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40. This work used eddy covariance data acquired by the FLUXNET community and in particular by the following networks: AmeriFlux [U.S. Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63917 and DE-FG02-04ER63911)], AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada (supported by CFCAS, NSERC, BIOCAP, Environment Canada, and NRCan), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, and USCCC. We acknowledge the support to the eddy covariance data harmonization provided by CarboEuropeIP, FAO-GTOS-TCO, Integrated Land Ecosystem-Atmosphere Processes Study, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, Université Laval and Environment Canada and U.S. Department of Energy and the database development and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California-Berkeley, and University of Virginia. Remotely sensed land cover, FAPAR, and LAI were available through the Joint Research Centre of the European Commission, the National Aeronautics and Space Administration, and the projects GLC2000 and CYCLOPES. Climate data came from the European Centre for Medium-Range Weather Forecasts, the Climate Research Unit of the University of East Anglia, and the GEWEX project GPCP. We thank Mahendra K. Karki at GMAO/NASA for extracting the MOD17 required surface meteorological variables from the GMAO reanalysis dataset and Maosheng Zhao at NTSG of University of Montana for calculating the respective daytime VPD. We further acknowledge support by the European Commission FP7 projects COMBINE and CARBO-Extreme and a grant from the Max-Planck Society establishing the MPRG Biogeochemical Model-Data Integration. C.B., D.P., M.R., P.C., D.B., and S.L. conceived the study. C.B., C.R., D.P., E.T., M.J., M.R., and N.C. contributed diagnostic modeling results. C.B., A.B., G.B.B., M.L., F.I.W., and N.V. contributed process model results. C.B., E.T., and M.R. performed the analysis. C.B. and M.R. wrote the manuscript. All other coauthors contributed with data or substantial input to the manuscript.

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Figs. S1 to S34

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Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level

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The respiratory release of carbon dioxide (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. We approximated the sensitivity of terrestrial ecosystem respiration to air temperature (Q_{10}) across 60 FLUXNET sites with the use of 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, by contrast, is highly variable among sites. The results may 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 sensitivities of soil respiration to temperature, with values of Q_{10} (here an indicator of the sensitivity of terrestrial ecosystem respiration to air temperature) 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), among other factors (13). On the other hand, global-scale

models often make use of globally constant Q_{10} values of 2 or below to generate carbon dynamics consistent with global atmospheric CO_2 growth rates (3, 14, 15). Nonetheless, several models have directly included empirical dependencies of the parameterization of respiratory processes to environmental dynamics (16–18). This inclusion is questionable, given that single-site studies have indicated that factors seasonally covarying with temperature can confound the experimental retrieval

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of the intrinsic temperature dependence of respiration (8, 9, 19). Davidson and Janssens (20) therefore proposed to distinguish intrinsic temperature sensitivities by 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).

Our aim here was 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, scale-dependent parameter estimation (SCAPE) (24), that investigates processes on different time scales. The SCAPE concept exploits the idea that measured time series $Y(i)$, $i = 1, \dots, N$, 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 ($Q_{10,\text{sc}}$) 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 $Q_{10,\text{sc}}$ 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 $Q_{10,\text{sc}}$ 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 $2.0 \lesssim Q_{10} \lesssim 2.6$, 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 $\langle Q_{10,\text{sc}} \rangle \approx 1.4$; the 95% confidence range collapses to the narrow interval of $1.3 \lesssim Q_{10,\text{sc}} \lesssim 1.5$. The observed systematic difference between apparent and short-term temperature sensitivities corresponds exactly to what was expected by theoretical considerations reported previously (9).

The reported range of $Q_{10,\text{sc}}$ values is low, given 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, such as the mobilization, transport, and transfer (e.g., via depolymerization) 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 is 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 $Q_{10,\text{sc}}$ values reported here are plausible estimates.

Despite a narrow range of identified $Q_{10,\text{sc}}$ values, the site-to-site variability in the $Q_{10,\text{sc}}$ estimates does not fully disappear. These differences may be partially caused by a propagation of noise in the nighttime 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

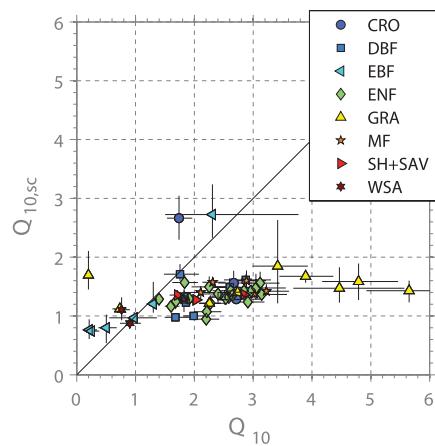


Fig. 1. Estimation of apparent Q_{10} values versus the approximated intrinsic $Q_{10,\text{sc}}$ values (SCAPE methodology) across 60 FLUXNET sites using nighttime observations of ecosystem-atmosphere CO_2 fluxes. Error bars show the 95% range of the parameter distributions. These uncertainties are identified via a bootstrapping approach (Q_{10}) or propagated from the SCAPE uncertainties of the time series decomposition [for $Q_{10,\text{sc}}$] (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; WSA, woody savanna.

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 because 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 $Q_{10,\text{sc}}$ and apparent Q_{10} (Fig. 2). The $Q_{10,\text{sc}}$ 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 $Q_{10,\text{sc}}$ value across climate zones and ecosystem types (see also Fig. 1) is identified. Using the conventional estimates of Q_{10} instead,

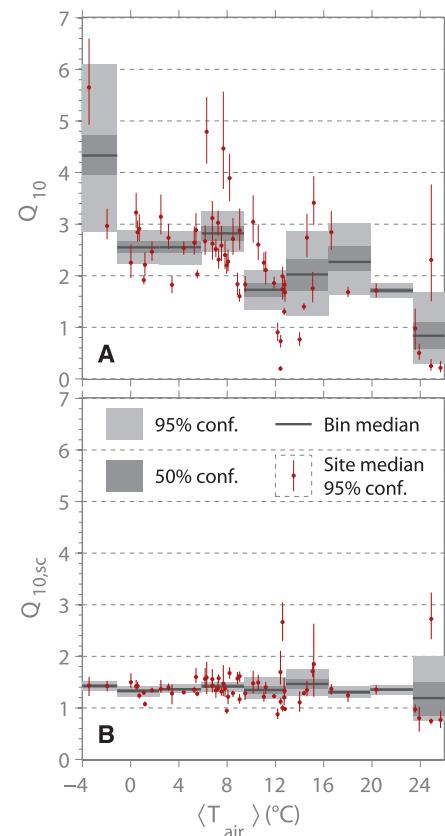


Fig. 2. Apparent Q_{10} and approximated intrinsic $Q_{10,\text{sc}}$ values binned over mean annual temperature (bin with 3.5°C). Bin medians and their 50% and 95% uncertainty ranges are estimated via block bootstrapping (24). Original site-level parameter medians (and 95% confidence ranges) are shown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

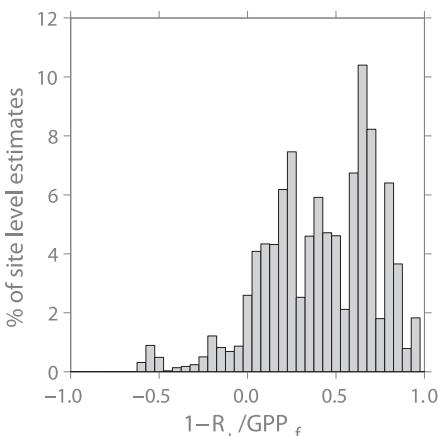


Fig. 3. Distribution of the ratio of base respiration to GPP_{f_j} , $1 - (R_b/GPP_{f_j})$. Base respiration is a low-frequency signal (periods >3 months) and is compared here to GPP fluctuations in the same frequency range (f_j) for all sites. The ratio is recomputed 1024 times per site from a randomly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

we reproduce the effects of an apparent temperature control on the sensitivity (Fig. 2A). This underscores the problem that some unconsidered process, such as substrate supply, can be erratically interpreted as an oversensitivity of ecosystem metabolic processes to temperature.

Our analysis further emphasizes that despite having comparable short-term temperature sensitivities, ecosystems strongly differ in their carbon metabolism 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_{f_j} (33) (fig. S6). If we allow R_b to respond to GPP_{f_j} 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 $1 - (R_b/GPP_{f_j})$ hints at how the low-frequency dynamics of carbon uptake is propagated to the metabolism 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 focusing on the short-term sensitivities. In particular, the role of intricate nonbiological stabilization processes versus carbon supply rates needs 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 also underlies recent observations of moderate global temperature responses of respiration in the long term (35). Also, modeling

studies reporting that the global carbon cycle can be well modeled only if it is 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 metabolism 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, whereas our analysis at ecosystem level included aboveground respiration. Furthermore, we suggest exploring the SCAPE methodology in other fields of research, where confounding factors at different scales obscure the intrinsic relation between two variables of interest.

Our findings offer 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 partly explain recent findings indicating a less pronounced climate–carbon cycle sensitivity (38) than assumed by current climate–carbon cycle model parameterizations. Contrary 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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Figs. S1 to S7

Table S1

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