



# Water limitation regulates positive feedback of increased ecosystem respiration

Received: 14 September 2023

Accepted: 8 July 2024

Published online: 07 August 2024

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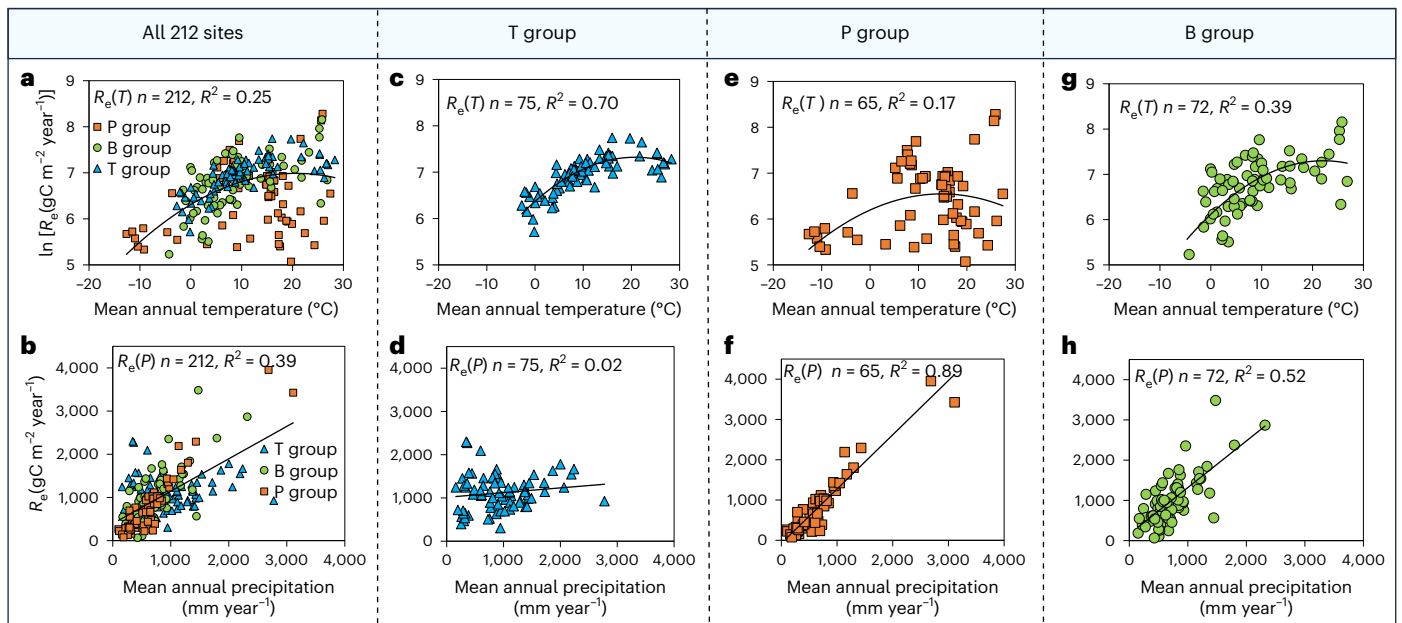
Terrestrial ecosystem respiration increases exponentially with temperature, constituting a positive feedback loop accelerating global warming. However, the response of ecosystem respiration to temperature strongly depends on water availability, yet where and when the water effects are important, is presently poorly constrained, introducing uncertainties in climate–carbon cycle feedback projections. Here, we disentangle the effects of temperature and precipitation (a proxy for water availability) on ecosystem respiration by analysing eddy covariance CO<sub>2</sub> flux measurements across 212 globally distributed sites. We reveal a threshold precipitation function, determined by the balance between precipitation and ecosystem water demand, which separates temperature-limited and water-limited respiration. Respiration is temperature limited for precipitation above that threshold function, whereas in drier areas water limitation reduces the temperature sensitivity of respiration and its positive feedback to global warming. If the trend of expansion of water-limited areas with warming climate over the last decades continues, the positive feedback of ecosystem respiration is likely to be weakened and counteracted by the increasing water limitation.

At present ecosystem respiration ( $R_e$ ) produces about one order of magnitude higher CO<sub>2</sub> than do anthropogenic emissions<sup>1</sup>, although  $R_e$  emissions are offset by plant primary production. The  $R_e$  increases exponentially with temperature, as typically described by  $Q_{10}$  (the factor by which respiration increases per 10 °C increase in temperature) and Arrhenius models<sup>2–4</sup>. These formulations are widely accepted in Earth system models (ESM) and suggest that the carbon transfer rate from soils and plants to the atmosphere will increase with warming, causing positive feedback that further accelerates warming<sup>5,6</sup>.

Recent observations, however, have led to debates<sup>7–20</sup> on the extent to which  $R_e$  may increase with warming. Uncertainty in the temperature sensitivity of  $R_e$  has been attributed mainly to a confounding effect of precipitation<sup>21,22</sup>. At the ecosystem level, respiration responds to temperature and precipitation through several mechanisms occurring

simultaneously and whose relative importance depends on biomes and climates<sup>7,20,23</sup>. Models solely driven by temperature can predict  $R_e$  well only over a limited temperature range<sup>8,23,24</sup> and in the absence of water limitation<sup>7</sup>. Recent field studies indicate that precipitation (a proxy for water availability) and supply of accessible substrates (photosynthates for plants or organic matter for decomposers) are confounding factors for the actual feedback of  $R_e$  to global warming that may unexpectedly lower the positive feedback in real-world scenarios, depending on local to regional conditions<sup>7,8,10,23–26</sup>.

Field experiments<sup>14,19</sup>, modelling studies<sup>27</sup> and meta-analyses<sup>7,8,20</sup> have suggested that  $R_e$  responds in different ways to changing hydro-thermal conditions depending on latitude and ecosystem type. The  $Q_{10}$  may decrease with increasing temperature<sup>4,7,8,23,26</sup>, often regulated by water availability<sup>10</sup>. However, the temporal and geographic influence



**Fig. 1 | The statistical performance of models of ecosystem respiration ( $R_e$ ) as a function of mean annual temperature ( $T$ ) and precipitation ( $P$ ),  $R_e(T)$  and  $R_e(P)$ . **a–h**, Models were constructed using: all data for  $R_e(T)$  (**a**); all data for  $R_e(P)$  (**b**); T group for  $R_e(T)$  (**c**); T group for  $R_e(P)$  (**d**); P group for  $R_e(T)$  (**e**); P group for  $R_e(P)$  (**f**); B group for  $R_e(T)$  (**g**); and B group for  $R_e(P)$  (**h**). Here, the empirical temperature-dependent respiration model  $R_e(T)$  refers to equation (11), while**

precipitation-dependent respiration model  $R_e(P)$  refers to equation (12). We first calculated site-year average of temperature ( $T$ ), precipitation ( $P$ ) and ecosystem respiration  $R_e$  across 212 FLUXNET sites. Then we used a mixture regression model (Methods) to statistically classify them into three groups: T group, P group and B group. Finally, we calculated statistics of both empirical models for each group.

of water availability on the temperature sensitivity of  $R_e$  remains to be determined. Moreover, the  $Q_{10}$  may change under future climate change scenarios<sup>7</sup>. This introduces more—and still poorly understood—complexity to terrestrial carbon budget estimates.

Disentangling the effects of temperature and precipitation on ecosystem  $R_e$  is a central challenge for reducing uncertainties in modeling of climate–carbon cycle feedbacks. There is therefore a pressing need to determine where and when the precipitation effects on  $R_e$  are important, which is the main research question addressed in this study.

## Results

### Statistical disentangling

We used statistical models on FLUXNET2015 data<sup>28</sup> to examine the effect of mean annual temperature ( $T$ ) and precipitation ( $P$ ) on  $R_e$ . Despite measurement challenges, FLUXNET2015 provides unique insights. Using a normal mixture regression model, we first identified 32 of the 212 sites of eddy covariance  $\text{CO}_2$  flux measurement as temperature limited (prototype T group, with >95% probability of temperature control) and 23 sites as precipitation limited (prototype P group, with >95% probability of precipitation control). Subsequent analyses allowed us to further classify sites into a T group, a P group and a group influenced by both temperature and precipitation (B group), based on relative residuals (Methods and Supplementary Information)

We used an existing empirical temperature-dependent respiration model  $R_e(T)$  (equation (10))<sup>29</sup> and a precipitation-dependent respiration model  $R_e(P)$  (equation (12))<sup>30,31</sup> to separately fit the data of the T group, P group and B group sites and further verify the effects of temperature and precipitation on  $R_e$  obtained from this statistical grouping (Methods and Supplementary Information). Owing to effect combinations, each of the empirical models  $R_e(T)$  and  $R_e(P)$  could partly explain the observed variability across all data (Fig. 1a,b). However,  $R_e(T)$  performed excellently for the T group (Fig. 1c) but poorly for the P group (Fig. 1e), while  $R_e(P)$  did poorly for the T group (Fig. 1d) but excellently for the P group (Fig. 1f). The  $R_e$  in the B group emerged as dependent on both temperature and precipitation (Fig. 1g,h).

This analysis shows that the grouping was effective in separating ecosystems that are predominantly limited by precipitation (where  $R_e(P)$  performs well) or temperature (where  $R_e(T)$  performs well). However, these empirical relations do not inform on the combinations of  $P$  and  $T$  where the transition from  $P$  to  $T$  limitation occurs, which we need to assess the temperature dependence of  $R_e$  under future climates.

### Empirical threshold function

We hypothesized that a threshold function exists that separates the biome climate space ( $T, P$ ) (Fig. 2a) into two distinct regions with: (1)  $R_e$  more limited by  $T$ ; and (2)  $R_e$  more limited by  $P$ .

We also expected the B group to straddle the boundary between the T and P groups, with  $R_e$  affected by both  $T$  and  $P$ . As a first step to test this and estimate the conditions under which  $R_e$  switches from  $T$  control to  $P$  control or vice versa, we used the climate data from the B group sites to obtain an empirical threshold precipitation function  $\tilde{P}$  of  $T$ ,

$$\tilde{P}(T) = 446 \times 10^{0.042T} \quad (1)$$

where  $\tilde{P}$  is mean annual precipitation (mm per year) and  $T$  is mean annual temperature ( $^{\circ}\text{C}$ ) (Extended Data Fig. 1).

### Theoretical basis of the threshold function

To investigate the theoretical basis of the empirical threshold precipitation function  $\tilde{P}(T)$ , we note that the surface net radiation  $R_n$  ( $\text{MJ m}^{-2}$  per year) is the sum of the sensible heat flux  $H$  ( $\text{MJ m}^{-2}$  per year) used to heat the air and the latent heat flux  $\lambda \text{ET}$  used to evaporate water from the soil and transpire water from plants. Here  $\text{ET}$  (mm per year) is evapotranspiration and  $\lambda$  ( $2.5 \text{ MJ kg}^{-1}$ ) is the latent heat coefficient. Considering the theoretical limits  $H \rightarrow 0, R_n \rightarrow \lambda \text{ET}$  we can find a theoretical maximum potential evapotranspiration  $\text{PET} = R_n/\lambda$  assuming the available energy  $R_n$  to be completely used for evapotranspiration without being constrained by water supply or atmospheric saturation. Budyko defined a dryness index  $\text{DI} = \text{PET}/P$ , providing essential

climatological water/energy limitation information in a straightforward way:  $DI < 1$  indicates wet (energy-limited) and  $DI > 1$  dry (water-limited) conditions<sup>32</sup>.

This framework can be illustrated in a two-dimensional space spanned by the dryness index  $DI$  and evapotranspiration index  $EI = AET/P$ , where  $AET$  is actual evapotranspiration<sup>32</sup>. In wet ( $DI < 1, P > PET$ ) regions,  $AET$  is limited by the available energy ( $R_n$ ) and hence  $EI$  is expected to be at or below the line  $EI = DI$  ( $AET = PET$ ; Fig. 2b). In dry ( $DI > 1, P < PET$ ) regions,  $AET$  is limited by the available water, so  $EI$  is expected to be at or below the line  $EI = 1$  ( $AET = P$ ; Fig. 2b).

The transition from temperature (energy) to precipitation (water) limitation of  $R_e$  is expected to occur at conditions that are neither too wet nor too dry. Therefore, we hypothesized the theoretical threshold function corresponding to the empirical function in equation (1) to be given by

$$P^* = PET(T), \text{ corresponding to } DI = 1 \quad (2)$$

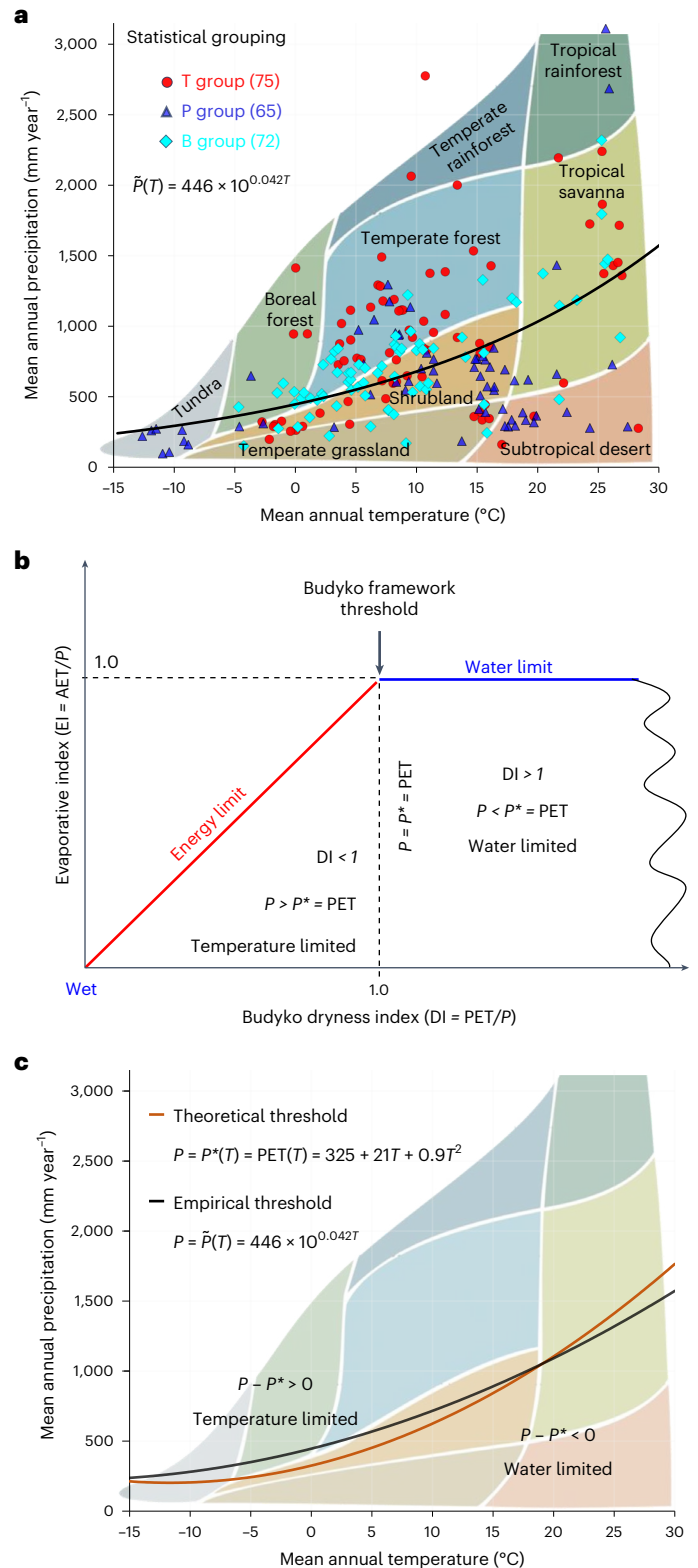
Thus,  $P^*$  is suggested to depend on temperature because the  $PET$  is solely determined by  $R_n$ . This threshold precipitation function can be estimated, for example, by the Langbein function<sup>33,34</sup>  $P^* = PET = 325 + 21T + 0.9T^2$ , originally derived from data for the eastern United States during 1921–1945 and further used, for example, for global water budget estimation<sup>35</sup>. Direct comparison finally shows that the empirical threshold precipitation function  $\tilde{P}(T)$  derived from FLUXNET2015 data closely agrees with the hypothesized theoretical threshold function  $P^*$  determined by  $DI = 1$  (Fig. 2c). To summarize, our analysis shows that ecosystem respiration is limited by energy (and thus temperature dependent) when the climate is wet ( $P > PET$ ) and is limited by water (and thus precipitation dependent) when the climate is dry ( $P < PET$ ).

### Discussion

The effects of temperature and precipitation on  $R_e$  can be disentangled empirically and mechanistically (Fig. 2). The condition  $DI = 1$  provides function  $P^* = PET(T)$  above which  $R_e$  is sensitive to  $T$ . As  $DI$  increases, respiration shifts from shifts from being temperature limited to being water limited (Fig. 2b). We used the FLUXNET2015 data of  $R_e$  to fit the  $Q_{10}$  model for the  $DI$  conditions of the different sites (Methods) and obtained apparent  $Q_{10}$  at the ecosystem level (Extended Data Figs. 2–4). In wet conditions, the apparent  $Q_{10}$  is high and decreases linearly with increasing dryness index ( $DI < 1$ ), while it is low and near-constant in water-limited conditions ( $DI > 1$ ) (Extended Data Fig. 2). The slope of the linear decrease of  $Q_{10}$  with temperature (the  $T$  sensitivity of  $Q_{10}$ ) is 3.7 times steeper when  $DI < 1$  than when  $DI > 1$  (Extended Data Fig. 3). Under the latter, dry conditions, the low substrate supply associated with the water (precipitation) limitation, reduces the biomass of both primary producers and consumers and thereby also reduces enzyme activities and capacity<sup>36</sup>. In fact, there is direct evidence of reduced carbon flux exchange between soil or canopy and the atmosphere under dry conditions, as the substrate supply to soil microorganisms

and the  $CO_2$  supply to the leaves are then reduced and both supply processes ultimately reduce  $R_e$  (refs. 37,38).

Interannual and intersite variations in  $R_e$  are confounded by a range of interlinked environmental factors with varying strengths<sup>39</sup>. Climatic variation and some non-climatic factors, such as topography, soil type, substrate availability and species composition, may account for those unexplained spatial variations in  $R_e$  of the three groups. They may also influence our grouping algorithm and explain why sites with similar



**Fig. 2 | Comparative threshold functions for mean temperature ( $T$ ) or mean precipitation ( $P$ ) regulation of ecosystem respiration ( $R_e$ ). a**, A threshold precipitation function  $\tilde{P}(T)$  emerging empirically from grouping of the observational eddy covariance flux data (Methods). **b**, A hypothesized comparative threshold precipitation function  $P^*(T) = PET(T)$  determined from the Budyko dryness condition  $DI = 1$ . **c**, Budyko theoretical threshold and empirical threshold. The empirical function  $\tilde{P}(T)$  in **a** was obtained from  $P$  and  $T$  values at sites belonging to the B group, which are colimited by temperature and precipitation. Then we linked this empirical result to the Budyko framework by assuming that Budyko dryness  $DI = 1$  provides the condition to determine a threshold relationship between precipitation with temperature. Thus, the space ( $T, P$ ) is divided by the threshold curve into two regions—one where  $R_e$  is dominated by temperature and one where it is dominated by precipitation.

temperatures and precipitation went to different groups. For instance, tropical rainforests may have been grouped into the P group owing to their low seasonal temperature variability (Fig. 2a). In addition, the correlation between  $R_e$  and gross primary production (GPP) is notably higher in the P group than in the T group (Supplementary Fig. 1). This is consistent with studies suggesting that substrate limitation leads to reduced temperature sensitivity.

Recent theoretical studies<sup>21,40–43</sup> indicate that temperature effects on metabolic fluxes at the ecosystem level can be obtained by integrating the kinetic effects of temperature on the rates of photosynthesis and respiration of individual organisms in the ecosystem. Temperature effects on metabolism at organism level can be described by an expression mathematically equivalent to Arrhenius equation ( $\sim \exp(-E_a/kT)$ ). These effects can be then scaled up to the whole ecosystem by considering the biomass of consumers and primary producers. Many modelling and observational studies have further shown that precipitation is a critical driver for site productivity<sup>44–47</sup> and many previous studies have reported that  $Q_{10}$  is not constant but decreases with increasing temperature<sup>7,8,23,26,27,48</sup>. In view of these studies, we here introduce and test DI ( $= R_n/\lambda P$ )<sup>32,49</sup>, expressing the ratio of available energy to precipitation, as a further quantitative explanatory parameter for both understanding and predicting under which conditions  $R_e$  is sensitive to temperature. For instance, precipitation in high-latitude ecosystems can be low, ranging from 150 to 250 mm per year, while the DI is also low because the available energy  $R_n$  is even more limited. Therefore, DI is a more informative predictor than  $T$  and  $P$  alone.

Our conclusions are drawn from broad patterns captured over long timescales across biomes and continents. We acknowledge a potential asymmetric effect of precipitation on  $R_e$ , particularly notable in arid and semi-arid ecosystems as a result of seasonal dynamics or spikes in soil respiration triggered by precipitation pulses after prolonged seasonal droughts<sup>30,50</sup>. Details on the assessment of such second-order effects at subannual timescales are discussed in Extended Data Figs. 5 and 6 and Supplementary Methods 2, while the main focus here is on the first-order effects at the annual timescale.

The temperature insensitivity of  $R_e$  under dry conditions indicates a water-availability control and regulation of the positive feedback of  $R_e$  to global warming. Expansion of arid areas and contraction of lake and wetland areas have been reported around the world<sup>51–55</sup>. Output data from climate models also indicate drying of land areas with mean annual temperature  $>16$  °C (ref. 51), while greenhouse gas emissions are expected to continue raising temperatures<sup>55</sup> with land-surface temperature reported to warm faster (0.27 °C per decade) than sea-surface temperature (0.11 °C per decade) since the 1970s<sup>56</sup>. Continuation of such drying trends under warming can be expected to reduce the positive feedback of  $R_e$  to future global warming.

More specifically, our findings indicate that this hydroclimatic trend will change the two main ecosystem carbon fluxes,  $R_e$  and GPP, and the balance of CO<sub>2</sub> exchanges between biosphere and atmosphere to weaker associated feedbacks to global warming. By analysing nine ESM outputs from Coupled Model Intercomparison Project Phase 6 (CMIP6), we also found that most models (seven out of nine) failed to reproduce the declining temperature sensitivity of  $R_e$  for drier conditions (Supplementary Fig. 3). The observation-based and theoretically/mechanistically supported threshold function between temperature- and precipitation-driven control on respiration rates represents an opportunity to assess if ESMs and land-surface models capture water versus energy limitations correctly and suggest ways to reduce associated model uncertainties in prediction of future climate change.

## Methods

### FLUXNET2015 data

The FLUXNET2015 dataset (<https://fluxnet.org/data/fluxnet2015-dataset/>) comes from 212 globally distributed eddy covariance sites (over 1,500

site-years) and provides CO<sub>2</sub>, water and energy exchange data between terrestrial ecosystem and atmosphere as well as meteorological observations<sup>28</sup>. This study used annual ecosystem respiration ( $R_e$ ) from the daytime partitioning method (RECO\_DT\_VUT\_REF, gC m<sup>-2</sup> per year), annual air temperature (TA\_F, °C) and annual precipitation (P\_F, mm per year) of all the 212 sites. Air temperature ( $T$ ) is consolidated from data gap-filled using marginal distribution damping method (TA\_F\_MDS) and downscaled from ERA-Interim reanalysis data product (TA\_ERA). Precipitation ( $P$ ) is consolidated from data measured and downscaled from ERA (P\_ERA). Site-average  $R_e$ ,  $T$  and  $P$  were averaged using the measurement period of each site. Site-average data rather than site-year data were used for the analyses in this study. In other words, each site contributed only one data point.

### Mixture regression model

The grouping method used in this paper is based on mixture regression, which uses the regression function of a response ( $R_e$ ) on covariates ( $T$  and  $P$ ) to cluster observations<sup>57,58</sup>. Mixture regression models are thus different from mixture models, which use the population mean to cluster observations<sup>59–61</sup>. Let  $m_1(T)$  and  $m_2(P)$  be the regression functions of  $R_e$  on  $T$  and  $P$ , respectively. That is,  $m_1(T) = E(R_e | T)$  and  $m_2(P) = E(R_e | P)$ . In other words,  $m_1(T)$  is used to model the regression function of the T group, while  $m_2(P)$  is used to model the regression function of the P group. Since most functions can be approximated well by polynomials, we use cubic polynomials to model both  $m_1(T)$  and  $m_2(P)$ ,

$$m_1(T) = a_0 + a_1T + a_2T^2 + a_3T^3 \quad (3)$$

and

$$m_2(P) = b_0 + b_1P + b_2P^2 + b_3P^3 \quad (4)$$

Formally, we can describe the mixture regression model in statistical terminology as follows. Let  $G$  be a latent group variable and the regression function of  $R_e$  on  $T$ ,  $P$  and  $G$ ,

$$E(R_e | T, P, G) = m_G(T, P) \quad (5)$$

with  $G = 1$  indicating the T group and  $G = 2$  indicating the P group and  $m_1(T, P) = m_1(T)$  and  $m_2(T, P) = m_2(P)$ . Since  $G$  is a latent group variable, it is not observed. Denote  $\pi_1 = p(G = 1)$  and  $\pi_2 = p(G = 2)$ , the probabilities of an observation belonging to the T and G groups, respectively (with  $\pi_1 + \pi_2 = 1$ ). Thus, this probability quantifies the likelihood that an observation belongs to a particular group. As a result, the probability may provide us a criterion to cluster observations. Further assume the random error  $\varepsilon$  in the regression model of  $R_e$  over  $T$ ,  $P$  and  $G$  follows a normal distribution with mean 0 and variance  $\sigma^2$ . That is,

$$R_e = m_G(T, P) + \varepsilon \quad (6)$$

where  $\varepsilon \sim N(0, \sigma^2)$ . This enables deriving the likelihood function of the mixture regression models based on a set of observations and finding maximum likelihood values of the model parameters,  $a_0, a_1, a_2, a_3, b_0, b_1, b_2, b_3, \pi_1, \pi_2$  and  $\sigma^2$ . Unlike with simple linear regression, there is no closed-form solution for these values and finding the maximum likelihood is in general challenging. In the literature of mixture regression model<sup>62,63</sup>, expectation maximization (EM)<sup>64</sup> algorithm is used to maximize the likelihood function. During the course of an iteration of the EM algorithm, we also obtain the probability  $p(G_i = 2, | T_i, P_i)$  for the observation  $(R_{e_i}, T_i, P_i)$  for  $i$ th site,  $k = 1, 2$ . This probability can be used to group observations and is also referred to as posterior probability, although there are no specifically Bayesian statistical concepts in this model. Sites whose probabilities do not meet this threshold are clustered into the B group.



## Grouping method

The first step in our data analysis is to identify sites in T and P groups with high confidence from the 212 eddy covariance sites. We apply the mixture regression model for the data collected from sites and obtain the posterior probability  $p(G_i = 1, | T_i, P_i)$  for the  $i$ th site,  $i = 1, \dots, 212$  and  $k = 1, 2$ . We determine the sites with >95% probability of belonging to T group or P group as two prototype subgroups. That is, if  $p(G_i = 1, | T_i, P_i) > 95\%$ , then the  $i$ th site belongs to the T group and if  $p(G_i = 2, | T_i, P_i) > 95\%$ , then the  $i$ th site belongs to the P group. On the basis of this criterion, 32 highly temperature-limited sites (>95% confidence) and 23 highly precipitation-limited sites (>95% confidence) were selected. Then the two prototype equations predict the annual  $R_e$  of any sites:

$$R_e^T(T) = m_1(T) = -0.20T^3 + 5.58T^2 + 22.3T + 538 \quad (7)$$

and

$$R_e^P(P) = m_2(P) = -(2.34 \times 10^{-7})P^3 + (7.26 \times 10^{-4})P^2 + 1.16P - 183 \quad (8)$$

The second step in our analysis is to cluster the sites on the basis of the dimensionless residual index<sup>65</sup>. The residual index is defined as:

$$\text{Residual index} = \frac{\varepsilon_P - \varepsilon_T}{\varepsilon_P + \varepsilon_T} \quad (9)$$

where  $\varepsilon_P = |(R_e^P - R_e^{\text{EC}})/R_e^{\text{EC}}| \times 100\%$  is a percentage error in  $R_e$  prediction by equation (8) for a site and  $R_e^{\text{EC}}$  is the semimeasured annual mean  $R_e$  of the site. Similarly,  $\varepsilon_T = |(R_e^T - R_e^{\text{EC}})/R_e^{\text{EC}}| \times 100\%$  is a percentage error in  $R_e$  prediction by equation (7) for a site. Intuitively, a large positive residual index value indicates that temperature controls the  $R_e$  while a large negative residual index value means that precipitation controls  $R_e$  of the site. A residual index value of around zero indicates that equations (7) and (8) have similar predictive ability. The  $R_e$  of the sites with a residual index near zero appear to be controlled by both temperature and precipitation. On the basis of equations (7), (8) and (9), we calculate the residual index for each site. We further group the 212 global distributed eddy covariance sites into three groups on the basis of their residual index values: temperature-limited group (T group, residual index > 30%); Precipitation-limited group (P group, residual index < -30%); both-limited by temperature and precipitation group (B group, -30% < residual index < 30%). There were a few sites (five) that we discovered were limited by neither temperature nor precipitation. We chose to leave those unusual sites in the B group. While these sites may demonstrate substantial deviations from the threshold function (Extended Data Fig. 1), most sites in the B group exhibit influences from both temperature and precipitation on ecosystem respiration.

We also calculated the residual index using datasets obtained from the daytime partitioning method; the results showed residual index values derived from night time and daytime partitioning methods show a robust agreement, closely following the 1:1 line (Supplementary Fig. 3).

## Empirical $R_e$ models

Equations (7) and (8) in polynomial form are essential for our grouping method and we aim for the purely mathematical fitting to be supported by observational evidence. We used the following model<sup>29</sup>:

$$R_e(T) = ae^{bT+cT^2} \quad (10)$$

as an empirical temperature-control model of ecosystem respiration. For convenience, we rewrote the equation (10) into a quadratic expression after log-transformation,

$$\ln R_e(T) = a' + b \times T + c \times T^2 \quad (11)$$

The statistical performances of  $R_e(T)$  with temperature for all data, T group, P group and B group are shown in Fig. 2a,c,e,g, respectively. The  $R_e$ -precipitation relationship is often described by a linear model with long-term site-based data<sup>30,31</sup>,

$$R_e(P) = a_1 \times P - b_1 \quad (12)$$

We used equation (12) as an empirical precipitation-control model of ecosystem respiration. The regression results of  $R_e(P)$  with precipitation in different data groups are shown in Fig. 2b,d,f,h, respectively.

## Apparent $Q_{10}$

We divided the 212 FLUXNET2015 sites into five groups according to their site-annual mean DI,  $0 < \text{DI} < 0.4$  (9 sites);  $0.4 < \text{DI} < 0.7$  (61 sites);  $0.7 < \text{DI} < 1.0$  (58 sites);  $1.0 < \text{DI} < 1.4$  (38 sites);  $1.4 < \text{DI} < 2.2$  (23 sites); and  $\text{DI} > 2.2$  (23 sites). The DI is defined as,

$$\text{DI} = \frac{P^*(T)}{P} \quad (13)$$

where  $P^*(T)$  is the threshold precipitation defined by equation (2) (Fig. 2c) and  $P$  is site mean annual precipitation (mm per year).

We estimated the apparent  $Q_{10}$  for each of the five groups through the van't Hoff  $Q_{10}$  model<sup>3</sup>,

$$R_e = \alpha e^{\beta T}, Q_{10} = e^{\beta 10} \quad (14)$$

where  $R_e$  is site-annual ecosystem respiration,  $T$  is site mean annual temperature in °C,  $\alpha$  and  $\beta$  are regression parameters.  $Q_{10}$  (temperature sensitivity) is the factor of 10 °C increase in temperature multiplied by the  $R_e$ .

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

All data used for this study are publicly accessible and downloadable and all results of this study can be reproduced according to the methods provided. The FLUXNET2015 dataset used here are publicly available at <https://fluxnet.org/data/fluxnet2015-dataset/>. The CMIP6 data are publicly available at <https://esgf-node.lnl.gov/projects/cmip6/>. Information on the 212 sites used in this paper and their groupings are available on GitHub (<https://github.com/chuixiangyi/Water-limitation>).

## Code availability

The Matlab code used for the analysis is available on GitHub (<https://github.com/chuixiangyi/>).

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## Acknowledgements

This work used eddy covariance data acquired and shared by the FLUXNET community, including these networks: AmeriFlux, AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia and USCCC. The FLUXNET eddy covariance data processing and harmonization were carried out by the ICOS Ecosystem Thematic Center, AmeriFlux Management Project and Fluxdata project of FLUXNET, with the support of CDIAC and the OzFlux, ChinaFlux and AsiaFlux offices. C.Y. completed this research when he was a Fulbright Visiting Professor at University of Innsbruck with support from the US-Austria Fulbright Program. D.C. is supported by the Swedish national strategic research area BECC. G.D. has received support for this research from the Swedish Research Council (VR; grant number 2022-04672). The research of M.R. is supported by

the European Research Council (ERC-Synergy project RESILIENCE, proposal no. 101071417) and by the Dutch Research Council (NWO ‘Resilience in complex systems through adaptive spatial pattern formation’, project no. OCENW.M20.169). S.M. was supported by ERC grant 101001608. G.W. acknowledges support from Austrian Research Promotion Agency grant 878893 and the Austrian Science Fund (10.55776/PAT2661823). N.K. acknowledges funding from National Oceanic and Atmospheric Administration Educational Partnership Program with Minority-Serving Institutions—Cooperative Science Center for Earth System Sciences and Remote Sensing Technologies cooperative agreement grant NA22SEC4810016.

## Author contributions

C.Y., Q.Z. and G.D. conceived the project. Q.Z. performed data processing with R.L., Z.T. and J.H. Q.Z. and C.Y. conducted data analysis. C.Y. wrote the first version of the manuscript with Q.Z., E.K., R.L., D.C., G.W., Y.K., G.D., S.M., M.R., G.H. and W.F. All authors discussed the results and contributed to the writing and to the final manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41559-024-02501-w>.

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41559-024-02501-w>.

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**Peer review information** *Nature Ecology & Evolution* thanks Jingfeng Xiao and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

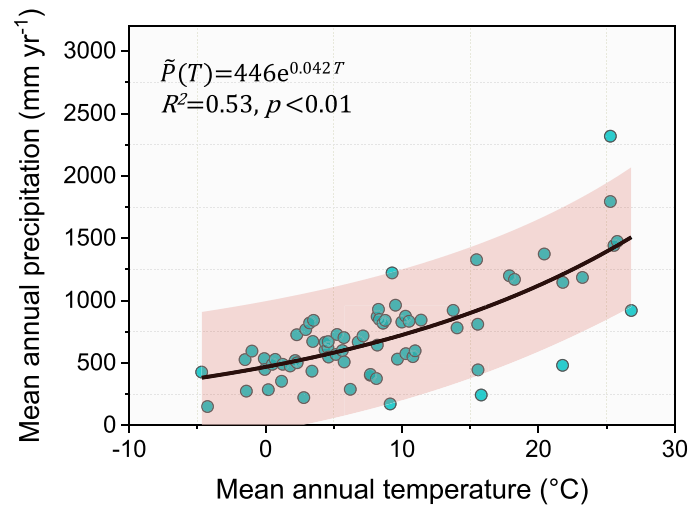
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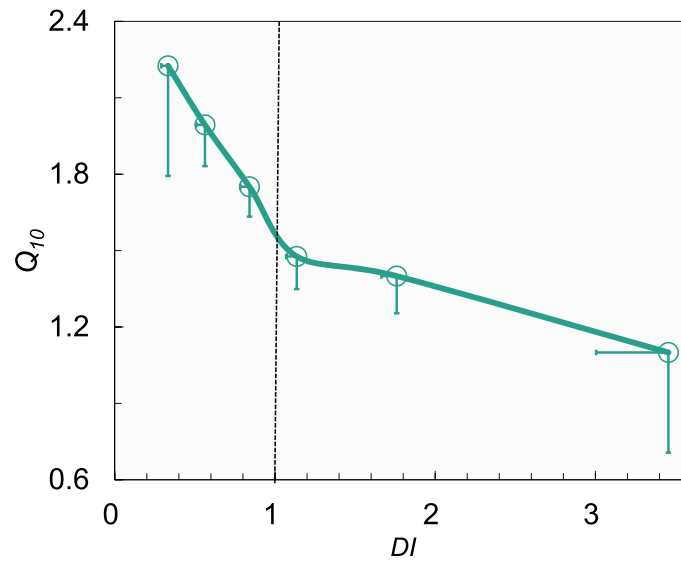
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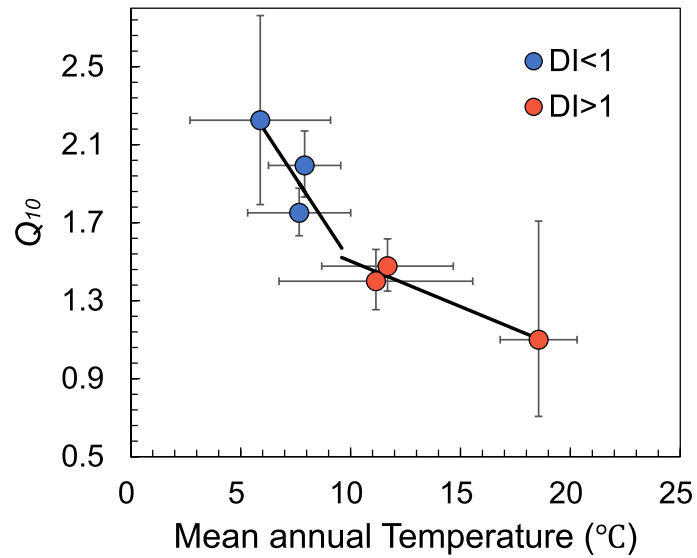


**Extended Data Fig. 1 | The statistics of the empirical threshold model  $\bar{P}(T)$ .** The blue filled circles are the data of mean annual temperature and mean annual precipitation in B-group. The threshold curve (black line) is the exponential regression line with 95% confidence interval (shaded area),  $R^2 = 0.53$  and  $p < 0.01$  for One-Tailed Test.



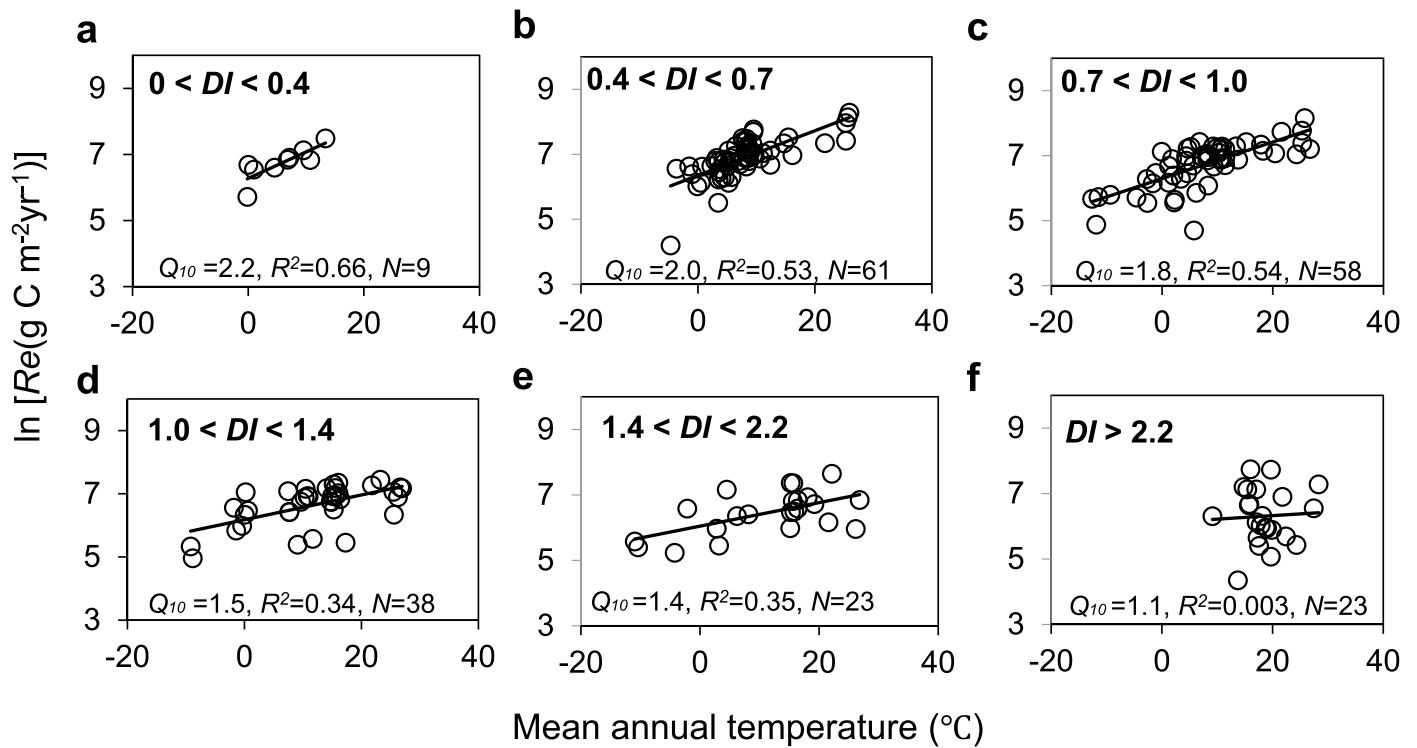


**Extended Data Fig. 2 | Differential sensitivity of  $Q_{10}$  to Dryness ( $DI$ ).** 212 sites of FLUXNET2015 were divided into six groups with six  $DI$  intervals:  $0 < DI < 0.4$  (9 sites);  $0.4 < DI < 0.7$  (61 sites);  $0.7 < DI < 1.0$  (58 sites);  $1.0 < DI < 1.4$  (38 sites);  $1.4 < DI < 2.2$  (23 sites); and  $DI > 2.2$  (23 sites). The apparent group average  $Q_{10}$  were estimated by  $Q_{10}$  models (see Methods).



**Extended Data Fig. 3 | Differential sensitivity of  $Q_{10}$  to temperature revealed by Dryness ( $DI$ ).** 212 sites of FLUXNET2015 were divided into six groups with six  $DI$  intervals:  $0 < DI < 0.4$  (9 sites);  $0.4 < DI < 0.7$  (61 sites);  $0.7 < DI < 1.0$  (58 sites);  $1.0 < DI < 1.4$  (38 sites);  $1.4 < DI < 2.2$  (23 sites); and  $DI > 2.2$  (23 sites). The filled

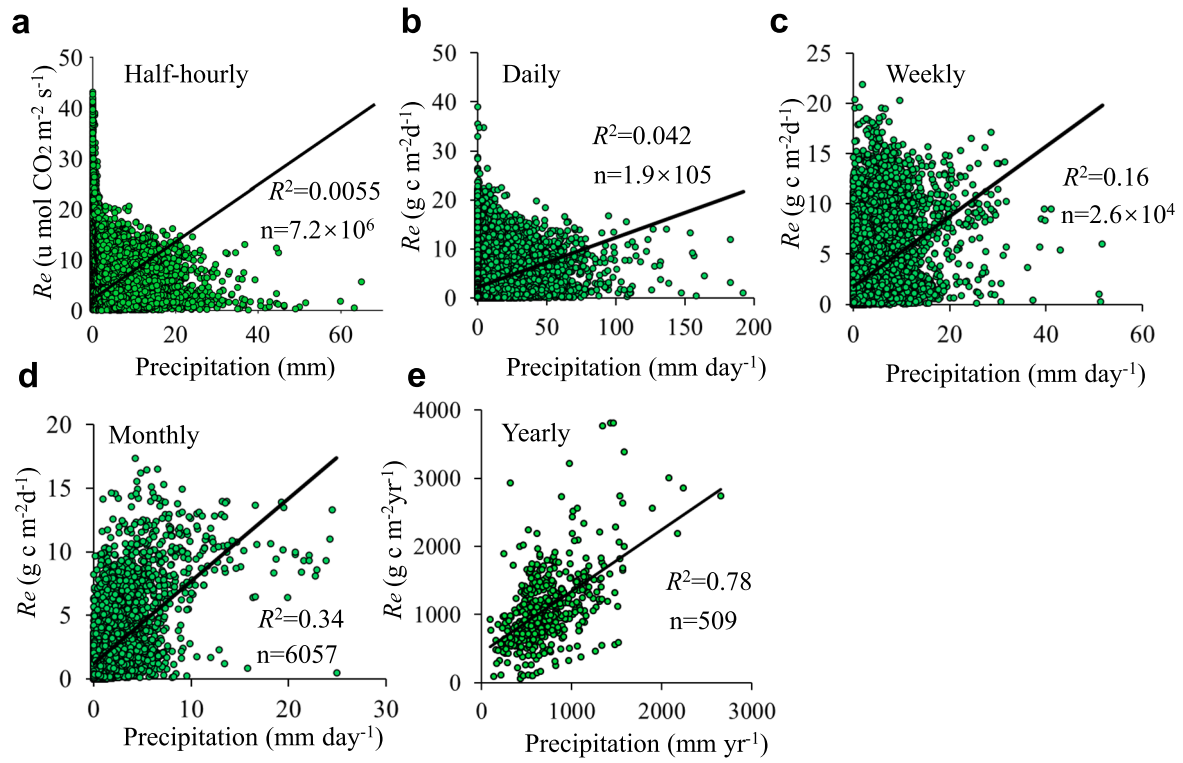
circles and error bars represent  $DI$ -group means and their standard deviations, respectively. The blue line is the regression ( $y = -0.1719x + 3.2197$ ,  $R^2 = 0.63$  for the data  $DI < 1$ , while the red line is the regression ( $y = -0.047x + 1.97$ ,  $R^2 = 0.93$ ) for the data  $DI > 1$ .



**Extended Data Fig. 4 | The distribution and statistics of  $Q_{10}$  for each  $DI$  group.**

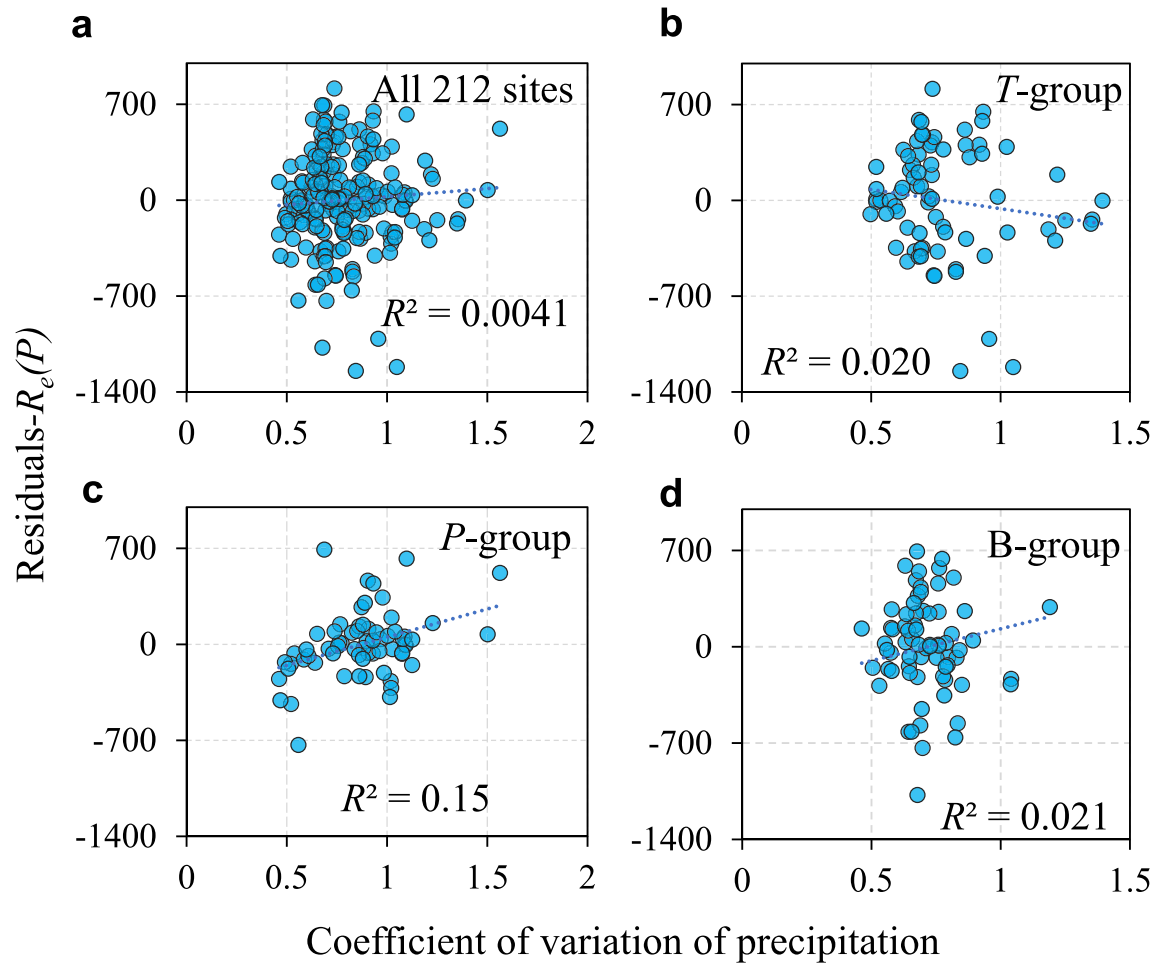
212 sites of FLUXNET2015 were divided into six groups with six  $DI$  intervals: (a)  $0 < DI < 0.4$  (9 sites); (b)  $0.4 < DI < 0.7$  (61 sites); (c)  $0.7 < DI < 1.0$  (58 sites);

(d)  $1.0 < DI < 1.4$  (38 sites); (e)  $1.4 < DI < 2.2$  (23 sites); and (f)  $DI > 2.2$  (23 sites).  $Q_{10}$  was calculated with  $Q_{10}$  model (equation (14)) based on FLUXNET2015 ecosystem respiration  $R_e^{EC}$  data and temperature data (see Methods).



**Extended Data Fig. 5 | The impact of precipitation (P) on ecosystem respiration ( $R_e$ ) across various time scales based on the data of  $R_e$  and P from the same P-group sites. (a) half-hourly; (b) daily; (c) weekly; (d) monthly; and (e) yearly.  $n$  is the number of scatter points.**





**Extended Data Fig. 6 | The asymmetric effect of precipitation (P) on ecosystem respiration ( $R_e$ ).** (a) all sites; (b) T-group; (c) P-group; and (d) B-group. The y-axis represents the residuals of model  $R_e(P)$  (equation(12)). The x-axis is coefficient of variation of monthly precipitation.

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Study description	We disentangle the impacts of temperature and precipitation (a proxy for water availability) on ecosystem respiration by analyzing eddy covariance CO <sub>2</sub> flux measurements across 212 globally distributed sites and reveal a threshold precipitation function separating temperature-limited and water-limited respiration.
Research sample	212 globally distributed eddy covariance sites (over 1500 site-years) used in this study.
Sampling strategy	We used all available data
Data collection	The FLUXNET2015 Dataset includes data collected at sites from multiple regional flux networks. The preparation of this FLUXNET Dataset has been possible thanks only to the efforts of many scientists and technicians around the world and the coordination among teams from regional networks
Timing and spatial scale	The FLUXNET2015 dataset used in this study comes from 212 globally distributed eddy covariance sites (over 1500 site-years). This study used annual ecosystem respiration (Re), annual air temperature, and annual precipitation of all the 212 sites. For different sites, the periods are different but all spanning the period 1992–2014.
Data exclusions	No data were excluded from the analyses.
Reproducibility	repository.
Randomization	Randomization is not relevant as we examined the effect over the entire study domain
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