Global convergence in leaf respiration from estimates of thermal acclimation across time and space

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Summary

• Recent compilations of experimental and observational data have documented global temperature-dependent patterns of variation in leaf dark respiration (R), but it remains unclear whether local adjustments in respiration over time (through thermal acclimation) are consistent with the patterns in R found across geographical temperature gradients.

• We integrated results from two global empirical syntheses into a simple temperature-dependent respiration framework to compare the measured effects of respiration acclimation-over-time and variation-across-space to one another, and to a null model in which acclimation is ignored. Using these models, we projected the influence of thermal acclimation on: seasonal variation in R; spatial variation in mean annual R across a global temperature gradient; and future increases in R under climate change.

• The measured strength of acclimation-over-time produces differences in annual R across spatial temperature gradients that agree well with global variation-across-space. Our models further project that acclimation effects could potentially halve increases in R (compared with the null model) as the climate warms over the 21st Century.

• Convergence in global temperature-dependent patterns of R indicates that physiological adjustments arising from thermal acclimation are capable of explaining observed variation in leaf respiration at ambient growth temperatures across the globe.

Introduction

Autotrophic respiration (i.e. respiration by photosynthetic organisms) is a critical component of the global carbon budget, releasing about half of the carbon fixed annually by photosynthesis (Amthor & Baldocchi, 2001; DeLucia *et al.*, 2007; Zhang *et al.*, 2009). As global temperatures are projected to rise over the 21st Century (IPCC, 2007), autotrophic respiration is expected to release a larger fraction of the CO_2 fixed by photosynthesis in terrestrial ecosystems (Luo, 2007). Anticipated temperature-related increases in respiration could potentially contribute to a progressive weakening of the global terrestrial carbon sink over the 21st Century (Friedlingstein *et al.*, 2006).

A review by Smith & Dukes (2013) on recent advances in modelling photosynthesis and respiration in terrestrial biosphere models (TBMs) highlighted two major challenges in quantifying temperature responses of autotrophic respiration. First, the biochemical processes controlling temperature-related variation in respiration rates are complex and poorly understood (Atkin &

Tjoelker, 2003), and so predictions for how temperature affects respiration rely largely on empirically derived relationships. Second, many TBMs ignore differences between short- and long-term responses of respiration to temperature variation. Terrestrial biosphere models commonly assume that instantaneous response functions – for example, an exponential relationship between respiration and variation in temperature over minutes to hours – can be applied to project respiration responses to temperature changes at seasonal and inter-annual time-scales. Although recent studies have begun to address these challenges (reviewed in Smith & Dukes, 2013), there remains considerable process uncertainty associated with model predictions of autotrophic respiration across time and space, particularly under new climatic conditions forecasted for the coming century.

Commonly used temperature response functions that are characterized by a doubling of respiration with each 10°C increase in temperature (i.e. $Q_{10} = 2.0$ in Eqn 1 below) are inadequate for describing autotrophic respiration over either short or long time-scales (Atkin & Tjoelker, 2003; Atkin *et al.*, 2005). One reason

for this is that the instantaneous response is itself temperature-dependent, with respiration appearing to exhibit a weaker response to temperature at higher temperature ranges (Tjoelker *et al.*, 2001). Further, individual plants exposed to colder or warmer temperatures over a period of days or weeks adjust their respiratory rates in a manner that partially compensates for shifts in ambient temperature (Lambers *et al.*, 2008). This process is known as thermal acclimation. Acclimation is associated with decreases in the rate of respiration at a common, set measuring temperature when plants are exposed to high growth temperatures for extended periods (Atkin & Tjoelker, 2003). Conversely, respiration rates at common temperature typically increase when plants acclimate to low growth temperatures. Acclimation may also affect the temperature sensitivity (Q_{10}) or temperature optimum of respiration, although we do not consider these aspects further here.

Acclimation has been shown to occur as quickly as in just a few days (Bolstad *et al.*, 2003; Lee *et al.*, 2005), which suggests that changes in the temperature response function of respiration probably have a very strong influence on realized rates. Over extended time-scales (days, weeks or longer), thermal acclimation weakens the realized temperature sensitivity of respiration by lessening differences in respiration when plants experience sustained changes in ambient temperature. The concept of acclimation can also explain how identical genotypes differ in respiration rates when grown at different ambient temperatures, as is the case in controlled environments and common garden studies. If we assume that closely related plants growing in different sites are genetically similar, then differences in respiration at a common temperature may reflect acclimation effects (although genetic differences in R could also be involved). Studies that have incorporated thermal acclimation of respiration into TBMs have concluded that this process has important effects on long-term carbon fluxes within biomes, although there is not a general agreement on its global effects (Wythers *et al.*, 2005, 2013; King *et al.*, 2006; Atkin *et al.*, 2008; Chen & Zhuang, 2013; Slot *et al.*, 2014). Discrepancies among models may be attributable to the different ways in which acclimation is formulated, as well as to the varying approaches for deriving acclimation parameters from local data sources. The assimilation of data on variation in leaf respiration into TBMs is currently an active area of research (Atkin *et al.*, 2014).

Quantitative estimates for the magnitude of thermal acclimation have been derived from experiments that measure the effects of recent growth temperature on leaf dark respiration (R) in local plant populations. The designs of such experiments vary, but typically rely on either natural variation in ambient temperature, common gardens with different ambient temperatures, or experimental warming and control treatments. Each type of experiment allows the assessment of how R acclimates to changes in temperature over a relatively short period. The degree of acclimation can be quantified by ratios of R between acclimated and control plants, either at a common set temperature or at the plants' respective growth temperatures (Loveys *et al.*, 2003). Slot & Kitajima (2015) recently performed a meta-analysis of 43 experimental studies of acclimation in plants from all major biomes, summarizing the overall size of thermal acclimation effects and their main sources of variation. Their analysis showed that, when compared at a common measuring temperature, acclimation effects on leaf respiration were strongly related to the magnitude of temperature change, but did not vary significantly by biome, growth form, or other factors.

In addition to direct experiments, indirect evidence for adjustments in R has been gleaned from comparative analyses of sites widely distributed across the globe. Databases such as Glopnet (Wright *et al.*, 2004, 2006), TRY (Kattge *et al.*, 2011), and GlobResp (Atkin *et al.*, 2015) contain hundreds of records for R across tropical, temperate, boreal and arctic biomes. Although these data lack the temporal resolution of experimental studies, they allow broad evaluations of how geographical patterns in respiration (which could result from both acclimation and long-term genetic adaptation) relate to climatic conditions. For example, in a comparison of R at 20 different sites (mostly temperate forests and woodlands), Wright *et al.* (2006) found that respiration at mid-growing season temperatures increased with mean annual temperature, but that this increase was much less than would be expected from a simple instantaneous response to temperature. The partial adjustment of R to ambient growth temperatures could reflect a combination of physiological acclimation, genetic adaptation, or variation in plant traits and species composition along climate gradients. To develop a more thorough understanding of global variation in R, Atkin *et al.* (2015) assembled data from 100 sites world-wide to describe relationships between R and both climate variables and leaf traits. Their analysis shows that R at ambient temperatures increases *c.* two-fold across a 20°C range in growth temperatures from the Arctic to the tropics.

The recent syntheses by Slot & Kitajima (2015) and Atkin *et al.* (2015) provide a valuable opportunity to assess whether plants locally adjust their respiration over time (through phenotypic acclimation) in a manner that corresponds with how plants across large spatial gradients differ in R with respect to temperature. In other words, is the change in R from 10°C to 20°C over time for a plant at a given site equivalent to the difference in mean R across sites with average temperatures of 10°C and 20°C? We address this question using a simple temperature-dependent framework for leaf respiration through which the measured effects of respiration acclimation-over-time and variation-across-space can be compared to one another, and to a null model in which acclimation is ignored. We use this framework, with model parameters obtained directly from the recent data syntheses described above, to simulate respiration rates at locations across the globe over the course of a year. We then compare predictions of various acclimation algorithms in terms of: seasonal variation in R at individual locations; spatial variation in mean annual R across a global temperature gradient; and expected increases in global leaf-level R rates under a representative climate change scenario. Output from these simple models illustrates how different formulations for thermal acclimation affect predicted global respiration patterns, and their future responses to climate warming.

Materials and Methods

The following analysis has been designed to predict temperature-dependent respiration rates in mature, fully expanded leaves, which primarily reflect demands for respiratory products associated with cellular maintenance and potentially phloem loading. In addition to temperature, respiration rates are known also to vary with growth, tissue composition (e.g. N concentration), and functional traits (e.g. maximum carboxylation rate). Although these other factors are certainly important to respiration overall, they do necessarily influence the degree of acclimation or the temperature response of fully expanded leaves in a systematic way (Atkin *et al.*, 2005, 2008).

We begin this section by describing the general form of instantaneous response and acclimation functions used in temperature-dependent respiration models. This is followed by descriptions of the model formulations that we have developed to incorporate the observed effects of acclimation-over-time and variation-across-space on R predictions. Next, we describe how we obtained parameter values for the various acclimation models from two independent, global data sets of experimental and observational variation in R. Last, we describe our procedures for constructing scenarios to evaluate differences in R across time and space under a set of different temperature-dependent models.

Temperature response framework for respiration

A common empirical framework for representing the instantaneous response of respiration to temperature uses the equation:

$$R_C = R_{REF} \cdot Q_{10}^{\left(\frac{T_C - T_{REF}}{10}\right)}, \qquad \text{Eqn 1}$$

(R_C, the respiration rate at a given current temperature; T_C, the current temperature; T_{REF}, an arbitrarily chosen reference temperature; R_{REF}, the baseline respiration rate at T_{REF}; Q_{10}, a constant (or temperature-dependent function) that describes the proportional change in R_C per 10°C change in temperature.) Local studies that use this framework normally set T_{REF} to a constant that is representative of growth temperatures for the plant population being studied (e.g. 10, 20 or 25°C), whereas models (Collatz *et al.*, 1991; Atkin *et al.*, 2008) and comparative analyses (Reich *et al.*, 1998; Wright *et al.*, 2006) have often employed a single T_{REF} of 25°C. The value $Q_{10} = 2.0$ has been adopted widely in TBMs that use the Q_{10} framework for autotrophic respiration (Raich *et al.*, 1991; Aber & Federer, 1992; Schimel *et al.*, 1997). More recently, empirical observations of decreasing Q_{10} with temperature (Tjoelker *et al.*, 2001) have led to models that treat Q_{10} as a temperature-dependent variable (Atkin & Tjoelker, 2003; Atkin *et al.*, 2005):

$$Q_{10} = 3.090 - 0.043 \cdot \left(\frac{T_C + T_{REF}}{2}\right). \qquad \text{Eqn 2}$$

Incorporating this temperature sensitivity in the instantaneous response leads to lower respiration rates in future climate scenarios than are observed in TBMs that use the static value $Q_{10} = 2.0$ (Wythers *et al.*, 2005; King *et al.*, 2006).

The framework above (Eqns 1 and 2) accounts for how the instantaneous response function changes across a biologically relevant temperature range. Acclimation responses can be accommodated in this framework by changing R_{REF} from a constant to a function of recent temperature history (Atkin & Tjoelker, 2003). In TBMs that have incorporated acclimation responses, respiration in future climate scenarios is moderated even further than with the temperature-sensitive instantaneous responses described by Eqn 2 (Wythers *et al.*, 2005; King *et al.*, 2006).

Alternative formulations of acclimation

We developed a set of six simple leaf-level respiration models that incorporate acclimation-over-time and/or variation-across-space in different ways. The models are each variations within the temperature response framework described above (Eqns 1 and 2, including a temperature-dependent Q_{10}), and employ different representations for reference temperature (T_{REF}) and baseline respiration at T_{REF} (R_{REF}) (Fig. 1; Table 1). The general functional form for baseline respiration in each of the models is:

$$\log_{10}(R_{REF}) = r_1 + r_2 \cdot T_{REF} + r_3 \cdot (T_A - T_{REF}), \qquad \text{Eqn 3}$$

(T_A, an exponentially weighted average of temperatures over preceding days (defined in the Model Simulations section below) to which plants acclimate; $r_1 - r_3$, empirical parameters from the syntheses by Slot & Kitajima (2015) and Atkin *et al.* (2015) (detailed further in the Model Parameterization section below). Eqn 3 provides a convenient means to separate different time-scales of thermal responses, and serves as an empirical framework for integrating thermal acclimation into model formulations of leaf-level respiration responses to temperature across both temporal and spatial scales. In the following paragraphs we describe the structure, rationale and assumptions of four of the different model formulations (another two models, which differ from those below only in their response to climate warming, are presented in the Model Simulations section).

Instant The simplest respiration model we consider, and which is similar to widely used formulations in current TBMs, calculates respiration rates at different temperatures using a fixed basal respiration rate at 25°C, along with a temperature-dependent instantaneous response (Eqn 2) to predict respiration rates at other temperatures (Fig. 1a). This model assumes that temperature-related variation in respiration rates is unaffected by acclimation or other long-term processes. Unlike each of the following models, the basal respiration rate (R_{25}) is a single constant value that applies across the globe.

Temporal This model modifies *Instant* by allowing for thermal acclimation processes to modulate R rates at a standard reference temperature based on the temperature history over recent days. In this case, basal respiration rates (R_{25}) are shifted up or down depending on whether temperatures over the preceding days have
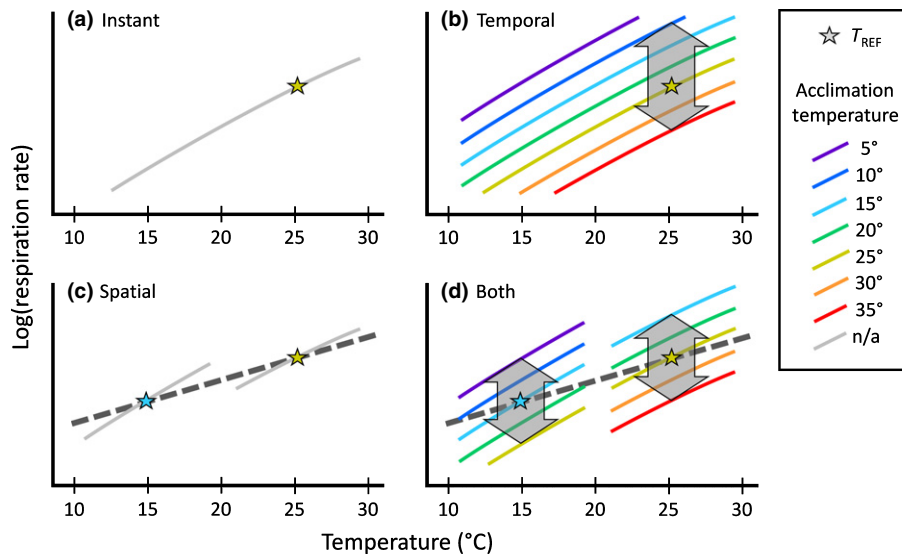
Fig. 1 Schematic illustration of temperature response curves under four alternative respiration models (Table 1). (a) In the most basic case, respiration rate at a given temperature is determined by applying the Q_{10}-based temperature response function from Eqn 2 (grey line) to the basal respiration rate (R_{REF}) at 25°C (yellow star). (b) Temporal acclimation changes respiration rates by shifting the temperature response function up or down depending on the acclimation temperature (T_A, different values of which are represented by the rainbow gradient of line colours) over preceding days. (c) To capture spatial variation in respiration at ambient growth temperatures across the globe, T_{REF} is set to the mean temperature of the warmest quarter (TWQ; hypothetical sites with TWQ = 15°C and 25°C represented by blue and yellow stars, respectively). The basal respiration rate at T_{REF} is a log-linear function of TWQ (indicated by the thick dashed line), with respiration at a given temperature then determined by the temperature-dependent Q_{10}-based response from Eqn 2 (solid grey lines). (d) When both spatial variation and temporal acclimation are represented, acclimation shifts the temperature response up or down relative to the curve where $T_A = $ TWQ, so that respiration responds separately to TWQ (moving along the thick dashed line), the acclimation temperature (moving up or down among the coloured lines), and the current temperature (moving along an individual coloured line). n/a, not applicable.

Table 1 Summary of temperature-dependent respiration model formulations and their ecophysiological interpretation

Model label [1]	T_{REF} [2]	$Log_{10}(R_{REF})$ [3]	Interpretation and notable characteristics
Instant	25°	$r_1 + r_2 \times 25$	Respiration rates are defined by a constant basal rate (R_{REF}) and a temperature-dependent, Q_{10}-based instantaneous response function. Acclimation processes are not represented. This corresponds with the respiration formulations in many current terrestrial biosphere models, and is used as a null model here for comparative purposes
Temporal	25°	$r_1 + r_2 \times 25 + r_3 \times (T_A - 25)$	Incorporates thermal acclimation of baseline respiration based on the temperature history over recent days. The structure of the model implies that thermal acclimation determines both intra-annual variation in respiration over time and variation among different locations across the globe
Spatial	TWQ_{FIX}	$r_1 + r_2 \times TWQ_{FIX}$	Describes the manner in which respiration varies across the globe by defining baseline respiration in relation to an ambient reference temperature (TWQ) at a given location. Like *Instant*, an instantaneous response function (Q_{10}) describes variation in respiration at all time-scales
Both	TWQ_{FIX}	$r_1 + r_2 \times TWQ_{FIX} + r_3 \times (T_A - TWQ_{FIX})$	Combines features of *Temporal* and *Spatial* to separately account for both spatial variation in respiration and acclimation responses over time. Long-term changes are described by both acclimation and instantaneous (Q_{10}) responses (because T_A rises relative to TWQ_{FIX} in future)
Spatial-Equil	TWQ_{DYN}	$r_1 + r_2 \times TWQ_{DYN}$	Equivalent to *Spatial* under a reference climate, but implies that future warming-induced respiration changes will mirror current spatial patterns across temperature gradients. The instantaneous response (Q_{10}) controls intra-annual variation in respiration
Both-Equil	TWQ_{DYN}	$r_1 + r_2 \times TWQ_{DYN} + r_3 \times (T_A - TWQ_{DYN})$	Similar to *Spatial-Equil*, but with an added effect of acclimation to account for seasonal temperature variation. The acclimation term does not reflect long-term changes in ambient temperature because T_A and TWQ_{DYN} are both presumed to increase in a warming climate

[1]All models share a common underlying framework where predicted respiration (R_C) at a given temperature (T_C) is modelled as $R_C = R_{REF} \times Q_{10}^{((T_C - T_{REF})/10)}$, $Q_{10} = 3.090 - 0.043 \times ((T_C + T_{REF})/2)$, and R_{REF} and T_{REF} are as specified in their respective columns.
[2]TWQ_{FIX}, the temperature of the warmest quarter (TWQ) in a historic reference period (e.g., 1961–1990) that does not change through time; TWQ_{DYN}, the temperature of the warmest quarter, either for the present or for a projected future climate.
[3]T_A, acclimation temperature, an exponentially weighted average temperature over recent days; r_1, r_2, r_3, model parameters derived from global empirical data in Atkin *et al.* (2015) and Slot & Kitajima (2015).

been cooler or warmer than the reference temperature (T_{REF}) of 25°C (Fig. 1b). This model accommodates thermal acclimation of respiration to intra-annual variation in the ambient

temperature at a particular location (e.g. summer versus winter). Importantly, when applied to multiple sites, the *Temporal* model also results in differences in leaf-level *R* across spatial temperature

gradients (e.g. tropical versus boreal biomes) through the same acclimation response to prior temperature that drives seasonal variation in *R*. Atkin *et al.* (2008) previously used this type of formulation to incorporate acclimation responses into the terrestrial biosphere model JULES.

Spatial This model explicitly accounts for leaf-level patterns of variation in respiration across space by allowing for spatially varying values of both R_{REF} and T_{REF} that are representative of ambient growing conditions. Following the approach outlined by Atkin *et al.* (2015), the *Spatial* model uses the mean temperature of the warmest quarter (TWQ; 1961–1990 reference period) in a given location as T_{REF}. Basal respiration rate (i.e. respiration at T_{REF}, with T_{REF} = TWQ in this model) is then assumed to vary across space according to empirical patterns derived from a global respiration data set (Fig. 1c). Because observed differences in respiration rates across climate gradients tend to be smaller (for a given temperature difference) than those arising from short-term temperature variation, this model moderates variation in leaf-level respiration rates across space much as acclimation does in the *Temporal* model outlined above. In this case, site-to-site variation in *R* could be underpinned either by phenotypic acclimation to the prevailing growth conditions or by genetic differences within and among species. Unlike the *Temporal* model, temperature responses in *Spatial* only describe variation across space, and do not account for seasonal patterns of acclimation over the course of a year. Yuan *et al.* (2011) used a similar formulation to redefine basal ecosystem respiration (analogous to R_{REF}) across different locations as ecosystem respiration at the mean annual temperature. Their approach yielded improved predictions of monthly respiration compared with a globally constant basal respiration value.

Both. This model incorporates acclimation over time into the *Spatial* model. Like *Spatial*, TWQ is used as a reference temperature for a given location. Acclimation-over-time acts to adjust R_{REF} depending on whether recent temperatures have been cooler or warmer than TWQ (Fig. 1d). Compared with rates of *R* predicted by *Spatial*, this formulation increases respiration at cooler times of the year (relative to the TWQ) and decreases it at warmer times of the year. Unlike the other models, *Both* explicitly separates out processes that modify *R* across space from acclimation responses that act over time. Of the four models, *Both* provides the greatest flexibility in responses to spatial and temporal variation in temperature at multiple scales.

Model parameterization

Baseline respiration (R_{REF}) in all of our models was controlled by three parameters ($r_1 - r_3$ in Eqn 3). Parameters r_1 and r_2 describe how mass-based baseline respiration rates for single leaves depend on the long-term mean ambient temperature. We obtained the values $r_1 = 0.546$ and $r_2 = 0.016$ from the Atkin *et al.* (2015) global analysis of leaf dark respiration rates; these values represent the coefficients of a least-squared regression between $\log_{10}(R_{TWQ})$ and TWQ for 1113 species–site combinations of *R* measurements in the GlobResp database, across all major biomes.

The relationship reported by Atkin *et al.* (2015) indicates that leaf-level respiration at the mean ambient temperature (TWQ) increases by *c.* 40% with each 10°C increase in TWQ across the globe, which is much less than expected from a simple instantaneous response (i.e. a Q_{10} of *c.* 2).

Parameter r_3 describes the strength of thermal acclimation to ambient temperatures over recent days. A meta-analysis by Slot & Kitajima (2015) showed that, at a given set temperature, acclimation effects on leaf-level respiration were strongly related to the magnitude of temperature change. Acclimation did not vary significantly by biome, growth form, leaf habit (deciduousness), or any of the other factors considered, however. Acclimation effects can be quantified by respiration ratios at a set temperature, defined as $\text{Acclim}_{SetTemp} = R_{REF, Control}/R_{REF, Acclim}$ (Loveys *et al.*, 2003). Here, we interpret control treatments as ones where $T_A = T_{REF}$. By using Eqn 3 and cancelling out all terms that are equal in the numerator and denominator, we obtain the expression $\text{Acclim}_{SetTemp} = 10^{(-r_3 \cdot (T_A - T_{REF}))}$. We then re-arrange this equation to estimate r_3 as:

$$r_3 = -\log_{10}(\text{Acclim}_{SetTemp})/\Delta T, \qquad \text{Eqn 4}$$

(ΔT, the temperature change relative to a reference temperature.) Using lab- and field-based data from the Slot & Kitajima (2015) meta-analysis, we obtained a global estimate of $r_3 = -0.0158$ for thermal acclimation effects (Table 2). Our model variants that do not include acclimation-over-time (*Instant*, *Spatial*) effectively assume $r_3 = 0$.

Model simulations

We applied each of the models in Table 1 across a sample of the global land area under both reference and projected future temperature conditions. We first selected 500 random locations from across the global land surface. For each of these locations, we retrieved monthly mean temperatures and TWQ over the 1961–1990 reference period from the Worldclim database (Hijmans *et al.*, 2005). To calculate respiration rates under reference conditions, we randomly selected for each location a single non-leap year between 1961 and 1990. For this single year per location, we obtained 6-hourly surface air temperature records (the shortest temporal resolution available) from the NCEP/NCAR reanalysis 1 climate data set (Kalnay *et al.*, 1996). The 6-hourly temperature data were used with Eqns 1–3 to calculate respiration rates at each location four times daily over the selected reference year. The 6-hourly respiration rates were then averaged for the entire year to estimate an annual mean respiration rate. To quantify the effects of parameter uncertainty in our models, we also calculated annual mean respiration when parameters $r_1 - r_3$ were varied by ± 2 SE. For simplicity, we assumed that respiration rates do not differ between day and night, other than through diurnal temperature changes.

In models that included acclimation-over-time, we used an exponentially weighted moving average to calculate acclimation temperature (T_A) as a recursive function of recent temperature history:

Table 2 Summary of thermal acclimation effects from a meta-analysis of lab (growth cabinet) and field (common gardens, *in situ* warming, ambient temperature changes) studies across boreal, temperate and tropical biomes (from Slot & Kitajima, 2015)

Biome	$N_{contrasts}$[1]	$N_{species}$[2]	$Acclim_{SetTemp}$[3] (mean $\pm$ SE)	ΔT[4] (mean $\pm$ SE)	$Log_{10}(Acclim_{SetTemp})/\Delta T$ (mean $\pm$ SE)
Boreal	17	6	1.31 ± 0.09	7.0 ± 0.91	0.0145 ± 0.0067
Temperate	156[5]	19	1.58 ± 0.05	11.2 ± 0.52	0.0161 ± 0.0014
Tropical	13	13	1.16 ± 0.06	4.9 ± 0.64	0.0132 ± 0.0035
All	186	33	1.53 ± 0.04	10.3 ± 0.47	0.0158 ± 0.0014

[1]Number of temperature contrasts included.
[2]Number of species included.
[3]Acclimation ratio under the set-temperature method ($R_{REF, Control}/R_{REF, Acclim}$, where $R_{REF, Control}$ and $R_{REF, Acclim}$ are the baseline respiration rates of control and acclimated plants, respectively).
[4]Temperature change applied to acclimated leaves.
[5]Excludes one outlier data point with only 0.3°C warming applied to *Eucalpytus pauciflora*.

$$T_{A,t+\Delta t} = 0.1 \cdot T_{C,t+\Delta t} + 0.9 \cdot T_{A,t}, \qquad \text{Eqn 5}$$

($T_{A,t}$, the acclimation temperature at time t; $T_{C,t}$, the current temperature in the 6-hourly time series; Δt, 6 h; $T_{A,0} = T_{C,0}$ (i.e. the temperature at 00:00 h on 1 January).) This formula allowed acclimation temperature to smoothly track the temperature history over previous days, with temperature weightings decreasing with elapsed time (e.g. temperatures on each of the past four days had total weights of 0.31, 0.20, 0.13, 0.09, etc., such that the past week's temperatures accounted for 95% of the exponentially weighted average temperature). This formulation is computationally efficient for modelling purposes, as it is calculated from a simple weighting of the current temperature and the immediately preceding acclimation temperature. The rate at which temperature weights decreased with time was somewhat faster than the duration of warming in the studies included by Slot & Kitajima (2015) (median of 10 d for fully expanded mature leaves), although studies that have specifically monitored the time-scale of acclimation have found that adjustments in respiration occur within 2–3 d (Bolstad *et al.*, 2003; Lee *et al.*, 2005).

To project changes in respiration under future climate warming, we retrieved projections of monthly temperature anomalies, relative to the reference period, for the period 2070–2099. We used data from the UK Met Office Hadley Centre coupled model 3 (HADCM3; Gordon *et al.*, 2000), whose projections are close to the mean of 23 general circulation models included in the IPCC AR4 synthesis report (IPCC, 2007). Data were obtained for an A1B emissions scenario, which, for this model, time period and set of sample locations, yielded average temperatures 4.5°C warmer than the reference period. We added the monthly temperature anomalies from the HADCM3 model to the 1-yr time series for each location to obtain a future time series with the same pattern of diurnal temperature fluctuations as the randomly selected year in the reference period. As before, 6-hourly respiration rates were averaged for the entire year to estimate an annual mean respiration rate under a warmer future climate. We again quantified uncertainty by varying model parameters by ± 2 SE.

In two of our respiration models (*Spatial* and *Both*), the reference temperature at a given location is specified by the TWQ. There are two possible ways to project future changes in

respiration using these models. In the first case, we fix future reference temperatures to TWQ values from the reference period (1961–1990; 'static TWQ'). This formulation implies that, as the climate warms, changes in R will be determined by short-term instantaneous responses (*Spatial*) and seasonal acclimation processes (*Both*). For example, if TWQ increases from 20 to 25°C at a particular site, the *Spatial* model would predict that R_{TWQ} would increase by 46% (from Eqns 1 and 2). In the second case, we update reference temperatures to projected TWQ values for the 2070–2099 period ('dynamic TWQ'). We designate this case by the model labels *Spatial-Equil* and *Both-Equil* to reflect the implicit assumption that respiration processes are, and will remain, in a dynamic equilibrium with climatic conditions at any given time. With this formulation, future changes in respiration rates over a 110-yr period will mirror spatial differences that are currently found across global climate gradients. In the example above, the *Spatial-Equil* model would predict that a 5°C increase in TWQ would increase R_{TWQ} by 20% ($= 10^{(r_2 \cdot 5)}$), the same difference that is observed across a spatial gradient in TWQ (Atkin *et al.*, 2015). The processes responsible for long-term changes in R could include acclimation, genetic adaptation, changes in species composition, or biogeochemical feedbacks (Smith & Dukes, 2013). It is not certain how much each of these processes contribute to differences in respiration rates, or how quickly they will respond to climate change. This scenario represents a useful basis for comparison with the first case (static TWQ), under the assumption that the key processes determining respiration rates keep pace with future climate warming.

Results

Incorporating direct estimates of thermal acclimation into our models changed respiration patterns in several ways. We illustrate these changes by examining three separate aspects of our projections in turn: seasonal variability in respiration rates at individual locations; spatial patterns in annual respiration rates across the globe; and global changes in respiration under future climate warming.

Models that incorporated acclimation-over-time based on Slot & Kitajima's (2015) meta-analysis data (*Temporal* and *Both*) each moderated seasonal variation in respiration relative to the model

that only accounted for variation-across-space (*Spatial*) (Fig. 2). In both acclimation-over-time models, respiration rates were higher during colder periods and lower during warmer periods in comparison to the *Spatial* model. The net result was a decrease in the intra-annual variance of respiration (30%, 40% and 50% smaller coefficients of variation in sites with TWQ = 10.3, 24.0 and 31.3°C, respectively), along with slightly higher mean annual values. Seasonal variation in respiration was very similar in the two models that included acclimation-over-time (< 2% difference in coefficient of variation between *Temporal* and *Both*), irrespective of how the models represented variation-across-space.

Acclimation-over-time yielded very similar changes in annual respiration rate across a global temperature gradient to variation-across-space, which was based on independent empirical observations from the GlobResp database (Atkin *et al.*, 2015) (Fig. 3). The model with no acclimation (*Instant*) implied that, across the globe, a 10°C increase in mean annual temperature was associated with a near doubling (96% increase) of mean annual respiration rates. Incorporating acclimation-over-time (*Temporal*) both increased respiration in locations with a mean annual temperature (MAT) less than *c.* 25°C and decreased respiration in regions with a higher MAT. These changes resulted in an overall increase in global respiration as well as lower spatial variability, with a 10°C increase in MAT now associated with only a 53% increase in respiration (47–60% when r_3 was varied by $\pm$ 2 SE). Importantly, the dampened increase in respiration with MAT mirrored that produced by both models derived from changes in observed ambient respiration with TWQ (*Spatial* and *Both*), where each 10°C increase in MAT increased respiration by 58% (52–65% when varying r_2 by $\pm$ 2 SE) and 53% (45–61%), respectively. The convergence of global variation in annual respiration between the *Temporal*, *Spatial*, and *Both* models implies that the direction and magnitude of thermal acclimation reported from local experimental studies are consistent with observed variation in ambient respiration (from GlobResp) across a global temperature gradient.

Projected respiration increases under climate warming were lessened by acclimation (Fig. 4). Models in which respiration responded to climate warming through short-term instantaneous responses (*Instant* and *Spatial*) projected a 34–36% global increase in respiration rates between the 1961–1990 and 2070–2099 periods. Relative increases were greatest in cold regions (51–52% where TWQ < 19°C) and lowest in hot regions (28% where TWQ > 27°C). Acclimation-over-time moderated the projected increase in respiration by slightly more than half in the *Temporal* and *Both* models, with climate warming projected to increase global respiration by 16% in both cases. Again, relative increases were larger in cold regions compared with hot ones (30% where TWQ < 19°C; 11% where TWQ > 27°C). The models in which we used ambient respiration across current spatial gradients to describe responses to climate warming (*Spatial-Equil* and *Both-Equil*) projected a 19–22% global increase in respiration. This change was considerably less than that produced by models that omitted acclimation-over-time (*Instant* and *Spatial*), but overlapped with the other models that included acclimation-over-time (*Temporal* and *Both*) when parameter uncertainty was considered. Unlike the other cases, the magnitude of warming-induced respiration increases in the two equilibrium models (*Spatial-Equil* and *Both-Equil*) was fairly consistent across the globe.

Discussion

We have used simple temperature-dependent models to scale up observational and experimental data on leaf respiration and project the effect of thermal acclimation on respiration rates across the globe. We show that the measured strength
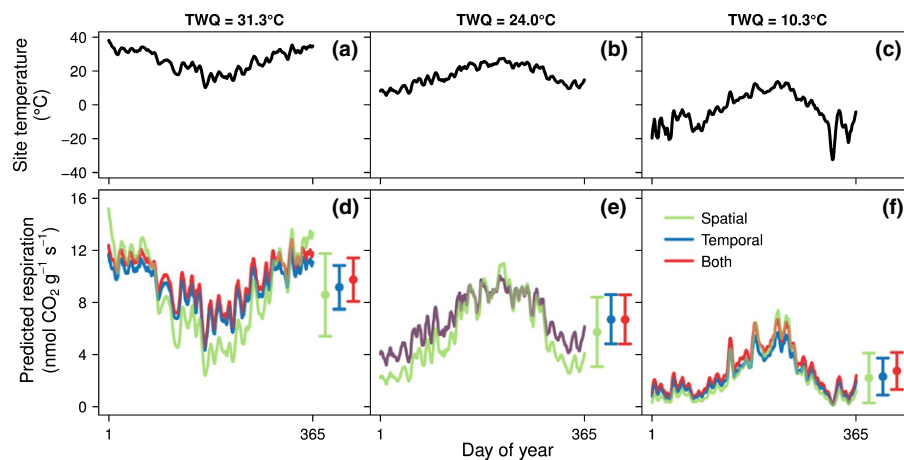

Fig. 2 Intra-annual variation in predicted respiration for individual sites representing the 90th, 50th and 10th percentiles of mean temperature of the warmest quarter (TWQ) under the three acclimation models illustrated in Fig. 1(b–d). The time series for site temperature (a, b, c) and predicted respiration rate (d, e, f) are each smoothed to 1-wk running means. The error bars at the right of each bottom panel show the annual mean and SD of respiration under each model. The *Temporal* acclimation model moderates respiration at both warm and cold parts of the year compared with the *Spatial* model, resulting in lower intra-annual variation. The model labelled *Both*, in which spatial and temporal variations in respiration are regulated independently of one another, yields predictions close to those produced by the *Temporal* model (producing overlapping lines that appear purple in (e)).
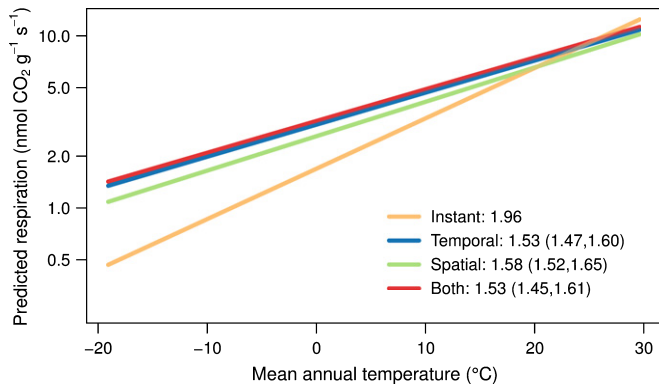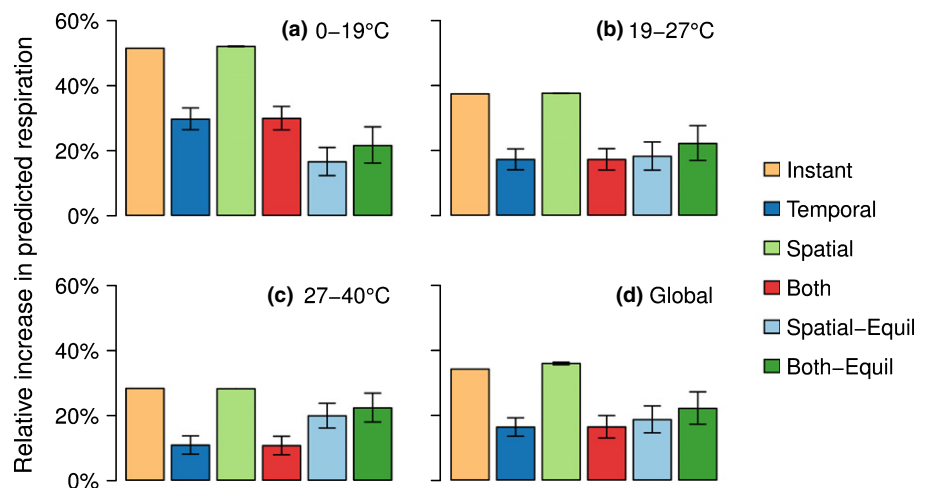
Fig. 3 Exponential relationships between predicted mass-based annual respiration rates and mean annual temperature (MAT) for the four respiration models illustrated in Fig. 1. Each line represents the fit of an exponential regression to model predictions for annual mean respiration at 500 sites across the globe ($R^2 = 0.96$–0.99; RMSE = 0.29–0.54). The numbers beside each model label indicate the proportional change in annual respiration per 10°C increase in MAT, followed in parentheses by the range when acclimation parameters were varied by ± 2 SE.

and of enabling a close analysis of the structure of the models themselves (i.e. the particular formulations of T_{REF} and R_{REF} in Eqns 1–3; Table 1). Our simple models also have limitations; for example, we do not attempt to represent growth (or growth respiration) responses to temperature variation, nor do we attempt to extrapolate from leaf-level respiration to other plant tissues or ecosystem-level fluxes. It is expected that total global leaf area will increase under climate change (Betts *et al.*, 1997; Li *et al.*, 2014), which would increase total leaf and autotrophic respiration (as well as photosynthesis) independently from changes that occur at the leaf level. Also, our climate simulations assume that daytime and nighttime temperatures will change by the same amount, but many projections indicate that daily minimum temperatures will increase more than daily maximum temperatures (IPCC, 2007). Given these types of simplifications, it would be inappropriate to formally compare predictions from our models to the quantitative effects of acclimation that have been estimated by TBMs. Nevertheless, our simple models occupy an important and largely unexplored space because, unlike TBMs, they are closely tied to global compilations of both data and results from empirical studies of respiration acclimation.

Comparing acclimation effects across time to spatial variation

As expected, acclimation-over-time moderated variation in respiration rates over the course of a year (Fig. 2). By increasing respiration in cold seasons and decreasing it in warm ones, acclimation (as represented in the *Temporal* model) produced less intra-annual variation in respiration than in the *Spatial* model (which captures the potential effects of acclimation across space, but not time). This finding is a useful proof-of-concept, and supports empirical studies (Tjoelker *et al.*, 2008, 2009) showing that seasonal variation in respiration is dampened by acclimation processes. We also found that, when spatial and temporal patterns of acclimation are both accounted for in a single model (*Both*), intra-annual variation is nearly equivalent to that in the model based on acclimation-over-time alone (*Temporal*). In each of these two models, the magnitude of intra-annual variation is

of acclimation-over-time (derived from a recent meta-analysis by Slot & Kitajima (2015)) produces differences in annual respiration across spatial temperature gradients that agree well (within limits of parameter uncertainty) with global empirical patterns of variation-across-space from an independent data set (Atkin *et al.*, 2015) (Fig. 3). Further, our simple models project that acclimation can greatly moderate future temperature-related increases in leaf-level dark respiration rates as the climate warms over the 21st Century (Fig. 4). These results contribute to a growing body of literature that highlights the importance of thermal acclimation of respiration to the global terrestrial carbon cycle (Wythers *et al.*, 2005, 2013; King *et al.*, 2006; Atkin *et al.*, 2008; Chen & Zhuang, 2013; Slot *et al.*, 2014).

While previous studies (such as those cited directly above) have incorporated acclimation into sophisticated TBMs, our approach rests on simple conceptual formulations for the temperature dependence of respiration. These model forms have the advantages of being readily parameterized from published data,

Fig. 4 Predicted increases in annual mean mass-based respiration rates from 1961–1990 to 2070–2099 in a projected A1B climate scenario in which the mean temperature increases by 4.5°C between these periods. Error bars show the range of predicted increase when acclimation parameters were varied by ± 2 SE. (not applicable for the *Instant* model, and a negligible effect in the *Spatial* model). The labels for each panel refer to different ranges of mean temperature of the warmest quarter (TWQ) in the 1961–1990 period.

controlled by the shared acclimation parameter r_3 (as depicted graphically in Fig. 1b,d), and so it is not unexpected that this particular aspect of R predictions is common to the *Both* and *Temporal* models.

Looking at spatial variation in mean annual respiration across the globe, models based on acclimation-over-time and variation-across-space all produced smaller increases in respiration with mean annual temperature than the model that excluded both of these effects (*Instant*; Fig. 3). Further, the rate at which respiration increased with mean annual temperature across global sites – the spatial equivalent of Q_{10} (Piao *et al.*, 2010) – was nearly the same between models incorporating acclimation-over-time (*Temporal*: 1.53 (1.47–1.60 given parameter uncertainty)) and variation-across-space (*Spatial*: 1.58 (1.52–1.65); *Both*: 1.53 (1.45–1.61)). The convergence of global temperature-dependent patterns of respiration between these models suggests that observed patterns in respiration at ambient temperatures (Atkin *et al.*, 2015) might be explained by the experimentally measured strength of thermal acclimation in diverse plant taxa (Slot & Kitajima, 2015), and may not necessarily be strongly related to longer term processes such as genetic adaptation or climate-related variation in species composition. Atkin *et al.* (2015) did not determine the relative importance of genotypic (i.e. inherent differences within and among species) and phenotypic variation (i.e. acclimation effects) in accounting for the observed global patterns.

Rates of leaf R are controlled by respiratory capacity, demand for respiratory products, and the availability of respiratory substrate (i.e. carbohydrates). Some of these factors are influenced by genetic traits; for example, respiratory capacity and demand for respiratory products are related to leaf nitrogen (N) and growth rate, respectively. Independent of species traits, acclimation is believed to operate through changes in leaf N and carbohydrates (Tjoelker *et al.*, 2008) that are related to thermal history. Are geographical patterns in R explained more by genetic factors or by thermal history, then? Common garden experiments in which warm- and cold-adapted populations of a species are grown together have frequently shown that local climatic conditions have a stronger influence on respiration than the location of source populations (Reich *et al.*, 1996; Oleksyn *et al.*, 1998; Gunderson *et al.*, 2000; Lee *et al.*, 2005; Tjoelker *et al.*, 2008, 2009; Van de Weg *et al.*, 2013). This general result implies that, within species, physiological acclimation exerts a greater degree of control over respiration processes than genetic adaptation. Among species, respiration tends to co-vary with leaf N (Wright *et al.*, 2004, 2006; Atkin *et al.*, 2015), but leaf N is only weakly associated with mean annual temperature and other climatic variables at a global scale (Reich & Oleksyn, 2004; Wright *et al.*, 2005). Species turnover across global temperature gradients is therefore unlikely to produce systematic differences in leaf respiration (at a common reference temperature) that could explain the observed climate-related variation in R. Taking these findings together with our current results, we may thus infer that physiological acclimation is largely responsible for temperature-dependent respiration patterns found across a global climate gradient.

Responses to long-term temperature increases

Our set of models describes three ways in which respiration rates may respond to climate warming at decadal to centennial time-scales: two models (*Instant* and *Spatial*) assume that respiration will increase according to a temperature-dependent instantaneous response function, two others (*Temporal* and *Both*) assume that respiration increases will be determined by thermal acclimation, and a third pair (*Spatial-Equil* and *Both-Equil*) assume that future changes in respiration will mirror current patterns found across spatial climate gradients. Models based on an instantaneous response only (like many TBMs) produced the largest increases in future respiration (Fig. 4). Because instantaneous responses are stronger at cold temperatures (under a temperature-dependent Q_{10}; Tjoelker *et al.*, 2001), projected increases were largest in cold regions and smallest in warm ones. It is widely appreciated that the instantaneous response does not apply at time-scales longer than days to weeks, however (Atkin *et al.*, 2000; Gifford, 2003; Dillaway & Kruger, 2011). Accounting for thermal acclimation in our models reduced projected 110-yr increases in leaf-level respiration by approximately one-half. Qualitatively, this result is in line with those of studies that have incorporated thermal acclimation into TBMs and projected that acclimation will act to reduce carbon fluxes from terrestrial vegetation to the atmosphere under climate warming (Wythers *et al.*, 2005, 2013; King *et al.*, 2006; Chen & Zhuang, 2013; Slot *et al.*, 2014).

Interestingly, we find that spatial patterns in respiration at ambient temperatures (as described by the parameters r_1 and r_2) and measured acclimation effects (r_3) each imply a similar global moderation of future warming-induced increases in leaf-level respiration. In the equilibrium models (*Spatial-Equil* and *Both-Equil* in Fig. 4), relative increases in respiration with climate warming were about the same in cold (TWQ < 19°C) and hot (TWQ > 27°C) environments because the models assumed a positive linear relationship between (log-scale) respiration and TWQ. If this assumption holds true under future conditions, our results imply that leaf-level respiration increases in warm biomes, such as tropical forests and hot deserts, might not be offset to the degree expected from measurements of acclimation-over-time (Fig. 4c). Acclimation responses in tropical regions are not as well studied as in temperate ones, and thus have somewhat higher uncertainty (Table 2). Nevertheless, experimental warming treatments applied to eucalypt populations of tropical and temperate origins have recently shown that warm-origin populations can have stronger thermal acclimation responses than cool-origin populations because they down-regulate photosynthetic capacity (which is metabolically linked to respiration) as temperatures increase (Drake *et al.*, 2015).

Comparative analyses with global respiration data sets (e.g. Wright *et al.*, 2006; Piao *et al.*, 2010) can be a useful means of assessing physiological acclimation, and may complement findings from experimental studies. Similar space-for-time substitutions have been applied in other areas of climate change biology, particularly in projecting how species' distributions track climatic niches (Guisan & Thuiller, 2005). Caution is warranted,

however, because models based on a space-for-time substitution may lack a sound biological basis if the processes governing changes in respiration do not keep pace with rates of climate change. However, as discussed above, it seems that physiological acclimation has considerable potential to moderate future increases in respiration even if species range shifts and genetic adaptation fail to keep pace with climate.

Testing respiration models against data

While the structure and parameter values for our models are well grounded in recently published data (Atkin *et al.*, 2015; Slot & Kitajima, 2015), it remains difficult to formally test the various models' predictions. Global databases of leaf traits such as TRY (Kattge *et al.*, 2011) provide some of the most spatially and taxonomically extensive information on respiration, but this is generally restricted to snapshot measurements at a single time and temperature. Such data do not provide information on variation in respiration over longer periods, nor do they record site temperature histories that could be used to model acclimation responses to recent temperature changes. Annual autotrophic respiration data are also available from a global database of ecosystem-scale forest carbon balance, which combines eddy-covariance measurements with other observations (Luyssaert *et al.*, 2007). These data have been useful in understanding controls over total annual respiration across the globe (Piao *et al.*, 2010), but unfortunately they do not have the temporal resolution needed to examine seasonal acclimation processes. Networks of eddy-CO_2 flux measurements (Baldocchi *et al.*, 2001) provide measurements of net ecosystem exchange (NEE) with both high temporal resolution (continuous half-hourly respiration measurements over multiple years) and extensive spatial coverage (over 500 tower sites world-wide). In this case, nighttime CO_2 fluxes provide a measure of ecosystem respiration, which is the sum of both autotrophic and heterotrophic respiration components. Eddy covariance measurements are often accompanied by measurements of soil respiration, which includes both heterotrophic respiration and below-ground autotrophic (root) respiration. However, soil respiration has different diel and seasonal patterns from ecosystem respiration (and by inference, above-ground respiration; Phillips *et al.*, 2010), and so it is still difficult to evaluate thermal acclimation of leaf respiration with eddy covariance measurements.

Algorithms representing the response of respiration to temperature within TBMs need careful scrutiny (Smith & Dukes, 2013). Without a mechanistic understanding for temperature-dependent *R*, the developers of TBMs have adopted simplistic model forms that do not necessarily hold up at large spatial and temporal scales. Vegetation modellers should always seek out ways to test the predictions of large-scale models, even if data sets such as those described above may be imperfect for this task. Here, we have shown that thermal acclimation effects from experimental studies are consistent with the best available data on global variation in respiration at ambient temperatures. These findings suggest there is considerable potential to improve our quantitative understanding of global carbon–climate dynamics by modifying respiration models to properly account for acclimation processes, and by ensuring that such models are well constrained by empirical data.

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