 13797-13802
471   (2016).
472

478   **Author contributions**

479   AJ conceived the idea and compiled and analysed the data; AJ and RS developed the methodology

480   and wrote the manuscript.

481

482   **Competing interests**

483   The authors declare no competing financial interests.

484