LETTER

Reconciling the temperature dependence of respiration across timescales and ecosystem types

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Ecosystem respiration is the biotic conversion of organic carbon to carbon dioxide by all of the organisms in an ecosystem, including both consumers and primary producers. Respiration exhibits an exponential temperature dependence at the subcellular and individual levels[1], but at the ecosystem level respiration can be modified by many variables[2-4] including community abundance and biomass[5], which vary substantially among ecosystems[6]. Despite its importance for predicting the responses of the biosphere to climate change, it is as yet unknown whether the temperature dependence of ecosystem respiration varies systematically between aquatic and terrestrial environments. Here we use the largest database of respiratory measurements yet compiled to show that the sensitivity of ecosystem respiration to seasonal changes in temperature is remarkably similar for diverse environments encompassing lakes, rivers, estuaries, the open ocean and forested and non-forested terrestrial ecosystems, with an average activation energy similar to that of the respiratory complex[3] (approximately 0.65 electronvolts (eV)). By contrast, annual ecosystem respiration shows a substantially greater temperature dependence across aquatic (approximately 0.65 eV) versus terrestrial ecosystems (approximately 0.32 eV) that span broad geographic gradients in temperature. Using a model[5] derived from metabolic theory[7], these findings can be reconciled by similarities in the biochemical kinetics of metabolism at the subcellular level, and fundamental differences in the importance of other variables besides temperature—such as primary productivity and allochthonous carbon inputs—on the structure of aquatic and terrestrial biota at the community level.

We assessed variability in the temperature dependence of ecosystem respiration within and among a range of aquatic and terrestrial environments using a global compilation of measurements of respiration from nine distinct ecosystem types that represent entire ecosystems or ecosystem components (Supplementary Information 1). We performed two analyses using these data. First, we assessed the sensitivity of ecosystem respiration to seasonal changes in temperature within sites for each ecosystem type, and quantified its variation among sites and across ecosystem types using daily (hereafter short-term) estimates of flux. Second, we determined the temperature sensitivity of respiration at longer timescales by comparing annual (hereafter long-term) fluxes across sites spanning broad geographic gradients in temperature. We reconcile the similarities and differences in the temperature dependence of ecosystem respiration across timescales and ecosystem types using a model[5] derived from metabolic theory[7].

To determine variation among sites in the seasonal temperature dependence of ecosystem respiration for the nine ecosystem types in our compilation, we fit the short-term respiration data to the Boltzmann–Arrhenius function using linear mixed-effects modelling[8] (see Methods Summary, Supplementary Information 2 and 5):

$$\ln R_s(T) = (\bar{E}_R + \varepsilon_E^s)(1/kT_C - 1/kT) + \overline{\ln R(T_C)} + \varepsilon_R^s \qquad (1)$$

In this expression, $\ln R_s(T)$ is the natural logarithm of respiration rate for some arbitrary site s at absolute temperature T (in kelvin (K)), $\bar{E}_R$ is an average among sites for the apparent activation energy, which characterizes the temperature sensitivity of ecosystem respiration, and k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}). We centred the temperature data using a fixed, arbitrary value ($= 288$ K $= 15\,°$C) so that $\overline{\ln R(T_C)}$ corresponds to an average among sites for the rate of ecosystem respiration at 15 °C, $R(T_C)$. We would expect $R(T_C)$ to vary among sites due to factors that affect the availability of reduced carbon substrates to support biomass, including net primary production[9,10] and allochthonous carbon inputs[6,11-13], as well as factors that affect the susceptibility of reduced carbon substrates to decomposition by biota, such as C:N:P stoichiometry[6] and water availability[14]. We would also expect $R(T_C)$ to vary seasonally within a site[2,3], resulting in a deviation of the apparent activation energy from $\bar{E}_R$ (Supplementary Information 2), owing to processes that co-vary with temperature, such as litterfall and nutrient turnover in the water column[15]. To account for these factors in our linear mixed-effects models, we treated the slope and intercept as random variables with averages of $\bar{E}_R$ and $\overline{\ln R(T_C)}$, respectively, and site-specific deviations from these averages of ε_E^s and ε_R^s for each site s.

Analyses of the short-term data revealed marked similarities in the seasonal temperature dependence of ecosystem respiration across all nine ecosystem types (Fig. 1). Estimates of the average apparent activation energy, $\bar{E}_R$, were statistically indistinguishable from each other (likelihood ratio test; $\chi_8^2 = 7.36$, $P = 0.50$), with an average of 0.62 eV (Table 1), which corresponds to a Q_{10}—that is, the proportional increase in respiration per 10 °C rise in temperature—of ~ 2.5 at 15 °C. Consistent with our model, the apparent activation energy varied between sites, as reflected by the significance of the term used to represent ε_E^s in eight of the nine models (Table 1), but this variation was not systematically different among ecosystem types (Supplementary Information 8 and 9). Recent work indicates that this variability partly reflects localized factors—for example, water availability, productivity, allochthonous carbon input—that seasonally co-vary with respiration, $R(T_C)$, and temperature, and can modulate the apparent temperature sensitivity at the site level[2,3]. Our model yields predictions on how the magnitude of this covariation affects the apparent activation energy at a given site, and thus provides a biological interpretation for differences among sites (Supplementary Information 2).

To set our results in a more general theoretical context, we can explore them further by applying a model derived from metabolic theory[5]. Because metabolic theory relates complex ecosystem-level phenomena to the effects of body mass and temperature on individual-level

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Table 1 | Estimates of the parameters used to characterize the temperature dependence of ecosystem respiration seasonally and annually

Ecosystem type	Short-term					Long-term	
	$\bar{E}_R$ (95% CI)	r^2	s.d. ε_E^s	s.d. ε_R^s	Cor[$\varepsilon_E^s, \varepsilon_R^s$]	E (95% CI)	r^2
Terrestrial							
Forests	0.62 (0.56–0.68)	0.56	0.17	0.43	0.33	0.42 (0.26–0.60)	0.46
Non-forests	0.70 (0.57–0.80)	0.63	0.20	0.95	0.26	0.00 (−0.30–0.32)	0.00
Soils	0.65 (0.53–0.68)	0.77	0.35	0.84	0.13	0.32 (0.26–0.37)	0.20
Aquatic							
Lake benthic	0.55 (0.44–0.68)	0.74	0.29	0.50	−0.03	0.64 (0.14–1.04)	0.27
Lake pelagic	0.63 (0.55–0.78)	0.73	0.38	1.65	−0.14	1.06 (0.14–2.15)	0.26
Rivers	0.58 (0.44–0.78)	0.81	0.16	0.62	−0.27	1.08 (0.49–1.60)	0.36
Estuarine benthic	0.63 (0.57–0.69)	0.77	0.10	0.53	0.16	0.93 (0.44–1.37)	0.22
Estuarine pelagic	0.59 (0.51–0.69)	0.87	0.29	1.56	−0.22	0.57 (0.22–0.94)	0.25
Oceanic microbial	0.57 (0.46–0.80)	0.72	NA	1.49	NA	NA	NA
All data combined	0.62 (0.60–0.66)	0.86	0.28	1.17	0.01		NA

A likelihood ratio test failed to detect significant differences in $\bar{E}_R$ among ecosystem types when all data were combined into a single mixed-effects analysis (Supplementary Information 5). The standard deviations (s.d.) of site-specific estimates for ε_E^s (equation (1)) were significantly >0 for the eight ecosystems tested ($P < 0.05$), indicating differences among sites in the short-term temperature dependence of ecosystem respiration. The standard deviations of site-specific estimates for ε_R^s (equation (1)) were significantly >0 for all ecosystem types ($P < 0.0001$), indicating differences among sites in the rate of ecosystem respiration at fixed temperature, $R(T_C)$. Cor[$\varepsilon_E^s, \varepsilon_R^s$] refers to the correlation between the site-specific slope and intercept estimates. NA, not applicable.

metabolism, it is particularly useful for understanding how physiology, community structure and abiotic variables combine to influence ecosystem metabolism[5,7]. Ecosystem respiration per unit area for J organisms in an area of size A is equal to the sum ($= (1/A) \sum_{i=1}^{J} r_i$) of the individual respiration rates[5,16], r_i. Separately performing this summation for autotrophs and heterotrophs yield expressions that relate total respiratory fluxes of the two groups, $R_A(T)$ and $R_H(T)$ (g C m^{-2} d^{-1}), to individual-level normalizations for respiration, r_o^A and r_o^H (g$^{1-\alpha}$ C d^{-1}), standing stocks of community biomass, M_A and M_H (g C m^{-2}), biomass-weighted averages for individual body mass, $\langle m_A^{\alpha-1} \rangle$ and $\langle m_H^{\alpha-1} \rangle$ (g$^{\alpha-1}$ C), and the size-dependence of individual respiration, characterized by α (Supplementary Information 3)[5]:

$$R_A(T) = r_o^A M_A \langle m_A^{\alpha-1} \rangle e^{-E_R/kT} \tag{2}$$

$$R_H(T) = r_o^H M_H \langle m_H^{\alpha-1} \rangle e^{-E_R/kT} \tag{3}$$

Ecosystem respiration, $R(T)$, is equal to the sum of these fluxes

$$R(T) = R_A(T) + R_H(T) = R(T_C) e^{E_R(1/kT_C - 1/kT)} \tag{4}$$

which implies that ecosystem respiration at fixed temperature, $R(T_C)$, is governed partly by the mass-corrected community biomass of autotrophs $M_A \langle m_A^{\alpha-1} \rangle$ and heterotrophs $M_H \langle m_H^{\alpha-1} \rangle$:

$$R(T_C) = \left(r_o^A M_A \langle m_A^{\alpha-1} \rangle + r_o^H M_H \langle m_H^{\alpha-1} \rangle \right) e^{-E_R/kT_C} \tag{5}$$

Remarkably, empirical estimates of $\bar{E}_R$ for all nine ecosystem types included in our analyses of the short-term data were statistically indistinguishable from the range of values expected for E_R, that is, 0.6–0.7 eV, based on the biochemical kinetics of the respiratory complex[1,5]. Thus, our findings suggest that the underlying physiological temperature dependence of ecosystem respiration is essentially the same across diverse aquatic and terrestrial environments, despite considerable variability in taxonomic composition and abiotic variables.

We now consider whether ecosystem-level variables, such as gross primary production and allochthonous carbon, modulate the temperature dependence of annual ecosystem respiration across sites that differ in their annual temperature regimes. Metabolic theory yields quantitative predictions for the temperature dependence of annual respiration across ecosystems in which community biomass and metabolism are constrained by the temperature dependence of photosynthesis[5], which is known to be weaker than that of respiration[5,17–19]. The temperature dependence of photosynthesis, although not exponential, can be approximated using an effective activation energy $E_p \approx 0.32$ eV over broad temperature gradients for both aquatic and terrestrial autotrophs[5,19,20], which corresponds to a Q_{10} of ~1.6 at 15 °C. If annual ecosystem respiration, $\tau \langle R(T) \rangle_\tau$, is limited by gross primary production, $\tau \langle P(T) \rangle_\tau$, over the time interval $\tau = 1$ yr, then

both quantities can be predicted by integrating short-term gross primary production, $P(T)$ (g C m^{-2} d^{-1}), with respect to temperature variation, $T(t)$, through time, t:

$$\tau \langle R(T) \rangle_\tau \approx \tau \theta \langle P(T) \rangle_\tau = \theta \int_\tau P(T(t)) dt =$$
$$\tau \theta p_o e^{-E_P/kT_C} M_A \langle m_A^{\alpha-1} \rangle \left\langle e^{E_P(1/kT_C - 1/kT)} \right\rangle_\tau \tag{6}$$

where p_o is an individual-level normalization for photosynthesis (g$^{1-\alpha}$ C d^{-1}), $\left\langle e^{E_P(1/kT_C - 1/kT)} \right\rangle_\tau$ is 'Boltzmann-averaged' temperature kinetics over the time interval $= (1/\tau) \int_\tau e^{E_P(1/kT_C - 1/kT(t))} dt$ (see Supplementary Information 4), and θ is the fraction of gross primary production respired by autotrophs and heterotrophs. The remaining non-respired fraction, $1 - \theta$, may accumulate in situ, may be released through alternative pathways such as fire or volatile organic carbon emissions[21], or may be exported as allochthonous carbon to other ecosystems, where it can potentially enhance respiration and heterotrophic biomass production[11,22]. Equation (6) implies a proportional relationship between ecosystem respiration and gross primary production, consistent with broad-scale comparative analyses of terrestrial ecosystems[10,23], based on the assumptions that allochthonous carbon inputs are much smaller than autochthonous primary production[24], and that heterotrophic respiration consumes most net primary production[5,10]. Although both assumptions seem to be reasonable first approximations in terrestrial ecosystems over sufficiently long timescales, for example, centuries[25], imbalances between terrestrial plant production and ecosystem respiration are well established over timescales of years to decades[26]. Nevertheless, equation (6) provides a useful framework for assessing the directions and magnitudes of such imbalances.

Equation (6) predicts that long-term ecosystem respiration should be governed by the temperature dependence of photosynthesis (≈ 0.32 eV) across terrestrial ecosystems, where long-term respiration is limited by gross primary production at the site level[23]. This assumption is clearly violated in many aquatic ecosystems because allochthonous carbon inputs can contribute to heterotrophic biomass production and ecosystem respiration, beyond that which could be supported by autochthonous primary production alone[11,22]. In addition, the fraction of autochthonous primary production consumed locally by heterotrophic respiration generally declines with increasing productivity in aquatic ecosystems[15]. Both of these processes may effectively decouple respiration from photosynthesis at the site level. This leads us to propose that there are fundamental differences in the long-term temperature dependence of ecosystem respiration between aquatic and terrestrial environments.
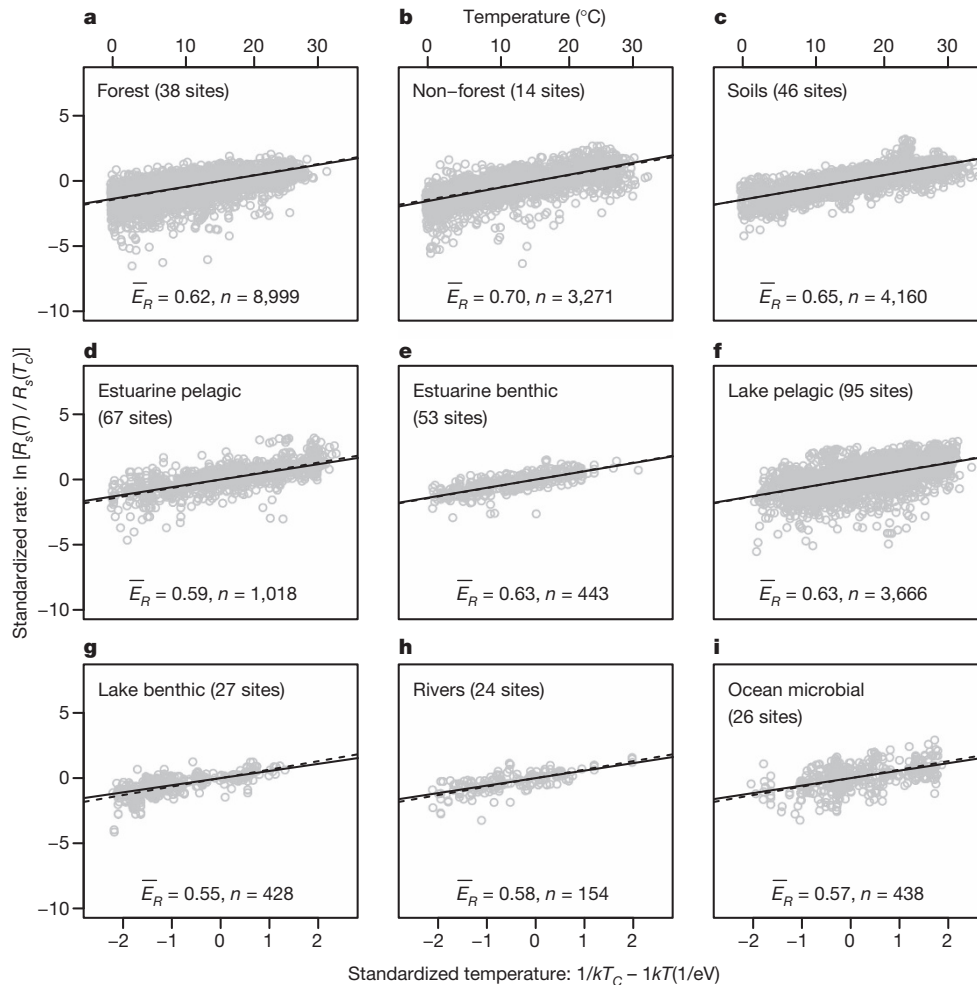
Figure 1 | Relationships between standardized short-term respiration and standardized inverse absolute temperature for 9 ecosystem types encompassing 373 sites. Standardized fluxes were expressed as $\ln[R_s(T)/R_s(T_C)]$, where $R_s(T)$ is the measured rate of respiration at site s. The site-specific estimates of respiration at fixed temperature, $R_s(T_C)$, and the average activation energies, $\bar{E}_R$, were determined using mixed-effects modelling (equation (1)). The temperature chosen for standardization ($T_C = 288\,\text{K} = 15\,^\circ\text{C}$) is arbitrary and does not substantively affect our results. Standardization of the fluxes was for visualisation of the data only; $R_s(T)$ values were used in the mixed-effects analysis to determine the temperature dependencies. The solid and dashed lines correspond to the fitted and predicted ($E_R \approx 0.65\,\text{eV}$) slopes, respectively. All data sets are consistent with this prediction (Table 1).

We evaluated this hypothesis using annually integrated rates of ecosystem respiration for eight ecosystem types (open oceans could not be analysed owing to insufficient long-term data; Supplementary Information 1). Across the terrestrial ecosystem types, annual respiration exhibited no significant correlation with temperature for non-forested systems (Fig. 2 and Table 1). This might be because warmer temperatures result in more negative water balances in such systems, depressing gross primary production[9,10] and thus respiration. Respiration was, however, positively correlated with temperature across forests and soils (Fig. 2 and Table 1) and, in agreement with our prediction, the temperature dependencies for the long-term rates were indistinguishable from that of photosynthesis ($E_P \approx 0.32\,\text{eV}$; Fig. 2 and Table 1). We obtained similar results for these two ecosystem types after controlling for growing-season length and daylight hours during the growing season (Supplementary Information 7). In contrast, for all of the aquatic ecosystem types, annually integrated rates of respiration yielded activation energies that were consistently greater than E_P, with 95% confidence intervals (CIs) that included E_R ($\approx 0.65\,\text{eV}$; Fig. 2 and Table 1). Overall, a likelihood ratio test indicated that the long-term temperature dependence of ecosystem respiration differed significantly ($\chi^2_1 = 17.14$, $P < 0.005$) between the terrestrial ($E = 0.32$ eV; 95% CI, 0.26–0.38 eV) and aquatic ecosystems ($E = 0.77$ eV; 95% CI, 0.57–0.98 eV), in agreement with our hypothesis.

In terrestrial ecosystems, where long-term respiration is constrained by gross primary production, equations (5) and (6) yield the prediction that the rate of ecosystem respiration at fixed temperature:

$$R(T_C) = \left(r_o^A M_A \langle m_A^{\alpha-1}\rangle + r_o^H M_H \langle m_H^{\alpha-1}\rangle\right) e^{-E_R/kT_C}$$
$$\propto \left\langle e^{E_P(1kT_C - /1kT)}\right\rangle_\tau \Big/ \left\langle e^{E_R(1kT_C - /1kT)}\right\rangle_\tau \tag{7}$$

should decline with increasing average temperature according to the ratio of the factors characterizing the Boltzmann-averaged temperature kinetics for photosynthesis and respiration. This predicted decline in $R(T_C)$ with increasing temperature in part reflects a reduction in mass-corrected heterotrophic biomass[5], $M_H \langle m_H^{\alpha-1}\rangle$ (Supplementary Information 4), which occurs because respiration rates of heterotrophic organisms increase more rapidly with temperature than autochthonous net primary production[5,18,20]. Warmer ecosystems should therefore support a lower standing stock of mass-corrected heterotrophic biomass per unit of carbon fixed by photosynthesis. On the contrary, in aquatic systems, empirical data demonstrate that heterotrophic metabolism is often not directly limited by autochthonous primary production over the long term, due either to allochthonous carbon subsidies, or because primary production exceeds heterotrophic metabolism[11,15,22]. Consequently, we would expect the temperature dependence of photosynthesis to have a weak or negligible effect on
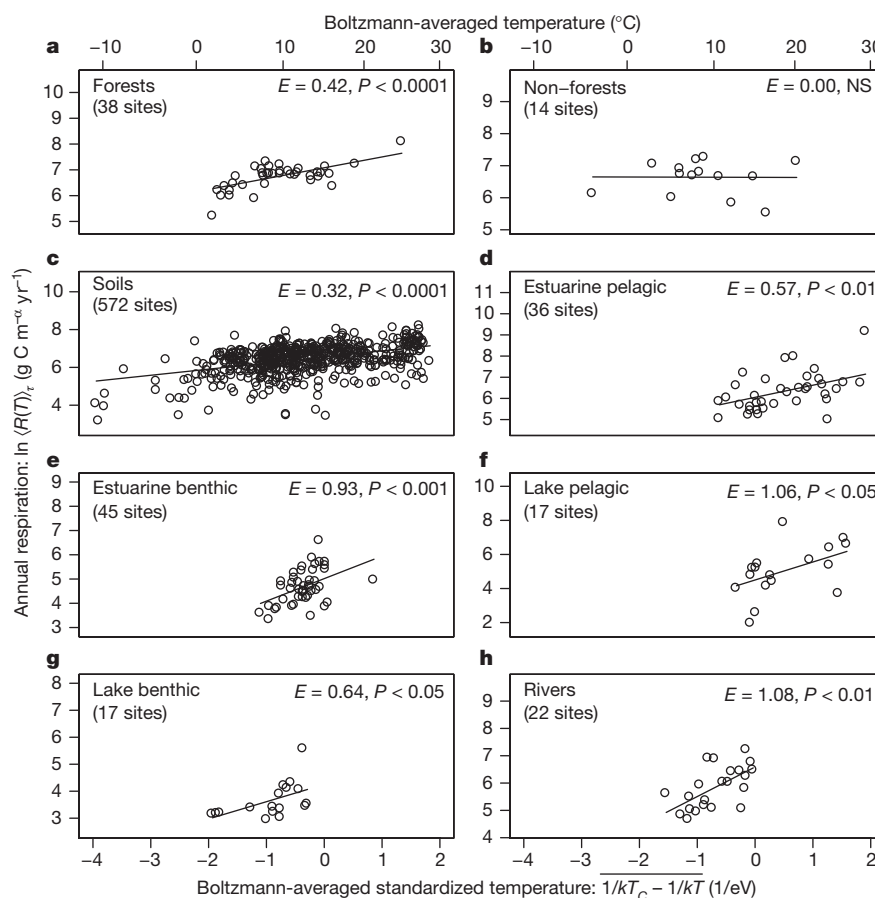
Figure 2 | Relationship between annual ecosystem respiration and Boltzmann-averaged standardized temperature. Units of fluxes are in $g\,C\,m^{-2}\,yr^{-1}$ for all ecosystem types except estuarine and lake pelagic zones, where fluxes are given in volumetric units ($g\,C\,m^{-3}\,yr^{-1}$). The long-term (that is, annual) temperature dependencies of respiration for all of the terrestrial ecosystems yielded slopes significantly less than the activation energy of

respiration ($E_R \approx 0.65$ eV; Table 1), consistent with the hypothesis that photosynthesis limits heterotrophic biomass and overall respiratory metabolism (equation (6)). By contrast, for all of the aquatic ecosystems, the 95% CIs encompassed E_R. Overall, these findings suggest fundamental differences in the factors structuring aquatic and terrestrial communities along geographic temperature gradients. NS, not significant.

$R(T_C)$ (Supplementary Information 4). We evaluated these predictions using the estimates of $R(T_C)$ obtained from the mixed-effects analyses above (equation (1)). As predicted by equation (7), $R(T_C)$ was negatively correlated with average temperature for forests, non-forested ecosystems and soils (Supplementary Information 10). Thus, because annual ecosystem respiration is the product of the sizes, abundances and metabolic rates of all the organisms comprising that ecosystem, declines in $R(T_C)$ with increasing annual temperature explain how the weaker apparent temperature dependence of long-term ecosystem respiration across terrestrial systems arises. By contrast, estimates of $R(T_C)$ were not correlated with average temperature for any of the aquatic ecosystem types (Supplementary Information 10), contrary to what was observed in terrestrial ecosystems, but in line with expectations given that the short-term and long-term aquatic flux data yielded similar apparent temperature sensitivities.

Our findings highlight marked similarities in the seasonal temperature dependence of short-term respiration across the major ecosystem types on the planet (Fig. 1), as well as a clear dichotomy between terrestrial and aquatic ecosystems with respect to the temperature dependencies of annual respiration (Fig. 2) and daily respiration at fixed temperature (Supplementary Information 10). These divergent patterns between terrestrial and aquatic ecosystems can be reconciled by assuming that, over long timescales, heterotrophic metabolism in terrestrial ecosystems is more tightly constrained by autochthonous primary production[10,23], which exhibits a weaker temperature dependence than respiration (equations (6) and (7)). In many aquatic ecosystems, the constraint of autochthonous primary production on

long-term respiration may be relatively weak due to a greater influence of other variables such as allochthonous carbon subsidies[11,22]. These assumptions are consistent with our compilation of long-term aquatic respiration data (with the important exception of open oceans, for which we had no long-term data), and with the observation that heterotrophic metabolism can exceed autochthonous primary production in many aquatic ecosystems over the long term[11,22]. Nevertheless, they clearly require direct empirical validation using commensurate community-level data on abundance and biomass, and ecosystem-level data on respiration and primary production. Still, our model and analyses provide a new way of reconciling the similarities and differences in the temperature dependence of ecosystem respiration across timescales and ecosystem types on the basis of the biochemical kinetics of photosynthetic and respiratory metabolisms.

METHODS SUMMARY

To estimate the seasonal temperature dependence of ecosystem respiration for each of the nine ecosystem types, linear mixed-effects models were fit to the data for each ecosystem type using the lme4 package in R statistical software (v.2.14.0)[27]. Mixed-effects modelling was also applied to all data combined to test for differences in the temperature dependence of respiration among ecosystem types. Significance was assessed using a likelihood ratio test[8], comparing a model with a common activation energy to models with different activation energies for each ecosystem type (see Supplementary Information 5).

The long-term temperature dependence of ecosystem respiration was determined by using maximum likelihood to estimate the activation energy, E, that best predicted annual ecosystem respiration based on Boltzmann-averaged temperature kinetics, $\left\langle e^{E(1/kT_C - 1/kT)} \right\rangle_\tau$ (equation (6); see Supplementary

Information 6). Boltzmann averaging is preferable to using arithmetic mean temperature to assess kinetics because this entails an approximation that becomes less accurate as seasonal variation in temperature increases[28]. Model fits are depicted graphically in Fig. 2 by re-expressing average kinetics as $\ln\left\langle e^{E(1/kT_C-1/kT)}\right\rangle_\tau \Big/ E$ and $(E/k)\Big/\left[E/kT_C-\ln\left[\left\langle e^{E(1/kT_C-1/kT)}\right\rangle_\tau\right]\right]-273$ along the lower and upper horizontal axes, respectively. However, the full distributions of temperatures (including temperatures $<0\,^\circ$C) were used to fit the models.

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Author Contributions G.Y.-D. and A.P.A. analysed the data, wrote the manuscript, and devised the research. A.C., J.M.C., M.D., P.d.G., J.M.G., J.M.M., J.P., P.A.S., M.T. and G.W. commented on the manuscript. G.Y.-D., A.P.A., P.d.G., J.M.M. and M.T. discussed ideas. A.C., J.M.C., M.D., P.d.G., J.P., M.T. and P.A.S. provided raw data.

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