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LETTER

When does temperature matter for ecosystem respiration?

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Abstract

The temperature response of ecosystem processes is key to understand and predict impacts of climate change. This is especially true for respiration, given its high temperature sensitivity and major role in the global carbon cycle. However, similar intrinsic temperature sensitivity for respiration does not mean comparable temperature effects across ecosystems and biomes because non-temperature factors can be more important. Here we analyzed soil and sediment respiration data and found that in temperature ranges corresponding to high latitude mean temperatures, absolute respiration rates are more sensitive to non-temperature factors than to projected direct temperature effects. However, at higher temperatures (>20 °C) the direct effect of temperature mediated by temperature sensitivity will likely be more important over changes in non-temperature factors in shaping how respiration change over time. This supports past suggestions that the relatively small projected temperature increase at low (tropical) latitudes may have a large direct impact on absolute respiration. In contrast, absolute respiration rates at high (boreal/arctic) latitudes will likely be more sensitive on the development of the non-temperature factors than on the direct effects of the large projected temperature increase there. Social media abstract. Respiration may be less dependent to changes in temperature at higher than lower latitudes.

Introduction

Heterotrophic respiration is a key process in the carbon cycle of terrestrial and aquatic ecosystems. Temperature is considered to control metabolic rates of heterotrophic processes (Davidson and Janssens 2006, Yvon-Durocher et al 2012), with implications for the fate of organic matter, i.e. storage versus release of carbon dioxide (CO₂) (Davidson and Janssens 2006, Gudasz et al 2010, Vachon et al 2021). There has been considerable interest in describing the temperature influence on ecological processes such as primary production and respiration. This temperature effect is central to the metabolic theory in ecology, e.g., in scaling metabolic processes from individual to ecosystem level (Allen et al 2005, Allen and Gillooly 2007). Several terms have been used to describe the change in metabolic rates with changing temperature, such as temperature dependence and temperature sensitivity, which are not necessarily interchangeable. Sierra (2011) defined a process that is temperature dependent if temperature is an explanatory or independent variable, unlike temperature sensitivity which is the rate of change of a process with temperature while other variables are held constant. Thus, temperature sensitivity directly links temperature and metabolism, and can be expressed as an absolute value or as the proportional metabolic rate change per unit change in temperature (Sierra 2011).

There are several mathematical formulations to describe the temperature sensitivity of heterotrophic respiration rates, many being variations of the simple exponential function:

\[ R = Ae^{bT} \]  

where \( A \) is pre-exponential factor, \( b \) is the exponent term of the equation that describes the temperature sensitivity and \( T \) is temperature in °C. This model has also been used to determine another common expression...
of relative temperature sensitivity, namely the \( Q_{10} \), which is the proportional change of respiration rates for a 10 °C temperature increase in the form of:

\[
Q_{10} = e^{\frac{b}{10}}
\]

Another mathematic formulation that has been widely used is the Boltzmann-Arrhenius function. It has a solid theoretical basis for describing change in reaction rates with temperature of single chemical compounds. The function describes chemical process rates at different temperatures using an exponential function:

\[
k = A e^{-\frac{E_a}{RT}}
\]

where \( k \) is the reaction rate constant, \( E_a \) is activation energy (e.g. J or eV), \( A \) is a pre-exponential factor, \( B \) is the Boltzmann constant \( 8.6173303(50) \times 10^{-5} \text{ eV} \text{ K}^{-1} \) and \( T \) is the absolute temperature (Kelvin). Its interpretation has been extended to temperature response of respiration and primary production in biological systems and the term \( E_a \) has been used analogous to temperature sensitivity (Yvon-Durocher et al 2012), e.g. as an analogue to the \( b \) term in equation (1).

The temperature effects on respiration have been extensively discussed and both the temperature sensitivity per se (Yvon-Durocher et al 2012) and variability in temperature sensitivity due to indirect or non-temperature related factors have been well documented (Conant et al 2011). The intrinsic temperature sensitivity for heterotrophic respiration was established at 0.64 eV (Yvon-Durocher et al 2012). However, due to that many indirect or non-temperature related factors changing respiration rates, many studies measure apparent rather than intrinsic temperature sensitivity (Conant et al 2011). For example, several studies have highlighted the influence of organic matter quality and soil moisture on apparent temperature sensitivity (Carey et al 2016, Meyer et al 2018). Complex interactions exist and interpreting the temperature effects on respiration based on the extent of temperature sensitivity change alone would be erroneous. For example, decreasing soil moisture can become a limiting factor resulting in a decrease temperature sensitivity at higher temperatures (Song et al 2014, Carey et al 2016). Accordingly, the apparent temperature sensitivity of terrestrial ecosystem respiration expressed as \( E_a \) derived from Arrhenius equation was found higher and lower at high and low latitudes, respectively, and soil water availability was an important factor behind this pattern (Song et al 2014, Carey et al 2016). As shown by this example, there has been an interest in the apparent temperature sensitivity and how it is modulated by other environmental variables.

Much of the literature using the exponential and Boltzmann-Arrhenius-type functions has focused on temperature sensitivity of respiration as a relative term (Yvon-Durocher et al 2012, Gudasz et al 2015), providing a relative measure of temperature impacts on process rates across systems. Temperature sensitivity of organic matter respiration in various ecosystems was a key parameter in assessing the climate impact on the carbon cycle (Lenton and Huntingford 2003). Lenton and Huntingford (2003) examined how the range in temperature sensitivity as \( Q_{10} \) of terrestrial carbon fluxes shaped the land carbon sink under the Last Glacial Maximum.

Temperature sensitivity directly links temperature control of respiration and carbon turnover. However, the absolute change in respiration at low temperatures is small with exponential models and it is not clear whether increasing influence of non-temperature related factors affecting respiration have a larger influence on respiration than higher or lower \( Q_{10} \). The temperature response of ecosystems processes in absolute terms is what eventually matters when assessing climate change feedbacks (Sierra 2011).

Hence, we ask under what temperature regimes is temperature sensitivity the most adequate property for assessments of absolute effects of temperature change. To address the question we use equation (1) and evaluate the importance of the temperature sensitivity (\( b \)-term, i.e. the direct effect of temperature) and the pre-exponential factor (\( A \), i.e. the potential respiration set by non-temperature factors) of contrasting temperature range and system properties. To determine \( A \), we choose a temperature reference point of 0 °C to stay in the frames of ecological relevance. Below freezing of water, the direct temperature response via \( b \) is inseparable from other limitations due to e.g. lack of liquid water, and transport limitations in and around cells (Mikan et al 2002). Hence, we hypothesize that: (1) At low temperatures, respiration rates are controlled by the pre-exponential factor (\( A \)) rather than directly through temperature sensitivity (\( b \)). (2) With increasing temperatures, the direct temperature effect on respiration expressed by temperature sensitivity (\( b \)) becomes progressively more influential—simply following the exponential relationship (Solomon et al 2007). (3) As a consequence of (1) and (2), the temperature regulates when \( A \) or \( b \) is most influential, i.e., when large direct temperature effects can be expected.

To consider the multiple types of temperature effects we conceptualized a multi-layered influence on respiration rates: The first layer is the direct impact via the temperature sensitivity (\( b \)). The second layer is that the temperature can determine if the non-temperature system features setting the respiration potential (\( A \)) or temperature sensitivity (\( b \)) is most important for overall absolute respiration rates (figure 1).

This second layer implies that respiration rates can shift between being controlled by indirect factors affecting \( A \) or by temperature sensitivity (\( b \)) as temperatures fluctuates over seasonal or day-night cycles in ecosystems. There is also a third layer, representing that temperature can affect the system features setting \( A \). The implications of this third layer can differ greatly among systems, and to keep the analysis generally valid we did...
not distinguish between different factors that can affect $A$. Hence, following discussions of implications of a change in $A$ acknowledge that several environmental factors, including temperature can contribute to changing $A$, and the first two layers, separating direct temperature effects via $b$, versus effects from combined non-temperature or indirect temperature effects via $A$, are in focus in this study.

**Methods**

We used temperature response data for sediment and soil respiration, i.e. two key components of the respiration of terrestrial and aquatic ecosystem (Pace and Prairie 2005, Luo and Zhou 2006). Sediment respiration data from Gudasz et al (2015) was derived from five months long incubations at water temperature ranging from 1 to 21 °C and with sediments composed by either primarily aquatic or terrestrial/humic organic matter, respectively, shown to be representative for a wide range of lake sediments globally (Cardoso et al 2014, Marotta et al 2014).

For soil respiration we used the Global Soil Respiration data set v5.0 (Jian et al 2021) and extracted 439 unique equations representing the response of respiration to soil temperature (annual temperature in year of study in °C; positive effect and moisture (positive and negative effects) that meet the criteria: at least 1 years of data, cover 0.75 of the year (fraction of annual coverage of soil respiration measurements, 1.0 = full year), provide full model parameters, model output units, biome characterization, a minimum, temperature between $-15$ and $25$ °C and maximum temperature between 15 and 37 °C. The extracted data represent measured soils respiration that span most common biomes and ecosystem types (see supplementary figure S1 (available online at stacks.iop.org/ERC/3/121001/mmedia)). Before use, the pre-exponential factor ($A$) was converted to the same unit of mg C m$^{-2}$ day$^{-1}$. We analyzed the distribution of the $A$ and $b$ model parameters and extracted the
respiration rates will eventually exceed respiration rates in the sediment with high respiration rates in sediment
For the sediments the Results to derive the information greater than between the two sediment types. Using the median (A plots were done using R version 3.5.1
Arrhenius function being common in ecological literature and to facilitate comparisons, we used the linear form of the Boltzmann-Arrhenius function in combination with the low A (brown line). (b) Soil respiration from Jian et al (2021) with A levels representing the 10th (grey line), 50th (black line), and 90th (blue line) quantiles of the data, and the same median b for all lines, are shown. The ΔA represented by $T_{A1,2,3}$ corresponds to a temperature shift of 10.3, 19.2 and 8.9 °C relative to the temperature response curves of the 10th–50th, 10th–90th, 50th–90th quantiles of A for the soil respiration equations, respectively.

10th, 50th and 90th quantiles (see supplementary figure S2) which we used to parameterize the temperature response curves in figure 2(b).

In order to express the temperature sensitivity (b) to the Boltzmann-Arrhenius-type activation energy ($E_a$) being common in ecological literature and to facilitate comparisons, we used the linear form of the Boltzmann-Arrhenius function (equation (3)), for which the natural logarithmic form is:

$$\ln k = \ln A_0 - \frac{E_a}{RT}$$

(4)
to derive the $E_a$ from the slope of the linear relationship between $\ln k$ and $1/RT$. In addition, and for other literature comparisons we also used the $Q_{10}$ function (equation (2)) to express $b$. Data analysis and Arrhenius plots were done using R version 3.5.1 (R Core Team 2020) and JMP version 14.0.

**Results**

For the sediments the $b$-term was slightly higher (not significantly different, Gudasz et al 2015) in the humic lake sediment ($b = 0.0822$, equivalent to $E_a = 0.59$ eV, $Q_{10} = 2.27$) with less reactive organic matter ($A = 16.7$ mg C m$^{-2}$ day$^{-1}$), than in the eutrophic lake sediment ($b = 0.0748$, $E_a = 0.53$ eV, $Q_{10} = 2.11$) with more reactive organic matter ($A = 50.9$ mg C m$^{-2}$ day$^{-1}$) (figure 2(a)). A visual analysis of figure 2(a) clearly show that higher absolute respiration rates are indicative of a sediment with higher A. Further, for sediments, a greater absolute increase in respiration rates with temperature was observed at high A in spite of a lower b in this sediment. The temperature increase (from a 0 °C reference temperature) required in the humic (low A, high b) sediments to reach the 0 °C respiration rate in the eutrophic (high A; low b) sediments, and thus to compensate for the low A, was as high as 13.5 °C (figure 2(a)). In the above example, the difference in $b$ was small, and scenarios with large differences in $b$ also need consideration. To investigate such a scenario, we projected a hypothetical doubling in $b$ in the low A lake sediment, making the doubled $b$ equivalent to $E_a$ of 1.17 eV ($Q_{10} = 5.18$). With such a double $b$ low A sediment, and progressively increasing the temperature, the respiration rates will eventually exceed respiration rates in the sediment with high A and lower b, but not until above 12.4 °C ($T_{b}$, figure 2(a) panel insert).

The soil respiration models yielded $b$ parameter values of 0.054, 0.09 and 0.137 representing 10th, 50th and 90th quantiles (equivalent to $E_a$ of 0.39, 0.64, 0.98 eV and $Q_{10}$ of 1.72, 2.46 and 3.94, respectively), whilst the A was 198, 500 and 1114 mg C m$^{-2}$ day$^{-1}$, representing the 10th, 50th and 90th quantiles (See supplementary information figure S2). The difference in respiration rates between 10th and 90th quantiles for soils was 5.6 times greater than between the two sediment types. Using the median $b$ and the 10th, 50th and 90th quantiles for A, yielded the temperature response curves depicted in figure 2(b). The hypothetical temperature changes needed to compensate for differences between the A levels (ΔA) of the three temperature response curves (from a 0 °C reference level) corresponded to 10.3, 19.2, and 8.9 °C when comparing the 10–50th, 10–90th, 50–90th

![Figure 2. Temperature response of sediment and soil respiration. (a) Sediment respiration from Gudasz et al (2015) with a low (brown line) and high (green line) pre-exponential factor (A) and similar b. $T_{A}$ represents the temperature where temperature response curves intersect and respiration rates are equal, whilst $T_{A}$ represents temperature changes (from a 0 °C reference level) needed to compensate for differences in A (see text for details). The panel insert represents a theoretical scenario with hypothetical doubling in $E_a$ (black line) in combination with the low A (brown line). (b) Soil respiration from Jian et al (2021) with A levels representing the 10th (grey line), 50th (black line), and 90th (blue line) quantiles of the data, and the same median b for all lines, are shown. The ΔA represented by $T_{A_{1,2,3}}$ corresponds to a temperature shift of 10.3, 19.2 and 8.9 °C relative to the temperature response curves of the 10th–50th, 10th–90th, 50th–90th quantiles of A for the soil respiration equations, respectively.](image-url)
The difference in sediment organic matter reactivity between the sediments was reflected by a 3-fold difference in $A$ levels. Higher $A$ is usually associated with faster decomposing sediment organic matter (Mikan et al 2002, Fierer et al 2005, Gudasz et al 2012). The large temperature increase required in the humic lake (low-$A$) sediments to compensate for the lower $A$ implies that a large temperature change is needed to override a difference or change in $A$. Although the hypothetical doubling in $b$ ($E_a = 1.18$ eV, $Q_{10} = 5.2$) used in the scenario test (figure 2(a)) is very high and outside the 95% confidence intervals of both short- and long-term lake sediment respiration (Yvon-Durocher et al 2012), it serves the purpose to illustrate a case where $E_a$ have maximum importance relative to the $A$ level. Hence, at low temperatures and $E_a$ values much larger than typically found for respiration, still temperature changes of $>10^\circ$C are required to make the direct temperature effects outweigh the difference in $A$. Overall, this show that the predominant organic matter source or other factors determining $A$ can have a dominant influence on absolute sediment respiration rates and on the response of increasing temperatures in low-temperature environments.

This result is highly relevant for environmental change feedbacks, because the difference in $A$ between the studied sediments correspond to shifting dominance between organic matter from within-lake primary production to catchment derived organic matter reaching the sediments (Gudasz et al 2012). Such shifts can happen in lakes through browning (Ask et al 2009), anticipated following northward expansion of the boreal forest into the lower arctic (Lenton et al 2008, Zhang et al 2018) or permafrost thaw and associated mobilization and export of previously frozen organic carbon stocks to lakes (Vonk et al 2015, Wauthy et al 2018) on one hand and through increased aquatic organic matter production as result of eutrophication on the other. This implies

Discussion

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that both direct temperature changes (via $b$), and indirect factors affecting $A$ levels, such as organic matter sources and characteristics, are key for reliable predictions of climate change effects and that $b$ should not be used alone to infer temperature feedbacks on sediment respiration.

When soil respiration was considered, our analysis show that changes in indirect factors affecting $A$, are likely to be very important for respiration rates in low-temperature environments such as the Boreal (figure 3(a)). Changes in the plant community composition, productivity, and soil microbial community composition and biomass, can play a larger role than direct effects of temperature changes, in spite of the large projected temperature change of $2.2\,^\circ{C}$–$8.3\,^\circ{C}$ by the year 2100 (Collins et al 2013). In high-temperature environments such as the tropics however, despite projected lower temperature changes of $0.9\,^\circ{C}$–$3.3\,^\circ{C}$ (Collins et al 2013), the direct temperature response of respiration (via $b$) may be of dominating importance for absolute respiration rates (figure 3(b)) following temperature changes (Crowther et al 2019).

Some studies have suggested a departure from the exponential function, with typically a decreasing temperature sensitivity with increasing temperatures above a threshold temperature (Hamdi et al 2016). Several explanations are possible, including enzyme degradation, thermal adaptation of microbial metabolism or decrease in soil moisture (Conant et al 2011, Carey et al 2016). This illustrates the third layer of temperature effects on respiration (figure 1), when temperature indirectly influences factors governing $A$. Such effects are generally expressed as an offset from equation (1) that is not always connected to $A$ in suggested equations, but in this context further strengthen the importance of factors behind $A$ relative to $b$ for absolute respiration rates also in the upper part of the temperature range suitable for biotic respiration.

There is a significant variability in the empirical temperature-respiration relationships (e.g. Yvon-Durocher et al 2012). One of the reasons has been attributed to the fact that the measured temperature sensitivity is apparent, which integrates the temperature response of the large number of processes leading to the net respiration measured. Ecosystem level observations integrate more factors that can interfere with respiration compared to plot or single core incubations studies; hence there are differences in the apparent temperature sensitivity among different types of assessments. Accordingly, apparent temperature sensitivity derived at long time scales for soil respiration were found diverging compared to that of short scales (Yvon-Durocher et al 2012) because more factors (including temperature acclimation) are integrated into the derived long-term rates. In a recent study, Niu et al (2021), suggest based on micrometeorological data that in a future warmer climate, spatial and temporal apparent temperature sensitivity ($Q_{10}$) of ecosystem respiration in diverse climates and biomes converge towards $Q_{10} = 1.38–1.5$ (i.e. 0.23–0.29 eV). If this is the case across longer time scales and at ecosystem levels, the $A$ levels would become even more important for the absolute ecosystem respiration rates relative to temperature sensitivity (i.e. $b$ terms). This further strengthens the point that the importance if $A$ for temperature effects on respiration has been overlooked.

This analysis highlights that absolute temperature has a multi-layered influence on respiration rates. The above examples collectively and clearly illustrates that at low temperatures, absolute respiration rates are controlled by indirect factors (expressed by $A$) modulating respiration and that with increasing temperatures, the direct temperature response of respiration expressed by $b$ becomes progressively more influential and changes associated with $b$ in warm climates could potentially have a large effect on respiration (Solomon et al 2007). Sediment and soil respiration, as considered in this study, represents respiration under many environmental conditions and are major components of ecosystem respiration. All types of respiration has been shown to respond similarly to temperature (Yvon-Durocher et al 2012) and are likely to follow the same fundamental regulation with regards to $A$ and $b$ as presented here. Therefore, the findings of this study appear generally relevant for all respiration processes and for overall ecosystem respiration, serving as a starting point for future studies using the multi-layered approach developed here to disentangle the importance of specific $A$ and $b$ factors for different habitats and organism groups.

Conclusions

Given the large projected changes in vegetation and hydrology due to climate change at high (boreal and arctic) latitudes, our results indicate that respiration will likely be more susceptible to the development of associated indirect factors than on the direct effects of the projected temperature increase there. Thus, predictions of temperature feedbacks on natural processes, such as respiration, should not solely rely on $b$ assessments, and the effect of changes (increase or decrease) in $b$ should also be evaluated in the context of $A$ levels and temperature ranges. In tropical regions, even small projected temperature increases could have a large effect on respiration via $b$ due to progressively larger absolute respiration changes as temperature increase (Townsend et al 1992, Marotta et al 2014). Consequently, even small changes in temperature, or in apparent $b$, can potentially exhibit large effects on absolute respiration if the starting temperature is high. On the other hand, properties setting the $A$ levels are particularly important for absolute respiration rates in colder regions such as the boreal, subarctic and
arctic biomes, in spite of largest expected temperature increases there (Anisimov et al 2007). We therefore propose that in many cold northern ecosystems, the indirect effects of climate change affecting A levels will have a greater impact on absolute respiration than the direct effect of temperature change.

Data availability statement
All data that support the findings of this study are included within the article (and any supplementary files).

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