Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level

Miguel D. Mahecha,[1,2]* Markus Reichstein,[1] Nuno Carvalhais,[1,3] Gitta Lasslop,[1] Holger Lange,[4] Sonia I. Seneviratne,[2] Rodrigo Vargas,[5] Christof Ammann,[6] M. Altaf Arain,[7] Alessandro Cescatti,[8] Ivan A. Janssens,[9] Mirco Migliavacca,[10] Leonardo Montagnani,[11,12] Andrew D. Richardson[13]

[1]Max Planck Institute for Biogeochemistry, 07745 Jena, Germany. [2]Institute for Atmospheric and Climate Science, ETH Zürich, Universitätsstrasse 16, 8092 Zürich, Switzerland. [3]Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal. [4]Norsk Institutt for Skog og Landskap, N-1431 Ås, Norway. [5]Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, USA. [6]Agroscope ART, Federal Research Station, Reckenholzstr. 191, CH-8046 Zürich, Switzerland. [7]McMaster Centre for Climate Change, McMaster University, Hamilton, Ontario L8S 4L8, Canada. [8]European Commission, Joint Research Center, Institute for Environment and Sustainability, I-21027 Ispra, Italy. [9]Department of Biology, University of Antwerpen, Universiteitsplein 1, 2610 Wilrijk, Belgium. [10]Remote Sensing of Environmental Dynamics Laboratory, DISAT, University of Milano-Bicocca, 20126 Milano, Italy. [11]Servizi Forestali, Agenzia per l'Ambiente, Provincia Autonoma di Bolzano, 39100 Bolzano, Italy. [12]Faculty of Sciences and Technologies, Free University of Bozen-Bolzano, Piazza Università 1, 39100, Bolzano, Italy. [13]Department of Organismic and Evolutionary Biology, Harvard University, HUH, 22 Divinity Avenue, Cambridge, MA 02138, USA.

*To whom correspondence should be addressed. E-mail: mmahecha@bgc-jena.mpg.de

The respiratory release of CO_2 from the land surface is a major flux in the global carbon cycle, antipodal to photosynthetic CO_2 uptake. Understanding the sensitivity of respiratory processes to temperature is central for quantifying the climate–carbon cycle feedback. Here, we approximate the sensitivity of terrestrial ecosystem respiration to air temperature (Q_{10}) across 60 FLUXNET sites using a methodology that circumvents confounding effects. Contrary to previous findings, our results suggest that Q_{10} is independent of mean annual temperature, does not differ among biomes, and is confined to values around 1.4 (±0.1). The strong relation between photosynthesis and respiration, instead, is highly variable among sites. Overall, the results partly explain a less pronounced climate–carbon cycle feedback than suggested by current carbon cycle climate models.

Quantifying the intensity of feedback mechanisms between terrestrial ecosystems and climate is a central challenge for understanding the global carbon cycle and a prerequisite for reliable future climate scenarios (*1*, *2*). One crucial determinant of the climate–carbon cycle feedback is the temperature sensitivity of respiratory processes in terrestrial ecosystems (*3*, *4*), which has been subject to much debate (*5–10*). On the one hand, empirical studies have found high temperature sensitivities of soil respiration with Q_{10} values well above 2 (*11*, *12*). Dependencies of Q_{10} values on mean temperatures (*12*, *13*) have been attributed to the acclimatization of soil respiration (*5*), amongst other factors (*13*). On the other hand, global scale models often employ globally constant Q_{10} values of 2 or below to generate carbon dynamics that is consistent with global atmospheric CO_2

growth rates (*3*, *14*, *15*). Nevertheless, several models have directly included empirical dependencies of the parameterization of respiratory processes to environmental dynamics (*16–18*). This inclusion is questionable, since single-site studies have indicated that factors seasonally covarying with temperature can confound the experimental retrieval of the intrinsic temperature dependence of respiration (*8*, *9*, *19*). Davidson and Janssens (*20*) therefore proposed to distinguish intrinsic temperature sensitivities quantifying the inherent kinetic properties of substrate decomposition from apparent temperature responses. Moreover, it has been recognized that the direct inference of process sensitivities from emergent ecosystem behavior is not possible (*19*, *21*).

Here we aim to retrieve the unconfounded (intrinsic) temperature sensitivities of ecosystem respiration across different climates and ecosystems, to resolve the question of whether we have to account for a globally varying and environmentally controlled Q_{10} in global carbon cycle modeling. The study is based on a global collection of eddy covariance CO_2 flux observations—the FLUXNET (*22*, *23*) LaThuile Database—which allows us to investigate greenhouse gas fluxes in response to meteorological variables across ecosystems. To minimize the influence of confounding effects, we apply a model-data fusion approach, the "Scale Dependent Parameter Estimation" (SCAPE) (*24*) where processes are investigated on different time scales. The SCAPE concept exploits that measured time series $Y(i)$, $i = 1$, ..., N result from superimposed modes of characteristic variability X_f where the index f indicates the attributable frequency class per subsignal (fig. S1). In SCAPE we can

distinguish rapid and slow system responses (here, direct responses to temperature versus long term organic matter dynamics described by the base respiration R_b). SCAPE differentiates the parameter estimation process according to identified time scales. We can therefore report temperature sensitivities ($Q_{10,sc}$) derived from specific (high frequency) subsignals X_f such that confounding factors that operate on other (generally low frequency) scales are excluded. Moreover, a nonparametric estimate of the low frequency R_b time series is directly provided (24). In an experiment with artificial data (24) (fig. S2) we show that with this methodology the unconfounded $Q_{10,sc}$ of respiration is retrieved within ±0.1 units, even under unfavorable conditions of noise (fig. S3) (25).

The examination of the ecosystem respiration data shows that the unconfounded $Q_{10,sc}$ values are generally lower than temperature sensitivities reported by conventional estimates (Fig. 1) with very few exceptions (table S1). Conventional estimates would suggest an average sensitivity to air temperature of $\langle Q_{10}\rangle \approx 2.3$ across sites. The corresponding 95% confidence range is $2.0 \leq Q_{10} \leq 2.6$, estimated via a block bootstrapping across sites (24). This large range of possible Q_{10} values is very likely caused by confounding factors. However, once we derive the sensitivities using SCAPE, the weighted arithmetic mean is $\langle Q_{10,sc}\rangle \approx 1.4$; the 95% confidence range collapses to the narrow interval of $1.3 \leq Q_{10,sc} \leq 1.5$. The observed systematic difference between apparent and short-term "intrinsic" temperature sensitivities corresponds exactly to what was expected by theoretical considerations reported previously (9).

The reported range of $Q_{10,sc}$ values is low considering that soil organic matter incubation experiments, which should not be hampered by seasonally confounding effects, typically find sensitivities of $Q_{10} > 2$ (7, 26, 27). We argue that this discrepancy is due to the controlled laboratory conditions, which partially exclude a number of factors relevant to ecosystem respiration. Measurements at ecosystem level always include multiple processes, *i.e.* the mobilization, transport, and transfer (*e.g.* via depolymerisation) of carbon compounds such that they are metabolizable in the mitochondria. At the end, the rate limiting step will determine the overall temperature response of a chemical reaction chain, and the overall Q_{10} is lower than for the individual processes (28). For instance, it has been shown that the mycorrhizal respiration is largely limited by the carbon supply from the roots, but virtually insensitive to temperature variations (29, 30). Moreover growth respiration of plants is largely independent of temperature (31). Because ecosystem respiration is a mixed response of temperature sensitive and insensitive subprocesses, we assume that the comparable low $Q_{10,sc}$ values reported here are plausible estimates.

Despite a narrow range of identified $Q_{10,sc}$ values, the site-to-site variability in the $Q_{10,sc}$ estimates does not fully disappear. These differences may be partially caused by a propagation of noise in the night time eddy covariance data into parameter estimates. Also slightly delayed system responses (32) can affect our estimates at ecosystem level. Minor confounding factors operating at comparable time scales as the effective system responses may also play a role. The latter are not easily distinguishable given that we are confronted with a signal comprising both soil and plant respiration at ecosystem level. Hence, it is very likely that the intrinsic temperature sensitivities of the involved subprocesses are confined to an even narrower range compared to our approximation at ecosystem level. This is remarkable since it implies a convergence of relative proportions of temperature sensitive and insensitive respiration fluxes among ecosystems.

To clarify whether a general environmental control might explain the site-to-site variability in the temperature sensitivities of ecosystem respiration, we investigated the relationship of mean annual temperature to the approximated intrinsic $Q_{10,sc}$ and apparent Q_{10} (Fig. 2). The $Q_{10,sc}$ estimates do not confirm the previously found or hypothesized patterns (Fig. 2B). Our results show a global convergence in the temperature sensitivity of terrestrial ecosystem respiration: an almost universal $Q_{10,sc}$ value across climate zones and ecosystem types (see also Fig. 1) is identified. Using the conventional estimates of Q_{10} instead, we reproduce the effects of an apparent temperature control on the sensitivity (Fig. 2A). This underscores the problem that some unconsidered process, for example substrate supply, can be erratically interpreted as an oversensitivity of ecosystem metabolic processes to temperature.

Our analysis further emphasizes that in spite of having comparable short term temperature sensitivities, ecosystems strongly differ in their carbon metabolization on longer time scales (Fig. 3): Low frequency ecosystem responses are reflected in the temporal dynamics of the base respiration R_b (fig. S5). These time series show a tight relationship with corresponding low frequency modes in independently estimated time series of gross primary productivity GPP_{fl} (33) (fig. S6). If we allow R_b to respond to GPP_{fl} with a time delay of a few days, which is a plausible assumption (32), all relationships are close to linear (fig. S7), confirming recent findings (34). The ratio $1 - (R_b/GPP_{fl})$ hints at how the low frequency dynamics of carbon uptake is propagated to the metabolization potential of labile soil organic carbon by autotrophic and heterotrophic respiration (19). Contrary to the global convergence in the temperature sensitivity, Fig. 3 shows that the low frequency dynamics within the ecosystem spreads over a wide range. Consequently, future analyses of the climate–carbon cycle feedback have to emphasize the role

of long term dynamics in the terrestrial carbon cycle rather than focus on the short term sensitivities. In particular the role of intricate nonbiological stabilization processes versus carbon supply rates need to be further investigated when trying to predict climate change effects on soil carbon dynamics.

The estimated average value for $Q_{10,sc}$ at ecosystem level likely underlies also recent observations of moderate global temperature responses of respiration on the long term (*35*). Also modeling studies reporting that the global carbon cycle can only be well modeled based on ecosystem level Q_{10} values below 2 (*36*) are empirically confirmed by our findings. Consequently, carbon process model results will need to be investigated for their capacity to predict similar short-term $Q_{10,sc}$ and the variation of R_b at ecosystem level. However, given the nontrivial ecophysiological interpretation of a multitude of processes summing up to the observed ecosystem respiration our results do not justify the prescription of $Q_{10} = 1.4$ for all rate constants in soil carbon models. Rather, a deeper understanding of the different factors and processes limiting soil carbon metabolization is needed for overcoming the "dead-soil box modeling paradigm" (*37*). Moreover, continuous time series of soil respiration, measured with automatic chambers should be analyzed with the presented methodology using soil temperature as a driving variable. Such studies could allow exclusive insights to the soil system, while our analysis at the ecosystem level included aboveground respiration. Furthermore, we suggest exploring the SCAPE methodology also in other fields of research, where confounding factors at different scales obscure the intrinsic relation between two variables of interest.

In summary, we provide substantial evidence for the existence of universal intrinsic temperature sensitivities of terrestrial ecosystem respiration. The empirically inferred results suggest a $Q_{10,sc} \approx 1.4$ at ecosystem level. These results reconcile the empirical evidence with findings that the global carbon cycle can be well modeled only with an ecosystem level sensitivity of $Q_{10} < 2$. Moreover, our results may explain recent findings indicating a less pronounced climate–carbon cycle sensitivity (*38*) than assumed by current climate–carbon cycle model parameterizations. Opposed to the global convergence in temperature sensitivities we find complex patterns in the low frequency influence of photosynthetic carbon uptake and available assimilates on ecosystem respiration dynamics. Future research should strive for an in-depth understanding of carbon pathways through slow pools in terrestrial ecosystems.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/science.1189587/DC1
Materials and Methods
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Figs. S1 to S7
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Fig. 1. Estimation of apparent Q_{10} values versus the approximated intrinsic $Q_{10,sc}$ values (SCAPE methodology) across 60 FLUXNET sites using night time observations of ecosystem-atmosphere CO_2 fluxes. Error bars show the 95% range of the parameter distributions. These uncertainties are identified via a bootstrapping approach (Q_{10}), or propagated from the SCAPE uncertainties of the time series decomposition (for $Q_{10,sc}$, (*24*)). The color code indicates the plant functional type at each site (CRO: cropland, SH: shrubs, SAV: savanna, DBF: deciduous broadleaf forest, EBF: evergreen broadleaf forest, ENF: evergreen needleleaf forest, GRA: grassland, MF: mixed forest, and WSA: woody savanna.)

Fig. 2. Apparent Q_{10} and approximated intrinsic $Q_{10,sc}$ values binned over mean annual temperature (bin with 3.5°). Bin medians, their 50%, and 95% uncertainty ranges are estimated via block bootstrapping (*24*). Original site level parameter medians (and 95% confidence ranges) are shown in red. A: The conventionally determined ecosystem level Q_{10} values suggest an apparent temperature dependence. B: The SCAPE $Q_{10,sc}$ estimates do not show any relationship with the mean annual temperature at the investigated FLUXNET sites.

Fig. 3. Distribution of the ratio of base respiration to GPP_{fl} [$1 - (R_b/GPP_{fl})$]. Base respiration is a low frequency signal (periods >3 months), and is compared here to GPP fluctuations in the same frequency range (f_l) for all sites. The ratio is recomputed 1024 times per site from a randomly chosen combination of subsignal estimates (of GPP_{fl} and R_b), such that the methodological uncertainty is considered (*24*).

Legend:
- CRO
- DBF
- EBF
- ENF
- GRA
- MF
- SH+SAV
- WSA

A

B