Methane fluxes show consistent temperature dependence across microbial to ecosystem scales

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1 **Temperature dependence of methane emissions: consistent scaling**
2 **from methanogenesis to ecosystem-level fluxes**

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28 Methane (CH₄) is an important greenhouse gas because it has 25 times the global
29 warming potential of carbon dioxide (CO₂) by mass over a century¹. Recent
30 calculations suggest that atmospheric CH₄ emissions have been responsible for
31 approximately 20% of planet's warming since pre-industrial times².
32 Understanding how CH₄ emissions from ecosystems will respond to expected
33 increases in global temperature is therefore fundamental for predicting the
34 magnitude of feedbacks between the carbon cycle and climate change.
35 Methanogenesis is the terminal step in the remineralisation of organic matter
36 and is carried out by strictly anaerobic Archaea³. Like most other enzymatically
37 mediated forms of metabolism, methanogenesis is temperature dependent^{4,5}.
38 However, it is not yet known how this physiological response combines with
39 other biotic – e.g. methanotrophy⁶, substrate supply^{3,7}, microbial community
40 composition⁸ – and abiotic – e.g. water-table depth^{9,10} – processes to determine
41 the temperature sensitivity of ecosystem-level CH₄ emissions. Nor is it known
42 whether CH₄ emissions at the ecosystem-level have a fundamentally different
43 temperature dependence than other key fluxes in the carbon cycle, such as
44 photosynthesis and respiration. Here we use meta-analyses to show that seasonal
45 variations in CH₄ emissions from a wide range of ecosystems exhibit an average
46 temperature dependence similar to that of CH₄ production derived from pure
47 cultures of methanogens and anaerobic sediment slurries. This average
48 temperature dependence (0.98 electron volts (eV)), which corresponds to a 61-
49 fold increase between 0 – 30°C, is considerably higher than previously observed
50 for respiration (approximately 0.65 eV)¹¹ and photosynthesis (approximately 0.3
51 eV)¹². As a result, we show that both the emission of CH₄ and the ratio of
52 CH₄:CO₂ emissions increase markedly with seasonal increases in temperature.

Our findings suggest that global warming may have a large impact on the relative contributions of CO₂ and CH₄ to total greenhouse gas emissions from continental aquatic ecosystems, terrestrial wetlands and rice paddies.

Biogenic methane (CH₄) fluxes are a major component of global CH₄ emissions, yet they are poorly constrained^{2,13,14}. There are large uncertainties not only in the current magnitude of these fluxes, but also in the factors that regulate them^{2,13}. In particular, there is substantial uncertainty in the parameterisation of the temperature dependence of natural CH₄ emissions in process-based biogeochemistry models¹⁵⁻¹⁸, which greatly hinders our ability to predict the response of this key component of the carbon cycle to global warming. For example, temperature sensitivities for ecosystem-level CH₄ emissions have reported apparent activation energies that range from 0.2 to 2.5 eV^{6,19-21} (1 eV = 96 kJ mol⁻¹).

In a bid to reduce this uncertainty, which is fundamental to improving projections of future carbon cycle-climate change feedbacks¹⁵⁻¹⁸, we quantified variation in the temperature dependence of CH₄ fluxes for three different types of experiments – i.e. methanogenic cultures, anaerobic sediment slurries, and seasonal field surveys of CH₄ emissions – that correspond to three distinct levels of biological organisation – i.e. population, community, and ecosystem, respectively. In particular, we assess whether ecosystem-level CH₄ emissions exhibit a temperature dependence similar to that of the underlying methanogenic process, and quantify the magnitude of between site deviations from this physiological response. To do this, we first establish the magnitude and variability of the temperature dependence of key metabolic rate processes (i.e. methanogenesis, growth) for populations of methanogens in culture, as well as the temperature dependence of CH₄ production for anaerobic microbial communities in slurries. We then assess whether these temperature dependencies

differ from those observed in an ecosystem-level analysis of the seasonal temperature dependence of natural CH₄ emissions from aquatic, wetland and rice paddy ecosystems (see S1 of the Supplementary Information). Our ecosystem analysis includes both new and previously published data that together encompass 1553 paired estimates of CH₄ emission and temperature taken from 126 field sites.

To directly characterise the physiological temperature dependence of key metabolic rate processes for methanogens, we compiled data on rates of methanogenesis and growth from laboratory cultures of methanogen populations as well as rates of CH₄ production from microbial communities in anaerobic sediment slurries (see S1 of the Supplementary Information). We then separately fit the data compiled for each type of experiment to a Boltzmann-Arrhenius function, which characterises the exponential relationship between metabolic rate and temperature assuming a single enzyme catalysed reaction is rate-limiting²², using a linear mixed-effects model (see S2 of the Supplementary Information) of the form²³

$$\ln F_i(T) = \left(\overline{E_M} + \varepsilon_{E_M,i} \right) \left(1 / kT_C - 1 / kT \right) + \left(\overline{\ln F(T_C)} + \varepsilon_{F,i} \right) \quad (1)$$

where $\ln F_i(T)$ is the natural logarithm of the measured rate of CH₄ production or growth rate at absolute temperature, T (K), for some arbitrary experimental unit, i . In this expression, each experimental unit, i , corresponds to a distinct strain of methanogen (culture analysis) or sediment community (slurry analysis) that has been subjected to a range of temperatures. The parameter $\overline{E_M}$ (in eV; 1 eV = 96 kJ mol⁻¹) corresponds to an average among experimental units for the apparent activation energy, which characterises the temperature sensitivity of $F_i(T)$, and k is the Boltzmann constant (8.62x10⁻⁵ eV K⁻¹). We centred the temperature data using the mean temperature, T_C , across experimental units, so that $\overline{\ln F(T_C)}$ corresponds to an

average rate at T_C . For each analysis, we expect estimates of E_M and $\ln F(T_C)$ to vary between experimental units due, for example, to differences between cultures in cell densities, and variation between slurries in community composition. We account for these factors in our linear mixed-effects models by treating the slopes and intercepts as random variables with averages of $\overline{E_M}$ and $\overline{\ln F(T_C)}$, respectively, and deviations from these averages of $\varepsilon_{E_M,i}$ and $\varepsilon_{F,i}$ for each experimental unit, i (see S2 of the Supplementary Information for details of the statistical analysis).

The population-level analysis of the culture data reveal that the average apparent activation energies, $\overline{E_M}$, for the rates of methanogenesis and growth are statistically indistinguishable (likelihood ratio test; $\chi^2 = 0.39$, d.f. = 1, $P = 0.53$), and therefore have a similar temperature sensitivity (Fig. 1a; $\overline{E_M} = 1.10$ eV, 95% confidence interval: 0.93 – 1.27 eV). The community-level analysis of CH₄ production rates in anaerobic slurries yields a similar value for $\overline{E_M}$ (0.93 eV, 95% confidence interval: 0.82 – 1.03 eV), indicating that the temperature dependence of CH₄ production at the community level largely reflects the kinetics of the physiological processes generating this flux. More detailed analyses indicate that the estimates of $\overline{E_M}$ for sediment slurries obtained from three broadly defined ecosystem types (i.e. aquatic, wetlands, rice paddies; see S1 of the Supplementary Information for details of the data) are statistically indistinguishable (likelihood ratio test: $\chi^2 = 1.62$, d.f. = 2, $P = 0.44$). Consistent with our expectations, E_M does vary between experimental units, i , as reflected by the magnitude of the standard deviation of the random effect on the slope of the Arrhenius model, $\varepsilon_{E_M,i}$, in both analyses (see Table 1).

To explore how the temperature dependence of methanogenic populations and communities, compare to that of natural ecosystem-level CH₄ emissions, we fit equation (1) – here experimental units, i , correspond to sites – to a database of 1553 measurements of CH₄ emission and temperature, measured seasonally for 126 field sites that span the globe and encompass three distinct ecosystem types (aquatic, wetlands, rice paddies – see S1 of the Supplementary Information for definitions). Analyses reveal that estimates of $\overline{E_M}$ are statistically indistinguishable among ecosystem types (likelihood ratio test: $\chi^2 = 4.97$, d.f. = 2, $P = 0.10$), and therefore that the average temperature dependence of CH₄ emissions from diverse ecosystem types can be characterised by a common apparent activation energy ($\overline{E_M} = 0.98$ eV; 95% confidence interval: 0.88 – 1.08; see Fig. 2). This average temperature dependence is strikingly similar to that observed for methane production in cultures and sediment slurries (Fig. 1), which is remarkable given the multitude of processes – e.g. methanotrophy⁶, water-table depth^{9,10}, substrate supply⁷, community composition⁸ – that may confound the temperature dependence of CH₄ emissions over a seasonal cycle at the ecosystem-level. Our analysis is broadly consistent with the hypothesis that the seasonal temperature dependence of CH₄ emissions at the ecosystem-level largely reflects the kinetics of the methanogenic process generating this flux (see S4 for further discussion of the potential mechanisms constraining the scaling of the temperature dependence of CH₄ emissions). Importantly, the average apparent activation energy we report here for the seasonal temperature dependence of ecosystem-level CH₄ emissions ($\overline{E_M} = 0.98$ eV) is considerably higher than that reported previously for CO₂ fluxes attributable to respiration (~ 0.65 eV)¹¹, which could have important implications for the effect of global warming on the balance of CH₄ and CO₂ emissions from ecosystems²⁴.

150 Given the average seasonal temperature dependencies of CH₄ emissions
 151 reported here ($\overline{E_M} = 0.98$ eV), and that previously documented for respiration (~ 0.65
 152 eV)¹¹, we expected the ratio of CH₄ to CO₂ emission to increase, on average, with
 153 seasonal increases temperature across a collection of sites (see S3 of the
 154 Supplementary Information). While the temperature dependence of this ratio is not
 155 expected to adhere to a Boltzmann-Arrhenius relationship, we can approximate it
 156 using an expression of the form (see S3 of the Supplementary Information for a
 157 derivation of Eq. 2)

$$158 \quad \ln Q_i(T) = \left(\overline{E_{M:C}} + \varepsilon_{E_{M:C},i} \right) \left(1/kT_C - 1/kT \right) + \left(\overline{\ln Q(T_C)} + \varepsilon_{Q,i} \right) \quad (2)$$

159 where $Q_i(T)$ is the ratio of CH₄ to CO₂ emissions for site i at temperature T , $\overline{E_{M:C}}$
 160 and $\overline{\ln Q(T_C)}$ are averages across sites for the temperature dependence of this ratio and
 161 the magnitude of the ratio at temperature T_C , and $\varepsilon_{E_{M:C},i}$ and $\varepsilon_{Q,i}$ are random-effects
 162 terms used to represent site-level deviations from these respective averages.

163 To test this prediction, we analyse ecosystem-level data for the subset of
 164 studies in our compilation that report simultaneous measurements of ecosystem-level
 165 fluxes of CH₄ and CO₂, enabling us to calculate the efflux ratio of these greenhouse
 166 gases in response to seasonal variation in temperature. This dataset comprises 177
 167 estimates from 38 field sites. In exactly the same way as for the analyses of CH₄
 168 emissions, we fit a linear mixed effects model using the Boltzmann-Arrhenius
 169 function to the natural logarithm of the CH₄:CO₂ flux data (see Eq. 2). As predicted,
 170 this ratio increases with increasing temperature for the majority of the field sites (35
 171 of 38), yielding average temperature dependence across sites of $\overline{E_{M:C}} = 0.71$ eV (95%
 172 confidence interval: 0.46 – 0.97; see Fig. 3). This finding suggests that, on average,
 173 the relative contribution of methane to total greenhouse gas emissions from aquatic

ecosystems increases with seasonal increases in temperature due to the differences in the biochemical kinetics of methanogenesis, respiration and photosynthesis.

Our analyses demonstrate that the average apparent activation energy of CH₄ emissions across a wide range of ecosystems scales consistently with that of populations of methanogens in culture, and laboratory incubations of microbial communities. Moreover, this temperature dependence is much higher than that of both respiration¹¹ and photosynthesis¹², resulting in a greater relative contribution of CH₄ to total C emissions from aquatic ecosystems at higher temperatures. While this scaling of the temperature dependence of CH₄ fluxes across levels of biological organisation is remarkable, our results also emphasise that temperature is not the only variable that controls CH₄ emissions. Indeed, the substantial site-to-site variation we report for the temperature dependence of ecosystem-level CH₄ emissions (characterized by $\varepsilon_{E_M,i}$ in our mixed-effects model; see also Fig. 2b & Table 1), highlights the importance of other variables in driving deviations from the underlying physiological response. It is also important to note, that the average within-site apparent activation energy we report here for CH₄ emissions ($\overline{E_M} = 0.98$ eV) does not hold for the temperature response derived from geographic variation in average CH₄ emissions and temperature across sites. For example, average site temperature is a poor predictor of spatial variation in average emissions for each ecosystem type (see Extended Data Figures 1 & 2), suggesting that other biotic – e.g. methanotrophy⁶, substrate supply^{3,7}, microbial community composition⁸ – and abiotic – e.g. water-table depth^{9,10} – variables, besides temperature, may be more important for driving differences in total CH₄ emissions among ecosystems.

Overall, our findings provide a robust basis for refining parameterisation of the temperature sensitivity of CH₄ fluxes in global coupled climate-carbon cycle

models, a factor that until now yielded significant uncertainty in these models¹⁵. Furthermore, the observation of a general increase in the CH₄:CO₂ ratio with increasing temperature, driven by the high temperature sensitivity of CH₄ production, has important implications for the magnitude of future positive feedbacks between global warming and the carbon cycle given the relative potency of CH₄ compared to CO₂ as a greenhouse gas^{2,13}. In fact, a recent sensitivity analysis of the temperature dependence of CH₄ production in CLM4Me¹⁶, a process-based wetland biogeochemistry model embedded within the land surface component of an Earth system model, demonstrates that a Q₁₀ value of 4, equivalent to the activation energies we identify ($\overline{E_M} \approx 1.0$ eV), would result in an 50% increase in high latitude CH₄ emissions over the 21st Century, relative to the model's baseline Q₁₀ of 2 at 20°C ($\overline{E_M} \approx 0.5$ eV). Our analyses give strong evidence to support temperature sensitivities for methanogenesis and CH₄ emissions that are substantially higher than other key fluxes in the carbon cycle, like heterotrophic respiration and photosynthesis, and suggest that current predictions of carbon cycle-climate change feedbacks²⁵, which fail to account for these differences, may be significantly underestimated.

References

1. Forster, P. *et al.*, *Changes in Atmospheric Constituents and in Radiative Forcing*. In: Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Eds: Solomon, S; Qin, D; Manning, M; Chen, Z; Marquis, M; Averyt, KB; Tignor, M; Miller, HL. Cambridge University Press. (2007).
2. Kirschke, S. *et al.* Three decades of global methane sources and sinks. *Nature*

- 224 *Geosci* **6**, 813–823 (2013).
- 225 3. Thauer, R. K., Kaster, A.-K., Seedorf, H., Buckel, W. & Hedderich, R.
 226 Methanogenic archaea: ecologically relevant differences in energy
 227 conservation. *Nature Reviews Microbiology* **6**, 579–591 (2008).
- 228 4. Westermann, P., Ahring, B. K. & Mah, R. A. Temperature compensation in
 229 *Methanoscina barkeri*. *Applied and Environmental Microbiology* **55**, 1262–
 230 1266 (1989).
- 231 5. Zinder, S. H., Anguish, T. & Cardwell, S. C. Effects of temperature on
 232 methanogenesis in a thermophilic (58-degrees-C) anaerobic digester. *Applied*
 233 *and Environmental Microbiology* **47**, 808–813 (1984).
- 234 6. Segers, R. Methane production and methane consumption: a review of
 235 processes underlying wetland methane fluxes. *Biogeochemistry* **41**, 23–51
 236 (1998).
- 237 7. Whiting, G. J. & Chanton, J. P. Primary production control of methane
 238 emission from wetlands. *Nature* **364**, 794–795 (1993).
- 239 8. Fey, A. & Conrad, R. Effect of temperature on carbon and electron flow and on
 240 the archaeal community in methanogenic rice field soil. *Applied and*
 241 *Environmental Microbiology* **66**, 4790–4799 (2000).
- 242 9. Moore, T. R., Roulet, N. T. & Waddington, J. M. Uncertainty in predicting the
 243 effect of climatic change on the carbon cycling of Canadian peatlands.
 244 *CLIMATIC CHANGE* {**40**}, {229–245} (1998).
- 245 10. Moore, T. R. & Roulet, N. T. Methane flux: Water table relations in northern
 246 wetlands. *Geophys. Res. Lett.* **20**, 587–590 (1993).
- 247 11. Yvon-Durocher, G. *et al.* Reconciling the temperature dependence of
 248 respiration across time scales and ecosystem types. *Nature* **487**, 472–476

- 249 (2012).
- 250 12. Allen, A. P., Gillooly, J. F. & Brown, J.H. Linking the global carbon cycle to
251 individual metabolism. *Functional Ecology* **19**, 202–213 (2005).
- 252 13. Bridgman, S. D., Cadillo-Quiroz, H., Keller, J. K. & Zhuang, Q. Methane
253 emissions from wetlands: biogeochemical, microbial, and modeling
254 perspectives from local to global scales. *Global Change Biology* **19**, 1325–
255 1346 (2013).
- 256 14. Bastviken, D., Tranvik, L. J., Downing, J. A., Crill, P. M. & Enrich-Prast, A.
257 Freshwater Methane Emissions Offset the Continental Carbon Sink. *Science*
258 **331**, 50 (2011).
- 259 15. Gedney, N. Climate feedback from wetland methane emissions. *Geophys. Res.*
260 *Lett.* **31**, (2004).
- 261 16. Riley, W. J. *et al.* Barriers to predicting changes in global terrestrial methane
262 fluxes: analyses using CLM4Me, a methane biogeochemistry model integrated
263 in CESM. *Biogeosciences* **8**, 1925–1953 (2011).
- 264 17. Spahni, R. *et al.* Constraining global methane emissions and uptake by
265 ecosystems. *Biogeosciences* **8**, 1643–1665 (2011).
- 266 18. Wania, R., Ross, I. & Prentice, I. C. Implementation and evaluation of a new
267 methane model within a dynamic global vegetation model: LPJ-WHyMe
268 v1.3.1. *Geosci. Mod. Dev* **3**, 565–584 (2010).
- 269 19. Christensen, T. R. *et al.* Factors controlling large scale variations in methane
270 emissions from wetlands. *Geophys. Res. Lett.* **30**, (2003).
- 271 20. Crill, P. M. *et al.* Methane flux from Minnesota Peatlands. *Global Biogeochem.*
272 *Cycles* **2**, 371–384 (1988).
- 273 21. Walter, B. P. & Heimann, M. A process-based, climate-sensitive model to

derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate. *Global Biogeochem. Cycles* **14**, 745–765 (2000).

22. Eyring, H. The Activated Complex and the Absolute Rate of Chemical Reactions. *Chem. Rev.* **17**, 65–77 (1935).
23. Zuur, A., Ieno, E., Walker, N. & Saveliev, A. *Mixed effects models and extensions in ecology with R*. (Springer Verlag, 2009).
24. Yvon-Durocher, G., Montoya, J. M., Woodward, G., Jones, J. I. & Trimmer, M. Warming increases the proportion of primary production emitted as methane from freshwater mesocosms. *Global Change Biology* **17**, 1225–1234 (2011).
25. Melton, J. R. *et al.* Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP). *Biogeosciences* **10**, 753–788 (2013).

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

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Author contributions. GY-D, DB & CG had initial discussions. GY-D conceived the study, analysed the data, and wrote the first draft of the manuscript. DB, PdG, CG, NT-D, RC & AS contributed original data. APA wrote the theory for the CH₄:CO₂ temperature dependence. All authors contributed to revisions of the manuscript.

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Tables

Table 1 Estimates of the parameters used to characterise the temperature dependence of CH₄ flux or the CH₄: CO₂ efflux ratio. The standard deviations (s.d.) of site or experimental unit-specific estimates for $\varepsilon_{E_M,i}$ (equation 1) were significantly > 0 for each of the analyses ($P < 0.05$), indicating differences among sites or experimental units in apparent activation energies. The standard deviations of site or experimental unit-specific estimates for $\varepsilon_{F,i}$ (equation 1) were significantly > 0 in all analyses ($P < 0.001$), indicating differences among sites or experimental units in CH₄ flux or the CO₂:CH₄ efflux ratio at the average temperature.

Flux Type	$\overline{E_M}$ (95% CI)	s.d. $\varepsilon_{E_M,i}$	s.d. $\varepsilon_{F,i}$
Laboratory Studies			
Pure culture methanogens	1.10 (0.93 – 1.27)	0.42	2.28
Slurries CH ₄ production	0.93 (0.82 – 1.03)	0.32	2.45
Whole Ecosystem CH ₄ Efflux	0.98 (0.88 – 1.08)	0.36	2.16
CO ₂ :CH ₄ ratio	0.71 (0.46 – 0.97)	0.59	1.03

315 Figures

Figure 1| The temperature dependence of CH_4 production. Analyses fitting the Boltzmann-Arrhenius function to rate data, reveal similar temperature dependencies for (a) pure cultures of methanogens, and (b) slurries of aquatic (red), wetland (green) and rice-paddy (red) sediment samples incubated at different constant temperatures in the laboratory. In (b), the temperature dependence of CH_4 production is not significantly different among ecosystem types (see main text for details of statistics). In all plots, data have been standardised by subtracting from each measurement the estimated experiment-specific deviation from the average intercept predicted by the mixed-effects model. This standardisation was used for visualisation of the data only; raw values were used in the statistical analyses.

Figure 2| The temperature dependence of CH₄ emissions at the ecosystem scale.

Analysis reveals a consistent temperature dependence for the emission of CH₄ from aquatic (red), wetland (green) and rice-paddy (red) ecosystems (a). Histogram of the site-level activation energies is also given (b), note that the majority of estimated apparent activation energies are very close to the average value derived from experiments using pure cultures and anaerobic sediment communities (see Fig. 1).

The red dashed line in (b) corresponds to $\overline{E_M} = 0.98$ eV, estimated from the mixed effects model. In the Arrhenius plot, data have been standardised by subtracting from each measurement the estimated site-specific deviation from the average intercept predicted by the mixed-effects model. This standardisation was for visualisation of the data only; raw values were used in the statistical analyses.

Figure 3| The temperature dependence of the $\text{CH}_4:\text{CO}_2$ emission ratio. Analyses reveal a high temperature dependence in the CH_4 to CO_2 emission ratio (a). A histogram of the site-level apparent activation energies is also given (b). The red dashed line in (b) corresponds to $\overline{E_{M:C}} = 0.71$ eV, estimated from the mixed effects model. As with Figs. 1 & 2, data for the Arrhenius plot have been standardised by subtracting from each measurement the estimated site-specific deviation from the average intercept predicted by the mixed-effects model. This standardisation was for visualisation of the data only; raw values were used in the statistical analyses.