

# Global patterns in lake ecosystem responses to warming based on the temperature dependence of metabolism

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## Abstract

Climate warming is expected to have large effects on ecosystems in part due to the temperature dependence of metabolism. The responses of metabolic rates to climate warming may be greatest in the tropics and at low elevations because mean temperatures are warmer there and metabolic rates respond exponentially to temperature (with exponents >1). However, if warming rates are sufficiently fast in higher latitude/elevation lakes, metabolic rate responses to warming may still be greater there even though metabolic rates respond exponentially to temperature. Thus, a wide range of global patterns in the magnitude of metabolic rate responses to warming could emerge depending on global patterns of temperature and warming rates. Here we use the Boltzmann–Arrhenius equation, published estimates of activation energy, and time series of temperature from 271 lakes to estimate long-term (1970–2010) changes in 64 metabolic processes in lakes. The estimated responses of metabolic processes to warming were usually greatest in tropical/low-elevation lakes even though surface temperatures in higher latitude/elevation lakes are warming faster. However, when the thermal sensitivity of a metabolic process is especially weak, higher latitude/elevation lakes had larger responses to warming in parallel with warming rates. Our results show that the sensitivity of a given response to temperature (as described by its activation energy) provides a simple heuristic for predicting whether tropical/low-elevation lakes will have larger or smaller metabolic responses to warming than higher latitude/elevation lakes. Overall, we conclude that the direct metabolic consequences of lake warming are likely to be felt most strongly at low latitudes and low elevations where metabolism-linked ecosystem services may be most affected.

**Keywords:** aquatic, carbon, climate change, fish, long-term, methane, temperature, tropics

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## Introduction

Metabolic theory provides a basis for using first principles of physics and chemistry to understand ecosystem responses to climate warming (Brown *et al.*, 2004). Metabolic theory suggests that warming influences ecosystem dynamics, in part, due to the fundamental temperature dependence of biochemical reactions underlying all of metabolism. Photosynthesis (Farquhar *et al.*, 1980), organismal lifespans (Munch & Salinas, 2009), and ecosystem-level methane emissions (Yvon-Durocher *et al.*, 2014) are all well-studied

metabolism-linked variables that exhibit a fundamental link between temperature and metabolism.

Empirically derived relationships between temperature and metabolism-linked variables have been used widely to estimate long-term responses of ecosystems to warming in the absence of long-term metabolism data (Cheung *et al.*, 2008; Daufresne *et al.*, 2009; Dillon *et al.*, 2010; Gardner *et al.*, 2011; Marotta *et al.*, 2014; Weber *et al.*, 2015). These estimations suggest that linear warming will increase metabolic rates exponentially, with consequences for all levels of biological organization from individuals to ecosystems. However, warming rates and the sensitivity of metabolism-linked variables to temperature vary substantially across ecosystem types (Dell *et al.*, 2011; O'Reilly *et al.*, 2015). Thus, estimations of the global responses of metabolism

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to climate warming in a specific ecosystem type will depend on how temperature variation in that ecosystem type intersects with its thermal sensitivity to give rise to metabolic change.

The relationship between temperature and metabolism-linked variables can be described by the Boltzmann–Arrhenius equation,

$$v = b_0 e^{-E_a/kT} \quad (1)$$

where  $v$  is the metabolism-linked variable,  $b_0$  is a normalization constant,  $e$  is Euler's number (2.718),  $E_a$  is the activation energy (in eV),  $k$  is the Boltzmann constant ( $8.617 \times 10^{-5}$  eV K<sup>-1</sup>), and  $T$  is the temperature (in °K). Metabolism-linked variables respond exponentially to temperature due to increases in the mean and variance of molecular kinetic energy as temperature increases. Boltzmann–Arrhenius model fitting has shown that Eqn (1) explains much of the seasonal and interannual variation in metabolism-linked variables (Dell *et al.*, 2011; Yvon-Durocher *et al.*, 2012, 2014). The sensitivity of a given metabolism-linked variable to temperature is related to its activation energy: higher activation energy connotes greater sensitivity to warming arising from a steeper exponential response to temperature.

Because metabolism-linked variables respond exponentially to temperature, regions where temperatures are high can have relatively strong absolute responses to climate warming (Dillon *et al.*, 2010; Marotta *et al.*, 2014). In some cases, the responses of metabolism-linked variables (hereafter, 'metabolic responses') to climate warming are expected to be greatest in the tropics, even when warming rates are relatively low there (Dillon *et al.*, 2010; Marotta *et al.*, 2014). Thus, the exponential relationship between temperature and metabolism-linked variables can make metabolic responses to warming incongruent with global patterns in warming rates. Work on the exponential response of metabolism to warming has added to a growing literature that suggests climate change may have larger direct effects on tropical ecosystems, which contain much of the world's biodiversity (Williams *et al.*, 2007; Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Loarie *et al.*, 2009; Kraemer *et al.*, 2015a; Radeloff *et al.*, 2015).

Nonetheless, if temperate and arctic sites are warming sufficiently faster than the tropics, the resulting metabolic responses could still be greater there despite the nonlinearity of metabolic responses to temperature. Using Eqn (1) with a moderate activation energy of 0.5 eV (common range: 0.2–1.2 eV; Dell *et al.*, 2011) for a simple calculation, an arctic/high-elevation site with an initial temperature of 5 °C would have to warm more than 3.4 times as fast as a tropical/low-elevation

site with an initial temperature of 25 °C to have a larger response in metabolism. The likelihood that temperate/mid-elevation and arctic/high-elevation metabolic responses will exceed tropical/low-elevation metabolic responses will also depend in part on the sensitivity to temperature of the metabolism-linked variable. A key feature of Eqn (1) is that as the activation energy approaches  $kT$ , the steepness of the relationship between temperature and the metabolism-linked variable is dampened (i.e., approaches a fixed linear slope). As a result, when activation energies are low, higher warming rates in temperate/mid-elevation and arctic/high-elevation ecosystems are more likely to lead to larger metabolic responses there. In contrast to our earlier example, if the activation energy of a metabolism-linked variable were only 0.25 eV, the arctic/high-elevation site would have to warm only 1.75 times faster than the tropical/low-elevation site to have a larger metabolic response. Thus, global patterns in metabolic responses to climate warming in a specific ecosystem type will depend on how warming rate variation across sites in that ecosystem type intersects with the thermal sensitivity of its metabolism-linked variables. Understanding how changes to environmental temperature intersect with the temperature sensitivity of key ecosystem processes could guide heuristics for predicting global ecosystem responses to warming.

Here we use long-term lake temperature data and published relationships between temperature and metabolism-linked variables in lake ecosystems to explore the magnitude and global geography of metabolic responses to climate warming. Lakes are ideal ecosystems for quantifying the effects of warming because their global geographic distribution and insularity make them sensitive sentinels of climate change (Adrian *et al.*, 2009; Schindler, 2009). Moreover, changes in metabolism-linked variables are likely to translate into shifts in global carbon cycling (Tranvik *et al.*, 2009), key ecosystem services (Wilson & Carpenter, 1999; Bennett *et al.*, 2009; Allan *et al.*, 2015), and freshwater biodiversity (Vadeboncoeur *et al.*, 2011). Lakes exhibit a wide range of baseline temperatures and warming rates (O'Reilly *et al.*, 2015), and the activation energies of key metabolism-linked variables within a lake also differ strongly (Dell *et al.*, 2011). Thus, combining temperature data from lakes worldwide with activation energy estimates from diverse metabolic processes should enable a powerful test of how metabolic responses to lake warming vary across latitude for lakes. Indeed, the 271 lakes included in this analysis contain the majority of the liquid surface freshwater on the planet and thousands of animal species that are found nowhere else on earth (Vadeboncoeur *et al.*, 2011).

## Materials and methods

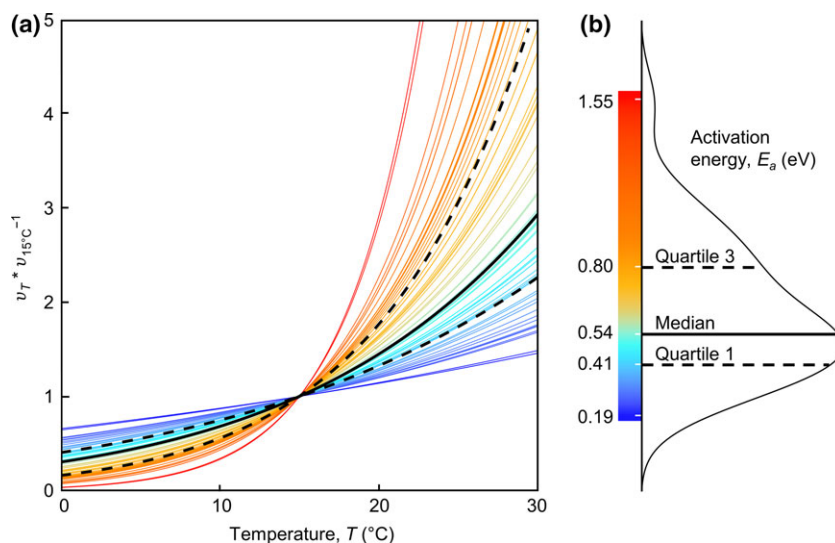
We estimated metabolic responses to climate warming in lakes by inserting long-term lake temperature time series into empirically derived Boltzmann–Arrhenius equations relating temperature to freshwater metabolism-linked variables. Our analyses made use of two large temperature datasets that each detail changes in environmental temperature of lakes over time. Together, these two data sources offer rich coverage of temperature measurements across lake depth and across the globe. The first dataset includes vertical profiles of water temperature measurements from 26 lakes that were monitored for 30 years on average (range: 6–41 years) spanning the time period from 1970 to 2010 (data from Kraemer *et al.*, 2015a; Text S1). Some lakes with nonseasonal temperature variability had only one profile per year, while others had daily profiles from high-resolution data loggers. Several lakes had data gaps of more than 1 year. The longest mean data gaps (average time between temperature profile measurements) were for Tanganyika (2 year), Kivu (3 year), Victoria (3 year), Nkugute (7 year), and Atitlan (8 year). To ascertain how metabolic rates in lakes are expected to respond to warming, we substituted time series of temperature measurements from the surface and near the bottom of the deepest point of each lake for  $T$  in the Boltzmann–Arrhenius equations (Eqn 1). Prior to the estimation of metabolic responses through time, temperature data were linearly interpolated to a daily time step (Text S2). The lake monitoring sites had a global distribution and represent a wide range of morphometric and geographic characteristics (surface area 0.02 to 68 800 km<sup>2</sup>, depth 2.3 to 1642 m, and elevation –212 to 1987 m above sea level). The second lake temperature dataset comes from a published repository which includes mean summer surface temperature from 271 lakes with broad geographic representation (Table S1) but with less temperature data per lake (annual summer surface mean temperature) (Sharma *et al.*, 2015). These temperature data are available for the period 1985–2009 and include both remote sensing and *in situ* measurements. The remote sensing data were validated using data from the Laurentian Great Lakes and were found to have a root-mean-squared error (RMSE) of 0.025 °C compared with *in situ* temperature measurements (Schneider & Hook, 2010). Mean summer surface temperature data during the summer (July 1–September 30 for lakes in the Northern Hemisphere and January 1–March 29 for lakes in the Southern Hemisphere) are available for at least 13 years of the study period. Some large, multibasin lakes had up to three monitoring sites within them to account for the substantial variation in warming rates that are observed within some lakes (Kraemer *et al.*, 2015b; Mason *et al.*, 2016). Nineteen lakes were represented in both summer mean and annual datasets. All lakes were functionally defined as high-latitude/elevation, mid-latitude/elevation and low-latitude/elevation based on their mean lake temperatures. Mean temperatures for arctic/high-elevation lakes (1st quartile,  $n = 65$ ) were <17 °C. Mean temperatures for temperate/mid-elevation lakes (2nd and 3rd quartiles,  $n = 135$ ) were between 17 and 22 °C. Mean temperatures for tropical/low-elevation lakes (4th quartile,  $n = 66$ ) were >22 °C.

To estimate metabolism through time as a function of lake temperature, temperature data from each lake were substituted for the  $T$  variable from Eqn (1) with  $E_a$  values from 64 different metabolism-linked variables spanning biological scales from individuals to populations to ecosystems. The output,  $v$ , from these calculations can be interpreted as an estimation of metabolic variables at specific lake temperatures through time. We caution that metabolic responses to temperature based on summer mean temperature do not represent an estimate of the summer mean metabolic rate or annual mean metabolic rate [see the fallacy of the average (Savage, 2004)]. Our interpretation of these results focuses on spatial and temporal patterns across lakes arising from differences in mean lake temperature, warming rates, and thermal sensitivity of freshwater metabolism-linked variables.

Activation energies for the metabolism-linked variables that we used in our analysis were derived empirically from published field and laboratory data. Data were obtained from published databases (Dell *et al.*, 2013) and extracted from peer-reviewed publications (Gillooly *et al.*, 2001, 2002; Savage, 2004; Munch & Salinas, 2009; Hein & Keirsted, 2012; Rall *et al.*, 2012; Yvon-Durocher *et al.*, 2012, 2014). Prior to Boltzmann–Arrhenius model fitting, we took the inverse of all responses to temperature where the unit in the response was time (e.g., gut clearance time). We fit the Boltzmann–Arrhenius model (Eqn 1) to data for each metabolism-linked variable. We only included measurements of metabolism at temperatures below the temperature of maximum performance that was observed, thereby avoiding complications from metabolic falls (Dell *et al.*, 2011). When more than one species or ecosystem type was represented for a given metabolic variable (Table S2), the median activation energy for that metabolic variable was used. The metabolic responses analyzed here included many important biogeochemical fluxes that differ strongly in their activation energies, such as methane emissions (0.96 eV) (Yvon-Durocher *et al.*, 2014), invertebrate metabolism (0.74 eV) (Gillooly *et al.*, 2001), pelagic ecosystem respiration (0.63 eV) (Yvon-Durocher *et al.*, 2012), and planktonic gross primary production (0.41 eV) (Yvon-Durocher *et al.*, 2010) (Fig. 1). Fifty-nine of 64 activation energies analyzed here represent processes that occur year-round in both surface and bottom waters of lakes (Table S2).

Measurements of metabolism-linked variables in lakes are rarely made over time periods sufficiently long to allow comparison to our results. However, long-term gross primary production data sets are available for lakes through the North Temperate Lakes Long-Term Ecological Research Site in Wisconsin, USA. We used data from two lakes with minimal changes in their watershed land cover (Sparkling Lake and Trout Lake) to estimate whether long-term trends (1987–2007) in gross primary production could be explained by observed warming trends (Figs S1 and S2).

We analyzed long-term trends in lake temperatures and in metabolic responses to warming using Theil–Sen nonparametric regressions (Theil, 1950) fit to annual averages using the ‘MBLM’ package in R (Komsta, 2013). We tested for the significance of warming trends in each lake without correcting for multiple comparisons ( $\alpha = 0.1$ ). We did not correct for



**Fig. 1** Exponential temperature dependence curves for 64 metabolism-linked variables based on Eqn (1). Metabolism-linked variables are expressed as,  $v_T$  (value of each metabolism-linked variable,  $v$ , estimated at temperature,  $T$ ) divided by  $v_{15\text{ }^\circ\text{C}}$  (the value of  $v$  estimated at  $T = 15\text{ }^\circ\text{C}$ ). The full density distribution of activation energies represented in this study is shown in Fig. 1b. The solid, black, horizontal line represents the median activation energy (0.54 eV) and the dashed lines represent the first and third quartiles (0.41 and 0.80 eV, respectively).

multiple comparisons because we only report the percentage of lakes with significant warming trends as an overall metric of lake temperature change and the significance of warming trends in specific lakes was not a concern. The slope of the Theil–Sen regression for each lake variable combination was used to represent the magnitude and direction of its metabolic response. To enable comparison across metabolic responses of different activation energies with different units, we express the long-term change in  $v$  (Theil–Sen slope) for each metabolism-linked variable as a proportion of the estimated value for that metabolism-linked variable at  $15\text{ }^\circ\text{C}$  ( $v_{15\text{ }^\circ\text{C}}$ ). All statistics were run using the R statistical computing environment (R Core Team, 2014).

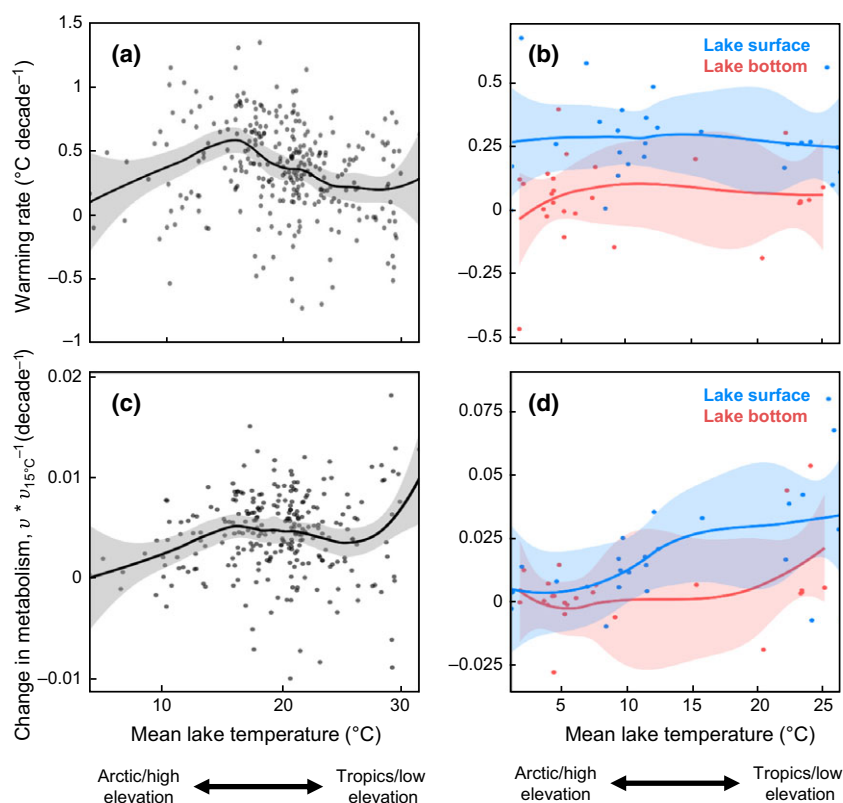
## Results

### *Geography of baseline lake temperatures and warming rates*

Mean lake temperatures varied predictably across the globe, with arctic/high-elevation lakes generally being colder than tropical/low-elevation lakes. Elevation and latitude together explained 65% of the variability in mean lake temperature. Earth's two subtropical high-pressure zones coincided with lower mean lake temperatures than would be expected at these latitudes due to the dominance of high-elevation lakes there. Lake depth and season affected the range of mean lake temperatures observed in our data. Summer surface temperatures had a wider range (3.81–31.49 °C) and higher median (20.23 °C) than annual surface (range:

1.14–26.35 °C, median: 11.40 °C) and bottom temperatures (range: 1.76–25.01 °C, median: 5.17 °C; Fig. 2b, d).

Mean summer surface temperatures increased by an average of  $0.36\text{ }^\circ\text{C decade}^{-1}$  from 1985 to 2009 based on data from all 271 lakes, with 233 (85%) of these lakes showing warming over the 24-year period of observation (positive Theil–Sen slopes) (Figs 2 and 3). The warming trend was significant in 53% of the 233 lakes with positive warming trends (Mann–Kendall,  $P < 0.1$ ). Of the 38 lakes with cooling trends (negative Theil–Sen slopes), only two trends were significant (Mann–Kendall,  $P < 0.1$ ). Summer lake warming rates were negatively correlated with mean summer lake temperature across lakes ( $r = -0.21$ ,  $P < 0.001$ ) which was consistent across the Northern Hemisphere and Southern Hemisphere (Fig. 2). Annual mean surface temperature has increased by  $0.29\text{ }^\circ\text{C decade}^{-1}$  over the period from 1970 to 2010 for the 26 lake monitoring sites with annual profile data (Fig. 2). Of these sites, all 26 were warming (positive Theil–Sen slopes), and 20 of those showed significant warming trends (Mann–Kendall,  $P < 0.1$ ). Average annual bottom temperature data have increased by only  $0.04\text{ }^\circ\text{C decade}^{-1}$  over the period from 1970 to 2010 on average. Eighteen of 26 lake monitoring sites with temperature profiles had increasing bottom temperatures (positive Theil–Sen slopes), but the increase was significant in only 10 of these lakes (Mann–Kendall,  $P < 0.1$ ). Eight lakes had cooling bottom temperature trends, two of which were significant (Mann–Kendall,  $P < 0.1$ ). Mean annual surface



**Fig. 2** Trends in lake temperature (a and b) and metabolism-linked variables (c and d), as they relate to mean lake temperature. Lakes are represented as individual dots. Lines and their associated ribbons represent the nonparametric, locally weighted regression lines (loess) and their 95% confidence intervals. Trends in metabolism are represented by the change (Theil–Sen slope) in  $v * v_{15\text{ }^{\circ}\text{C}}^{-1}$  ( $\text{decade}^{-1}$ ), where  $v$  is the metabolism-linked variable with the median activation energy from Fig. 1 (0.54 eV), and  $v_{15\text{ }^{\circ}\text{C}}$  is the estimated value for that metabolism-linked variable at 15 °C. The left panels (a and c) represent summer temperature and metabolism trends in 271 of the world’s lakes from 1985 to 2009. The right panels (b and d) represent full annual temperature and metabolism trends in 26 of the world’s lakes from 1970 to 2012.

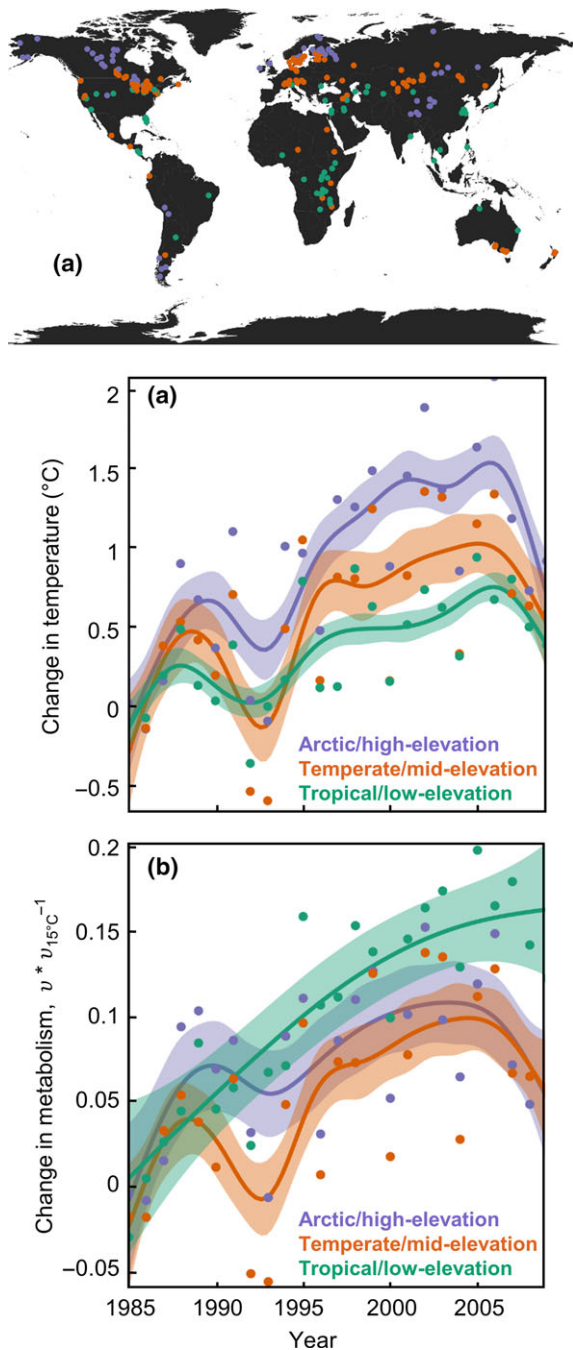
warming and mean annual bottom warming were only weakly correlated with mean lake temperatures (surface  $r = -0.01$  and  $P = 0.96$ , bottom  $r = -0.19$  and  $P = 0.35$ ) (Fig. 2).

#### Metabolic responses to warming

All activation energies for metabolic processes in lake ecosystems fell between 0.019 and 1.55 eV (Fig. 1). The first, second, and third quartiles of the distribution of activation energies fell at 0.41 eV (mass-scaled fish respiration), 0.54 eV (invertebrate growth rate), and 0.80 eV (mass-scaled arthropod embryonic development time) (Fig. 1). We use the first, second, and third quartiles of the activation energy distribution as important benchmarks in Figs 1 and 4. The mean activation energy (0.63 eV) was slightly higher than the median, indicating slight right skewness in agreement with previous work (Dell *et al.*, 2011). There was no evidence suggesting that activation energies for any particular

metabolism-linked variable used in our study varied systematically with latitude (Fig. S3).

There was wide variation in the estimated direct effects of temperature on metabolism across metabolism-linked variables with different activation energies. Using the median activation energy and annual surface temperature variation to calculate metabolic responses to warming, we estimate that lake surface metabolism has increased by  $0.015 * v_{15\text{ }^{\circ}\text{C}} \text{decade}^{-1}$ , where  $v_{15\text{ }^{\circ}\text{C}}$  is the estimated metabolism-linked variable at 15 °C (Fig. 2). The metabolic response to warming for the metabolism-linked variable with an activation energy at the first quartile (mass-scaled fish respiration, 0.41 eV) averaged  $0.009 * v_{15\text{ }^{\circ}\text{C}} \text{decade}^{-1}$  across lakes based on mean annual lake surface temperature. However, the metabolic response to warming for the metabolism-linked variable with an activation energy at the third quartile (mass-scaled arthropod embryonic development time, 0.80 eV) was  $0.027 * v_{15\text{ }^{\circ}\text{C}} \text{decade}^{-1}$  on average when based on mean annual surface warming.



**Fig. 3** Global changes in temperature (b) and metabolism (c) across 271 lakes (a) since 1985. Points are changes in mean temperature (annual mean across lakes) for arctic/high-elevation lakes ( $n = 65$ , mean temperature  $<17$  °C), temperate/mid-elevation lakes ( $n = 135$ ,  $17$  °C  $<$  mean temperature  $<22$  °C), tropical/low-elevation lakes ( $n = 66$ , mean temperature  $>22$  °C) (a). Change in temperature and metabolism is expressed as a difference from the average value for each geographical lake category from 1985 to 1987. Lines are locally weighted regression lines and shaded ribbons around each line represent 95% confidence intervals. The median activation energy (0.54 eV) was used to calculate metabolic change through time.

This represents a threefold difference in the magnitude of metabolic responses to warming in lakes over the middle half of activation energies reported here.

There was also wide variation in the metabolic response to warming across depth and season. Using the median activation energy, metabolic responses at the bottom of lakes were estimated to have changed more slowly ( $0.004 * v_{15} \text{ °C decade}^{-1}$ ) than at lake surfaces due to the slower warming rates at the bottom of lakes on average (Fig. 2b). The metabolic response of the metabolism-linked variable with the median activation energy increased to a rate of  $0.044 * v_{15} \text{ °C decade}^{-1}$  (Fig. 2d) when based on summer surface temperature.

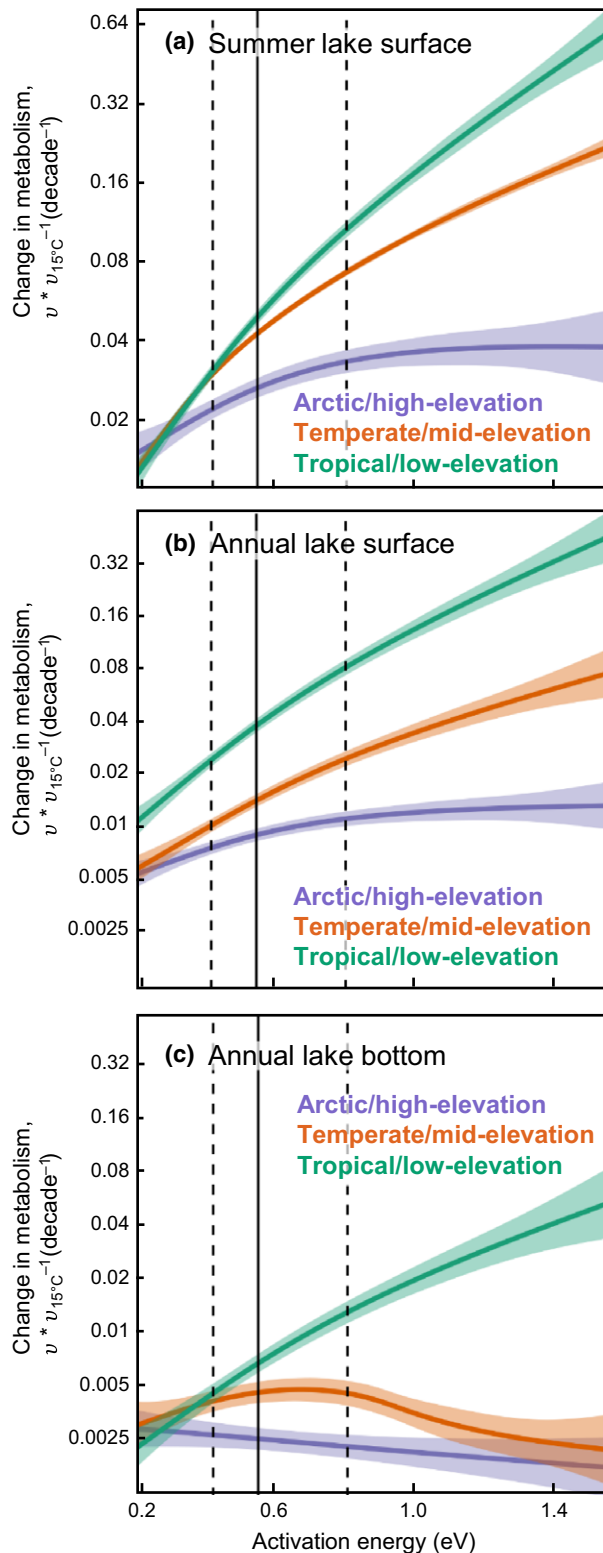
For the bulk of activation energies analyzed here, metabolic responses to warming were greatest for tropical/low-elevation lakes in stark contrast to global patterns in warming rates (Fig. 4). For instance, Lake Superior is one of the top five fastest warming lakes in our analysis, but its median metabolic response is only in the 63rd percentile due to its low mean temperature. Metabolic responses in tropical/low-elevation lakes were larger than in temperate/mid-elevation and arctic/high-elevation lakes for metabolic responses with moderate to high activation energies (Fig. 4). However, at the lowest activation energies (e.g.,  $<0.3$  eV), metabolic responses were greater in temperate/mid-elevation lakes or arctic/high-elevation lakes (Fig. 4) because they tended to be warming faster (Figs 2 and 3) based on summer surface temperatures.

## Discussion

Our calculations suggest that climate warming accelerated metabolism in the world's lakes since 1970. The acceleration of metabolism in lakes has likely changed the functioning of lake ecosystems by altering food web dynamics (e.g., consumption rates), animal behavior (e.g., predatory attack distances), life histories (embryonic development times), species interactions (e.g., prey escape velocities), and ecosystem carbon cycling (e.g., primary production; Table S2). These changes are known to have consequences for human populations through their effects on water quality, fisheries productivity, and greenhouse gas emissions. For instance, based on its high thermal sensitivity alone, we estimate that ecosystem-level methane emissions ( $E_a = 0.96$ ) will increase by 4% per decade on average, representing a substantial increase in aquatic emissions of a potent greenhouse gas.

### *Metabolic response heterogeneity*

Variation across metabolism-linked variables in their thermal sensitivity may give rise to asymmetrical



metabolic responses to warming (Dell *et al.*, 2014). For instance, metabolism-linked variables related to ecosystem primary production ( $E_a$  range: 0.30–0.45; Table S2) were consistently less sensitive to temperature than for

**Fig. 4** Responses of metabolism-linked variables to climate warming in relation to activation energy and geographical lake category (tropical/low-elevation, temperate/mid-elevation, and arctic/high-elevation). Colored lines represent the loess regression of metabolic change against activation energy for each geographical lake category. Shaded ribbons surrounding each line represent  $\pm 95\%$  confidence intervals. Estimated change in each metabolism-linked variable is divided by the estimated value at 15 °C for that variable to facilitate comparison across metabolism-linked variables with different units and different normalization constants ( $b_0$ ). The response of metabolism-linked variables is split into separate panels according to whether summer surface temperatures (years 1985–2009, a), annual surface temperatures (years 1970–2010, b), or annual lake bottom temperatures (years 1970–2010, c) were used. The vertical solid reference lines indicate the median activation energy (0.54 eV) across 64 metabolic responses considered in this study. Dashed lines represent the first (0.41 eV) and third (0.80 eV) quartiles of the distribution of activation energies.

ecosystem respiration ( $E_a$  range: 0.55–0.63 eV), suggesting asymmetrical responses to warming across trophic levels (Dell *et al.*, 2014). The asymmetry between the temperature sensitivity of primary production and ecosystem respiration could have implications for greenhouse gas emissions (Yvon-Durocher *et al.*, 2010) and dissolved oxygen dynamics (Staehr *et al.*, 2012). Furthermore, the activation energy for benthic ecosystem respiration (0.55 eV) was lower than that for pelagic ecosystem respiration (0.63 eV). Thus, pelagic respiration may comprise a relatively larger proportion of total lake respiration as temperatures rise.

Activation energies also provide a simple heuristic for predicting the geography of metabolic responses to warming. Our findings show that global patterns in the response of lake ecosystems to climate warming varied widely among metabolism-linked variables, using empirically derived estimates of their thermal sensitivity. The bulk of metabolic responses to warming showed larger absolute changes in tropical/low-elevation lakes even when such lakes were warming more slowly than arctic/high-elevation and temperate/mid-elevation lakes. Our analyses corroborate other work that showed that metabolic impacts of warming on terrestrial ectotherms may be greatest in the tropics despite lower air temperature warming rates there (Dillon *et al.*, 2010). However, we caution against generalizations about nonlinear responses to temperature always leading to disproportionately strong responses to warming at low latitudes and elevations; variation in activation energy among metabolic processes precludes such a sweeping conclusion. For instance, metabolic responses with low thermal sensitivity (e.g., photosynthesis, 0.30 eV; and ectotherm consumption rate, 0.20 eV) were greatest in temperate lakes because they

have sufficiently high mean temperatures and warming rates to counteract the nonlinear temperature dependence of metabolism. Thus, for processes with low activation energies, lakes with low mean temperatures are warming sufficiently fast in the summer to maintain larger metabolic responses than warmer lakes despite nonlinear responses. This finding contrasts with similar analyses of terrestrial ectotherm respiration rate change through time showing consistently larger effects on the respiration rates of tropical terrestrial ectotherms across activation energies (Dillon *et al.*, 2010). This difference is attributable to the inclusion of a broader range of metabolic responses in our study [0.019–1.55 eV among our 64 metabolism-linked variables compared with 0.46–0.74 eV for terrestrial ectotherm respiration rates (Dillon *et al.*, 2010)] including those with low activation energies. Therefore, we emphasize the importance of considering the full range activation energies observed in nature in studies of the global geography of metabolic responses to climate warming.

Due to reduced warming rates at the bottom of lakes relative to the surface (Winslow *et al.* 2015, Kraemer *et al.*, 2015a,b), absolute metabolic responses to temperature depend heavily on the depth at which each process occurs. Lake surface temperatures are determined predominantly by direct heat exchange across the air–water interface, and hence, they are correlated with air temperature on many timescales (Livingstone & Lotter, 1998; Livingstone, 2003). In contrast, the temperature of deep water is determined primarily by lake mixing behavior (Ambrosetti & Barbanti, 1999). Of the 64 metabolism-linked variables that we analyzed, 59 represent traits that are likely present at all locations within a particular lake, while the remaining five are likely concentrated at particular depths. For instance, methanogenesis primarily occurs in the anoxic benthos of lakes, while primary production primarily occurs at lake surfaces where light is most available. Given the strong difference between metabolic responses estimated here for lake surfaces and lake bottoms (Fig. 2), surface temperature change alone may be a poor indicator of lake-wide metabolic responses for the metabolism-linked variables that occur across all lake depths. Thus, predictions of lake-wide metabolic responses to warming based on metabolic theory will require *in situ* temperature profiles that cannot be derived from satellite imagery. Such monitoring data are scarce, especially in the tropics.

#### *Direct vs. indirect drivers of metabolism*

We have focused on estimating the direct effect of temperature rise on metabolism-linked variables. However, the actual change in metabolism through

time as a result of climate change will depend on the sum of direct and indirect effects of temperature on metabolism. Comparing our estimates based on warming alone to long-term primary production measurements in two Wisconsin lakes suggests no statistical evidence for major indirect effects (Figs S5 and S6). However, the direct effect of warming on metabolism-linked variables may be outweighed in other lakes with large changes in nutrient loads, species invasions, or other factors. Warming-driven shifts in lake mixing (O'Reilly *et al.*, 2003; Ndebele-Murisa *et al.*, 2014; Brighenti *et al.*, 2015) and oxygenation (Cheung *et al.*, 2012; Deutsch *et al.*, 2015) may also affect long-term trends in lake metabolism, and such changes have not been accounted for in our analysis. Whether indirect effects swamp the direct temperature dependence of metabolism in most lakes remains a stimulating research topic.

Incorporating all direct and indirect effects of climate change into models of lake metabolic processes will be required to generate accurate modeled estimates of changes in metabolism through time for specific lakes. This is especially the case for metabolic responses that have large standard deviations in site-specific activation energies (e.g., 0.59 eV standard deviation for methane emissions across sites; Yvon-Durocher *et al.*, 2014). There is a strong need to evaluate whether variability in site-specific activation energies can be explained by site traits (Irlich *et al.*, 2009; Dillon *et al.*, 2010). In some cases, ecological differences between sites (e.g., geomorphology, organic carbon recalcitrance, nutrient stoichiometry, community structure, local adaptation) may constrain or amplify the apparent sensitivity of metabolic responses to temperature change (Jankowski *et al.*, 2014; Yvon-Durocher *et al.*, 2014). Thus, site-specific conditions could dampen or amplify the underlying temperature dependence of a specific metabolic response (Jankowski *et al.*, 2014). At present, there is no evidence that site-specific activation energies in lakes vary systematically across the globe (Perkins *et al.*, 2012; Yvon-Durocher *et al.*, 2012, 2014), but some evidence for such a pattern has been found in terrestrial ectotherms (Irlich *et al.*, 2009). In our compilation of freshwater activation energies, we found no significant relationship between activation energy and the average temperature, or environmental context (laboratory vs. field) for metabolic data used to calculate activation energies (Dell *et al.*, 2011). Similarly, estimated activation energies were not correlated with the latitude at which metabolic data were collected (Fig. S3), although tropical ecosystems are clearly underrepresented, underscoring an acute need for further assessment of activation energies in tropical lakes. A better understanding of drivers of site-specific



activation energies would enable more accurate estimates of the direct effect of climate change on metabolism in lakes at the global scale.

Increases in metabolic demands of organisms estimated here also assume that they will acclimate to their new thermal environment. If behavioral and physiological acclimation is not possible, or if organisms are already above their thermal optima or critical thermal maxima, the impacts of warming on organisms could be magnified. Maintenance of metabolic stasis through relocation to deeper, colder water has been invoked as an adaptation strategy for aquatic ectotherms in the face of environmental temperature change (Cheung *et al.*, 2012; Burrows *et al.*, 2014); however, such forced shifts may raise a host of new problems by separating aquatic fauna from habitats whose depth distribution is constrained by light and nutrient gradients (Cheung *et al.*, 2012).

Understanding the consequences of metabolic acceleration for lake ecosystems is critical for predicting shifts in the benefits that lakes provide to society. The lakes included in this analysis are globally significant repositories of freshwater biodiversity and ecosystem services. In aggregate, they contain the vast majority of liquid surface freshwater on the planet. The large ancient lakes in our analysis (Tanganyika, Hovsgol, Baikal, Biwa, Kinneret, Van, Valencia, Titicaca, etc.) hold thousands of animal species found nowhere else on Earth (Martens, 1997). The African rift lakes support highly productive fisheries that are vital to local food security. Lakes Tahoe, Atitlan, and Zurich are deeply integrated into regional economies through recreation and tourism. The consequences of metabolic acceleration for biodiversity and ecosystem services in lakes will also depend on shifts in lake physics (Kraemer *et al.*, 2015a), the global distribution of lake area (Downing *et al.*, 2006), and complex ecological interactions that are beyond the scope of this study. However, our work suggests that substantial metabolic acceleration has already occurred since 1970, and is most pronounced in the tropics where metabolism-linked ecosystem services (e.g., water clarity, fishery productivity, and greenhouse gas sequestration) may be most affected.

Joint consideration of metabolic thermal sensitivity and global patterns of warming rates indicates that warming has had greater direct effects on tropical lake ecosystems than temperate and arctic lake ecosystems for most, but not all metabolism-linked variables. Like analyses of climate velocity (Loarie *et al.*, 2009; Burrows *et al.*, 2014), climate novelty (Williams *et al.*, 2007; Radeloff *et al.*, 2015), and the thermal tolerances of organisms (Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey & Kingsolver, 2011), our

findings demonstrate that global patterns in warming rates alone can be misleading as predictors of ecosystem responses to climate change (Fig. 4). For the critical biological processes analyzed herein, metabolism provides a powerful foundation for understanding such decoupling and the resulting patterns of metabolic responses to climate warming.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Long-term trends in gross primary production and temperature in Sparkling Lake and Trout Lake, WI, USA.

**Figure S2.** The interannual temperature dependence of gross primary production in Sparkling Lake and Trout Lake, WI, USA.

**Figure S3.** Relationship between activation energy and latitude for the 9 metabolism-linked variables in our study fit to data which span the widest range in latitude.

**Table S1.** Lake characteristics for all 271 lakes used in our analysis.

**Table S2.** Activation energies and data sources for 64 freshwater activation energies used in our study.

**Text S1.** Temperature profile data sources.

**Text S2.** Temperature profile data interpolation procedure.