A temperature threshold to identify the driving climate forces of the respiratory process in terrestrial ecosystems

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Abstract. Terrestrial ecosystem respiration (R_e) is the major source of CO_2 release and constitutes the second largest carbon flux between the biosphere and atmosphere. Therefore, climate-driven changes of R_e may greatly impact on future atmospheric CO_2 concentration. The aim of this study was to derive an air temperature threshold for identifying the driving climate forces of the respiratory process in terrestrial ecosystems within different temperature zones. For this purpose, a global dataset of 647 site-years of ecosystem flux data collected at 152 sites has been examined. Our analysis revealed an ecosystem threshold of mean annual air temperature (MAT) of 11±2.3℃. In ecosystems with the MAT below this threshold, the maximum R_e rates were primarily dependent on temperature and respiration was mainly a temperature-driven process. On the contrary, in ecosystems with the MAT greater than 11±2.3℃, in addition to temperature, other driving forces, such as water availability and surface heat flux, became significant drivers of the maximum R_e rates and respiration was a multi-factor-driven process. The information derived from this study highlight the key role of temperature as main controlling factor of the maximum R_e rates on a large fraction of the terrestrial biosphere, while other driving forces reduce the maximum R_e rates and temperature sensitivity of the respiratory process. These findings are particularly relevant under the current scenario of rapid global warming, given that the potential climate-induced changes in ecosystem respiration may lead to substantial anomalies in the seasonality and magnitude of the terrestrial carbon budget.

1 Introduction

Among the greenhouse gases, carbon dioxide (CO_2) is the one that contributes mostly to the contemporary climate change (IPCC, 2007) and characterized by large global fluxes between the atmosphere, the biosphere, and the anthroposphere. Terrestrial ecosystem respiration (R_e) is the major source of CO_2 release and the second largest carbon flux

between the biosphere and atmosphere (Raich and Potter, 1995). Therefore, climate-induced change in R_e may profoundly impact the global carbon cycle (Yvon-Durocher et al., 2012).

The total ecosystem respiration is composed of heterotrophic respiration and autotrophic respiration, which may response to different driving forces, including biotic and abiotic factors (Falge et al., 2002). However, among the major
5 ecological factors, temperature is prominent to determine the natural distribution of plants and to regulate activities of microbial communities (Lipson et al., 2000). It has been shown that R_e rates increase exponentially with temperature (Enquist et al., 2003; Gillooly et al., 2001). However, the temperature dependence of respiration can be modified by many variables at the ecosystem level (Allen et al., 2005; Luo, 2007; Mahecha et al., 2010). According to the metabolic theory of ecology, the temperature dependence of R_e has been quantified by a constant activation energy ($E = 0.60$ eV) (Brown et al.,
10 2004; Enquist et al., 2003; Gillooly et al., 2001). By contrast, some other authors have shown varied average E values of R_e with ecosystem types and climate zones (Price and Sowers, 2004; Song et al., 2014). Similarly, inconsistent results of temperature sensitivity of R_e quantified by Q_{10}, which is the proportional increase in respiration per 10℃ rise, have been reported in the literature. A constant Q_{10} value of R_e has been utilized in several ecosystem models (Xu and Qi, 2001). Curiel Yuste et al. (2004) found that the Q_{10} values of soil respiration were similar among different vegetation types at short-
15 term time scale. Mahecha et al. (2010) showed that Q_{10} values of R_e were independent of temperature and converged on aconstant value across biomes. On the contrary, Q_{10} values have been shown to change with different ecosystem types or even different vegetation types within an ecosystem (Lavigne et al., 2003; Melillo et al., 2002; Song et al., 2014; Zheng et al., 2009).

Besides temperature, other environmental factors can affect R_e values (Han et al., 2007; Schaefer et al., 2009; Wiseman
20 and Seiler, 2004). Some micrometeorological factors can affect the assimilatory process of plants and therefore the substrate quantitity and quality for respiration (Högberg et al., 2001; Rogers and Humphries, 2000; Sage and Kubien, 2007). In particular water availability (e.g., soil water content and precipitation) is often reported as a key co-acting or controlling factor of R_e in different temperature regimes (Conant et al., 2000; Li et al., 2006). The apparent inconsistency in the literature about these processes are often due to the combined effect of different driving forces on the respiratory process that
25 may ultimately lead to different apparent temperature sensitivities of R_e rates.

The concept of ecological threshold has been widely recognized as an important paradigm to assess the effect of environmental limiting factors on biological processes (Holling, 1973; Larsen and Alp, 2015). As a turning point, the ecological threshold divides the ecosystems into two groups, between which the driving forces of ecological process are different (Andersen et al., 2009; Scheffer and Carpenter, 2003). The ecological threshold is also linked to alternatively
30 stable states in the structure and function of ecosystems. Therefore, the alternatively stable states represent different combinations of ecosystem components (e.g., assemblage of species, productivity) and environmental conditions that may stably persist at certain spatial and temporal scales (Suding et al., 2004).

According to the review of R_e and the concept of ecological threshold, here we hypothesize that there is a temperature threshold that can be utilized to identify the driving climate forces of the respiratory process in terrestrial ecosystems within

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different temperature zones. Therefore, the objectives of this study were to investigate the effects of air temperature and other micrometeorological factors, including greenhouse gases (e.g., atmospheric CO_2 concentration and atmospheric H_2O content), heat flux (e.g., soil heat flux, sensible heat flux, and latent heat flux), and water availability (e.g., precipitation, relative humidity, and soil water content), on R_e at different latitude regions and to quantify the temperature threshold for

5 respiratory process in different terrestrial ecosystems. This study was carried out using a global dataset covering broad environmental gradients.

2 Materials and Methods

2.1 Data

In total, 647 site-years data were collected at 152 eddy flux sites globally. Basic information of the database, including

10 site ID, latitude, longitude, PFT, climate class, year of data collection, and reference of each data set, is listed Table S1 (Supplement). Annual ecosystem respiration rates were estimated from the mean NEE values measured during nighttime. At least five data points for each day and at least 255 measurements in each site were required for the estimation (Mahecha et al., 2010). Mean annual air temperatures (MAT) and other mean annual values of selected micrometeorological factors (i.e., greenhouse gases, heat flux, and water availability), including atmospheric CO_2 concentration (denoted by CO_2),

15 atmospheric H_2O content (H_2O), soil heat flux (G), sensible heat flux (H), latent heat flux (LE), precipitation (P), relative humidity (RH), and soil water content (SWC), over the same periods for CO_2 flux measurements were used as the corresponding data for analysis.

2.2 Data analysis

If temperature is the primary determinant of R_e rates (i.e., temperature-driven pattern), the maximum realizable R_e rate

20 (i.e., the upper bound of R_e rate) should increase with MAT (Kätterer et al., 1998; Rustad et al., 2001). If other micrometeorological factors in addition to temperature control R_e rates, the change of maximum realizable R_e rate with MAT is expected to be different from that of the temperature-driven pattern (Flanagan and Johnson, 2005; Xu et al., 2004). Based on the hypothesis above, the quantile regression was applied to evaluate relationships between R_e rate and MAT, and other micrometeorological factors (i.e., CO_2, H_2O, G, H, LE, P, RH, and SWC). Following the procedure of Cade and Noon

25 (2003), we applied the quantile linear regression at the quantile levels of $\tau \in (0.90, 0.95, 0.99)$ to evaluate relationships of the maximum realizable R_e rates vs. temperature and other micrometeorological factors. For a tested factor, if quantile slopes at all τ levels are significantly different from zero, the maximum realizable R_e rates are significantly correlated to the factor. If the correlation (i.e., positive or negative) trends between the maximum realizable R_e rates and a factor at the three linear quantiles are not consistent, the quantile linear regression should be further tested at more quantiles. Many changes in

30 ecological processes occur with gradual transitions (Sankaran et al., 2005). Thus, we used a bent-cable model as a more

flexible model to describe the gradual changes from one ecological state to another to form a piecewise linear model (Chiu et al., 2006). The model was implemented in the 'quantreg' library in the statistical package R (http://www.r-project.org).

In addition to analyzing patterns of the maximum R_e rates, a regression tree analysis was conducted to determine the effects of temperature and other micrometeorological factors on the mean realizable R_e rates. After tree construction, cross-validation procedures were used to refine the trees to better represent relationships among the variables (De'ath and Fabricius, 2000). The regression tree analysis was implemented in 'rpart' library in the statistical package R. Further details on the methodology are provided in the Supplement.

3 Results

3.1 Relationship between the maximum realizable R_e rate and MAT

Using the quantile piecewise linear regression at $\tau = 0.99$, we evaluated the upper bound of R_e rates (i.e., the maximum realizable R_e rates) changing with MAT. As shown in Fig. 1, a threshold of MAT was identified as $11\pm2.3\,℃$. Within a MAT range below the threshold, the relationship between the maximum realizable R_e rate and MAT was characterized with a linear equation $R_e = 0.19(MAT) + 2.49$. In ecosystems with MAT $>11\pm2.3\,℃$, the relationship between the maximum realizable R_e rates and MAT was characterized with a linear equation $R_e = 0.07(MAT) + 3.81$.

According to the MAT threshold, terrestrial ecosystems across the globe can be divided into two regions (Fig. 2). Basically, terrestrial ecosystems with MAT $\leqslant$ the threshold are within the high-latitude regions and terrestrial ecosystems with MAT $>$ the threshold are within the lower-latitude regions.

3.2 Relationships between the maximum realizable R_e rate and other micrometeorological factors

Based on the temperature threshold, the data was divided into two groups: one for sites with MAT $\leqslant$ the threshold and another for sites with MAT $>$ the threshold. The quantile linear regression at $\tau \in (0.90, 0.95, 0.99)$ was applied to evaluate the relationships between the maximum realizable R_e rates and MAT as well as the micrometeorological factors, or the driving forces for the maximum realizable Re rates. In the ecosystems with MAT $\leqslant 11\pm2.3\,℃$, the maximum realized R_e rates increased with MAT (Fig. 3a), but decreased with H (Fig. 3b). However, the maximum realized R_e rates were not significantly correlated with other micrometeorological factors of CO_2, G, H_2O, LE, P, RH, and SWC (Table 1, Fig. 3c-j).

In sites with MAT $> 11\pm2.3\,℃$ (i.e., the lower-latitude sites), besides temperature, some micrometeorological factors also profoundly affected the maximum realizable R_e rate. As shown in Fig. 4 and Table 2, the maximum realizable R_e rates were positively correlated to MAT, H2O, and SWC, and negatively correlated to H and LE. For the data of maximum realizable R_e rates vs. LE, the quantile slopes at 90*th*, 95*th* and 99*th* percentiles were significantly different from zero (Table 2), but did not show consistently positive or negative relationships. Therefore, further quantile linear regressions at τ levels

of 10*th*– 80*th* were conducted, which confirmed the negative relationship between the maximum realizable R_e rates and LE (Fig. 4f).

Since temperature is a function of sensible heat (Lindau, 2001), the correlation between the maximum realizable R_e rate and H indeed refers to the relationship of R_e rate and temperature.

3.3 Effects of environmental factors on the mean realizable R_e rate

A regression tree analysis of mean R_e rates for a restricted subset of sites showed that MAT was the principal driving force of respiratory process of terrestrial ecosystems (Fig. 5). In sites with MAT < 2.96℃, the mean R_e rates were typically low and other micrometeorological factors rarely regulated the R_e rates. In sites with MAT > 2.96℃, RH became a controlling factor to reduce R_e rates below the MAT-controlled upper bound. At the next level in the tree, LE became a relevant factor in regulating the mean R_e rates. Within a certain RH value, a lower LE resulted in a higher R_e rate. The sequence in Fig. 5 indicated that besides temperature, water availability and heat flux were the key factors to regulate the respiratory process of terrestrial ecosystems.

4 Discussion

4.1 Patterns of R_e response to temperature

Physiological processes of ecosystems are dependent on the enzyme kinetics, which are largely controlled by temperature (Brown et al., 2004). Higher temperatures generally increase biochemical reaction rates, metabolic rates, and rates of other biological activities (Brown et al., 2004). Although R_e rates increased with temperature across all sites in this study, R_e rates in different regimes responded to temperature differently. In the high-latitude region with low temperatures, root respiration of plants and microbial metabolism are primary controlled by temperature (Bond-Lamberty et al., 2004; Lavigne et al., 2003). The decomposition rates of soil organic matter are relatively low in these regions so that substrate is abundant (Davidson and Janssens, 2006). According to Michaelis-Menten kinetics (Michaelis and Menten, 1913), if substrate is abundant and temperature does not exceed the optimum temperature, the reaction rate is determined by temperature (Atkin and Tjoelker, 2003). This state of R_e rates responding to temperature indicates that the maximum realizable R_e rates are primarily controlled by temperature.

In lower-latitude regions with higher temperatures, besides temperature, other micrometeorological factors also affect Re rates (Rustad et al., 2000). In these regions, the decomposition rates of soil organic matter are relatively high (Davidson and Janssens, 2006), which results in low substrate availability. Water availability may also limit the substrate accessibility of microbes. Therefore, besides temperature, substrate quality, availability, and accessibility become relevant for enzyme-catalysed reaction rates (Berry and Raison, 1981; Davidson et al., 2006). This state of R_e rates responding to temperature implies that the respiratory process of terrestrial ecosystem is in a multi-factor-driven pattern.

At the ecosystem level, temperature changes may be associated with changes in the water balance via evapotranspiration and altered precipitation regimes (IPCC, 2007; Swann et al., 2016). Temperature increases enhance evapotranspiration and reduce water availability.On the other hand, the physiological response of plants to warming climate with the stomatal conductance reduction may decrease water losses from the land surface (Swann et al., 2016). These two opposite processes make the respiratory process of ecosystem more complicated in the high temperature regions (Balogh et al., 2015; Kool et al., 2014). The temperature effect on microbial communities may also alter ecosystem carbon and nutrient balances (Högberg et al., 2007; Karhu et al., 2014). Evidence shows that microbial communities and activities are different at the two end members of the temperature range (7-14℃) (Allison and Treseder, 2008; Crowther and Bradford, 2013; Karhu et al., 2014; Nie et al., 2013).

4.2 Relationships between R_e and other micrometeorological factors

Water availability influences autotrophic respiration by controlling plant growth and development (i.e., production of substrate), photosynthesis and carbon allocation patters (i.e., distribution of substrate) (Flanagan and Johnson, 2005). Water availability can also affect heterotrophic respiration through controlling microbial growth and development, and the supply and quality of respiratory substrate provided by plants (Raich and Tufekciogul, 2000). Therefore, many studies have shown that soil moisture can influence soil respiration (Curiel Yuste et al., 2003; Janssens and Pilegaard, 2003; Lavigne et al., 2004; Reichstein et al., 2002). The thin soil water films in a dry condition should obstruct enzyme diffusion and reduce substrate availability, while oxygen deficit in saturated soils creates anaerobic conditions. There is an optimal soil water content for respiration (Davidson and Janssens, 2006). Generally, within a certain range of soil moisture content, soil respiration increases with water content (Flanagan and Johnson, 2005; Reichstein et al., 2003). In semi-arid and arid regions, soil moisture is the second most important abiotic variable for soil respiration (Qi and Xu, 2001). Even in Mediterranean ecosystems, water availability is the main environmental constraint for plant growth and reproduction (Pausas, 1999) and may become an even more limiting resource under the increasing aridity predicted for this region by most climate models (Kéfi et al., 2007).

The effect of precipitation on soil respiration extends beyond its direct effect via soil moisture (Reichstein et al., 2003). Because of highly spatial and temporal variability of rainfall (Bowling et al., 2002; Curiel Yuste et al., 2003; Huxman et al., 2004; Xu et al., 2004), we did not observe any relationship between the maximum realizable R_e rate and precipitation.

Sensible and latent heat fluxes (H and LE) are non-radiative pathways for energy transfer from the Earth surface to the atmosphere. Both H and LE are important components of the Earth's surface energy budget (Rebmann et al., 2012). More available energy of ecosystem partitioning to H leads to high vapour pressure deficit, which is a major impact factor on the rate of net photosynthesis (Lambers et al., 1998). It has been shown that the vapour pressure deficit negatively affects R_e rates (Ekblad et al., 2005; Seneweera et al., 1998). Thus R_e rates are negatively correlated to H. The evapotranspiration is a function of LE (Gentine et al., 2007), and increased evapotranspiration will reduce water availability of ecosystems. Therefore, the R_e rates are negatively correlated with LE.

As one of greenhouse gases (Rodhe, 1990), atmospheric H_2O content (water vapour) increase may accelerate respiratory process of terrestrial ecosystem (Wang et al., 2016). In addition, elevated H_2O reduces the vapour pressure deficit, resulting in higher R_e rates(Ekblad et al., 2005; Seneweera et al., 1998). Therefore, R_e rates are positively correlated to H_2O.

5 **4.3 Temperature sensitivities under different temperature zones**

Temperature is the primary factor in regulating respiratory process of terrestrial ecosystem. Since the regression tree in Fig. 4 split data based on variance of the predictor variables, different temperature thresholds were obtained in the terminal nodes. Several authors pointed out that Q_{10} values of R_e rates decrease with temperature (Atkin and Tjoelker, 2003; Hamdi et al., 2013; Schipper et al., 2014). Similarly, as indicated in Fig. 1, the temperature dependence of R_e at low temperatures
10 (or in high-latitude regions) is stronger than that at high temperatures (or in lower-latitude regions). In other words, the temperature sensitivity of R_e at low temperatures is higher than that at high temperatures. Biochemical reactions require appropriate activation energies under different initial ambient temperatures, according to the Arrhenius equation (Blankenship, 2013; Laidler, 1996). More activation energy is required to complete the reaction at a lower temperature (Cai et al., 2014). R_e in response to a temperature change may be interpreted as respiration acclimation to temperature (Atkin and
15 Tjoelker, 2003). Temperature acclimation indicates that with increasing global temperature, plants and microorganisms may generate reversible changes in a way that can optimize their functioning under warmer environment, a process also described as temperature adaptation (Saxe et al., 2001). Such adaptation mechanism may result in compensation of ecological processes (e.g., R_e) in response to a change in temperature and subsequently reduce the temperature sensitivity of ecological processes (Luo et al., 2001; Tjoelker et al., 2008). Using field measurement data, Reich et al. (2016) demonstrated strong
20 acclimation of plant respiration to seasonal temperature increase. The acclimation mechanism reduces plant respiration rate greatly and decreases Q_{10} values (Reich et al., 2016).

5 Conclusions

The results from this global scale analysis indicate that temperature is the main driving force of the maximum realizable R_e rates in almost all terrestrial ecosystems, while other micrometeorological factors (e.g., water availability and heat flux)
25 reduce the maximum realizable R_e rates in higher temperature regions. A temperature threshold was derived to identify the driving forces of the respiratory process in terrestrial ecosystems under different climate regions. These findings highlight the key importance of climate drivers on the terrestrial carbon balance and may have important implications for the benchmarking and refinement of biogeochemical land models (Flanagan and Johnson, 2005; Frank et al., 2010; Reynolds et al., 2015). Better understanding of the driving forces of ecosystem respiration should enhance the capacity to accurately
30 estimate ecosystem carbon fluxes and predict future climate trajectories.

6 Data availability

The measured CO_2 fluxes and meteorological data are obtained from the La Thuile Dataset, which are freely available at the FLUXNET community (http://fluxnet.fluxdata.org/data/la-thuile-dataset/). The mean annual temperature data are gathered from the MODIS subset product, and they are freely available at the MODIS subset website
5 (https://gmao.gsfc.nasa.gov/reanalysis/MERRA/).

Author Contributions

This study was conceived and designed by Z.Z., R.Z. Calculations and analysis was performed by Y.Z. The data were collected by J.Z. Z.Z., R.Z., A.C., G.W. and V.M. wrote the paper, with contributions and comments from all other authors.

References

25 Allen, A. P., Gillooly, J. F., and Brown, J. H.: Linking the global carbon cycle to individual metabolism, Funct. Ecol., 19, 202-213, 2005.

Allison, S. D. and Treseder, K. K.: Warming and drying suppress microbial activity and carbon cycling in boreal forest soils,

Global Change Biol., 14, 2898-2909, 2008.

Andersen, T., Carstensen, J., Hernández-García, E., and Duarte, C. M.: Ecological thresholds and regime shifts: approaches to identification, Trends Ecol. Evol., 24, 49-57, 2009.

Atkin, O. K. and Tjoelker, M. G.: Thermal acclimation and the dynamic response of plant respiration to temperature, Trends in Plant Science, 8, 343-351, 2003.

Balogh, J., Fóti, S., Pintér, K., Burri, S., Eugster, W., Papp, M., and Nagy, Z.: Soil CO_2 efflux and production rates as influenced by evapotranspiration in a dry grassland, Plant Soil, 388, 157-173, 2015.

Berry, J. A. and Raison, J. K.: Responses of Macrophytes to Temperature. In: Physiological Plant Ecology I: Responses to the Physical Environment, Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H. (Eds.), Springer Berlin Heidelberg, Berlin, Heidelberg, 277-338 pp., 1981.

Blankenship, R. E.: Molecular mechanisms of photosynthesis, John Wiley & Sons, 2013.

Bond-Lamberty, B., Wang, C., and Gower, S. T.: Contribution of root respiration to soil surface CO_2 flux in a boreal black spruce chronosequence, Tree Physiol., 24, 1387-1395, 2004.

Bowling, D. R., McDowell, N. G., Bond, B. J., Law, B. E., and Ehleringer, J. R.: [13]C content of ecosystem respiration is linked to precipitation and vapor pressure deficit, Oecologia, 131, 113-124, 2002.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B.: Toward a metabolic theory of ecology, Ecology, 85, 1771-1789, 2004.

Cade, B. S. and Noon, B. R.: A gentle introduction to quantile regression for ecologists, Front. Ecol. Environ., 1, 412-420, 2003.

Cai, J., Wu, W., and Liu, R.: An overview of distributed activation energy model and its application in the pyrolysis of lignocellulosic biomass, Renew. Sust. Energ. Rev., 36, 236-246, 2014.

Chiu, G., Lockhart, R., and Routledge, R.: Bent-Cable regression theory and applications, J. Am. Stat. Assoc., 101, 542-553, 2006.

Conant, R. T., Klopatek, J. M., and Klopatek, C. C.: Environmental factors controlling soil respiration in three semiarid ecosystems, Soil Sci. Soc. Am. J., 64, 383-390, 2000.

Crowther, T. W. and Bradford, M. A.: Thermal acclimation in widespread heterotrophic soil microbes, Ecol. Lett., 16, 469-477, 2013.

Curiel Yuste, J., Janssens, I. A., Carrara, A., and Ceulemans, R.: Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity, Global Change Biol., 10, 161-169, 2004.

Curiel Yuste, J., Janssens, I. A., Carrara, A., Meiresonne, L., and Ceulemans, R.: Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest, Tree Physiol., 23, 1263-1270, 2003.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165-173, 2006.

Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}, Global Change Biol., 12, 154-164, 2006.

De'ath, G. and Fabricius, K. E.: Classification and regression tree: A powerful yet simple technique for ecological data analysis, Ecology, 81, 3178-3192, 2000.

Ekblad, A., Boström, B., Holm, A., and Comstedt, D.: Forest soil respiration rate and $\delta^{13}C$ is regulated by recent above ground weather conditions, Oecologia, 143, 136-142, 2005.

Enquist, B. J., Economo, E. P., Huxman, T. E., Allen, A. P., Ignace, D. D., and Gillooly, J. F.: Scaling metabolism from organisms to ecosystems, Nature, 423, 639-642, 2003.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K. J., Elbers, J. A., Goldstein, A. H., Grelle, A., Granier, A., Guðmundsson, J., Hollinger, D., Kowalski, A. S., Katul, G., Law, B. E., Malhi, Y., Meyers, T., Monson, R. K., Munger, J. W., Oechel, W., Paw U, K. T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., and Wofsy, S.: Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements, Agr. Forest Meteorol., 113, 53-74, 2002.

Flanagan, L. B. and Johnson, B. G.: Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland, Agr. Forest Meteorol., 130, 237-253, 2005.

Frank, D. C., Esper, J., Raible, C. C., Buntgen, U., Trouet, V., Stocker, B., and Joos, F.: Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate, Nature, 463, 527-530, 2010.

Gentine, P., Entekhabi, D., Chehbouni, A., Boulet, G., and Duchemin, B.: Analysis of evaporative fraction diurnal behaviour, Agr. Forest Meteorol., 143, 13-29, 2007.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L.: Effects of size and temperature on metabolic rate, Science, 293, 2248-2251, 2001.

Hamdi, S., Moyano, F., Sall, S., Bernoux, M., and Chevallier, T.: Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions, Soil Biol. Biochem., 58, 115-126, 2013.

Han, G., Zhou, G., Xu, Z., Yang, Y., Liu, J., and Shi, K.: Biotic and abiotic factors controlling the spatial and temporal variation of soil respiration in an agricultural ecosystem, Soil Biol. Biochem., 39, 418-425, 2007.

Högberg, M. N., Högberg, P., and Myrold, D. D.: Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three?, Oecologia, 150, 590-601, 2007.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Lofvenius, M., and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789-792, 2001.

Holling, C. S.: Resilience and stability of ecological systems, Annu. Rev. Ecol. Evol. S., 4, 1-23, 1973.

Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D. R., Potts, D. L., and Schwinning, S.: Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, Oecologia, 141, 254-268, 2004.

IPCC: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Climate Change 2007: The Physical Science Basis, Cambridge University Press, Cambridge, UK and New York, NY., 2007.

Janssens, I. A. and Pilegaard, K. I. M.: Large seasonal changes in Q_{10} of soil respiration in a beech forest, Global Change Biol., 9, 911-918, 2003.

Karhu, K., Auffret, M. D., Dungait, J. A. J., Hopkins, D. W., Prosser, J. I., Singh, B. K., Subke, J.-A., Wookey, P. A., Agren, G. I., Sebastia, M.-T., Gouriveau, F., Bergkvist, G., Meir, P., Nottingham, A. T., Salinas, N., and Hartley, I. P.: Temperature sensitivity of soil respiration rates enhanced by microbial community response, Nature, 513, 81-84, 2014.

Kätterer, T., Reichstein, M., Andrén, O., and Lomander, A.: Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models, Biol. Fert. Soils, 27, 258-262, 1998.

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., and de Ruiter, P. C.: Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems, Nature, 449, 213-217, 2007.

Kool, D., Agam, N., Lazarovitch, N., Heitman, J. L., Sauer, T. J., and Ben-Gal, A.: A review of approaches for evapotranspiration partitioning, Agr. Forest Meteorol., 184, 56-70, 2014.

Laidler, K. J.: A glossary of terms used in chemical kinetics, including reaction dynamics (IUPAC Recommendations 1996), Pure Appl. Chem., 68, 149-192, 1996.

Lambers, H., Chapin, F. S., and Pons, T. L.: Photosynthesis, Respiration, and Long-Distance Transport. In: Plant Physiological Ecology, Lambers, H., Chapin, F. S., and Pons, T. L. (Eds.), Springer New York, New York, NY, 10-153 pp., 1998.

Larsen, S. and Alp, M.: Ecological thresholds and riparian wetlands: an overview for environmental managers, Limnology,

16, 1-9, 2015.

Lavigne, M. B., Boutin, R., Foster, R. J., Goodine, G., Bernier, P. Y., and Robitaille, G.: Soil respiration responses to temperature are controlled more by roots than by decomposition in balsam fir ecosystems, Can. J. Forest Res., 33, 1744-1753, 2003.

5 Lavigne, M. B., Foster, R. J., and Goodine, G.: Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching, Tree Physiol., 24, 415-424, 2004.

Li, Y., Xu, M., and Zou, X.: Heterotrophic soil respiration in relation to environmental factors and microbial biomass in two wet tropical forests, Plant Soil, 281, 193-201, 2006.

Lindau, R.: Sensible Heat Flux. In: Climate Atlas of the Atlantic Ocean: Derived from the Comprehensive Ocean
10   Atmosphere Data Set (COADS), Lindau, R. (Ed.), Springer Berlin Heidelberg, Berlin, Heidelberg, 383-397 pp., 2001.

Lipson, D. A., Schmidt, S. K., and Monson, R. K.: Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass, Soil Biol. Biochem., 32, 441-448, 2000.

Luo, Y., Wan, S., Hui, D., and Wallace, L. L.: Acclimatization of soil respiration to warming in a tall grass prairie, Nature,
15   413, 622-625, 2001.

Luo, Y.: Terrestrial carbon-cycle feedback to climate warming, Annu. Rev. Ecol. Evol. S., 38, 683-712, 2007.

Mahecha, M. D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S. I., Vargas, R., Ammann, C., Arain, M. A., Cescatti, A., Janssens, I. A., Migliavacca, M., Montagnani, L., and Richardson, A. D.: Global convergence in the temperature sensitivity of respiration at ecosystem level, Science, 329, 838-840, 2010.

20 Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S.: Soil warming and carbon-cycle feedbacks to the climate system, Science, 298, 2173, 2002.

Michaelis, L. and Menten, M. L.: Die kinetik der invertin wirkung, Biochem. Z., 49, 334-336, 1913.

Nie, M., Pendall, E., Bell, C., Gasch, C. K., Raut, S., Tamang, S., and Wallenstein, M. D.: Positive climate feedbacks of soil microbial communities in a semi-arid grassland, Ecol. Lett., 16, 234-241, 2013.

25 Pausas, J. G.: Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach, J. Veg. Sci., 10, 717-722, 1999.

Price, P. B. and Sowers, T.: Temperature dependence of metabolic rates for microbial growth, maintenance, and survival, P. Natl. Acad. Sci. USA, 101, 4631-4636, 2004.

Qi, Y. and Xu, M.: Separating the effects of moisture and temperature on soil CO_2 efflux in a coniferous forest in the Sierra

Nevada mountains, Plant Soil, 237, 15-23, 2001.

Raich, J. W. and Potter, C. S.: Global patterns of carbon dioxide emissions from soils, Global Biogeochem. Cy., 9, 23-36, 1995.

Raich, J. W. and Tufekciogul, A.: Vegetation and soil respiration: Correlations and controls, Biogeochemistry, 48, 71-90, 2000.

Rebmann, C., Kolle, O., Heinesch, B., Queck, R., Ibrom, A., and Aubinet, M.: Data acquisition and flux calculations. In: Eddy Covariance: A practical guide to measurement and data analysis, Aubinet, M., Vesala, T., and Papale, D. (Eds.), Springer Science & Business Media, 79-80 pp., 2012.

Reich, P. B., Sendall, K. M., Stefanski, A., Wei, X., Rich, R. L., and Montgomery, R. A.: Boreal and temperate trees show strong acclimation of respiration to warming, Nature, 531, 633-636, 2016.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J.-M., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biogeochem. Cy., 17, 1104, 2003.

Reichstein, M., Tenhunen, J. D., Roupsard, O., Ourcival, J.-M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., and Valentini, R.: Severe drought effects on ecosystem CO_2 and H2O fluxes at three Mediterranean evergreen sites: revision of current hypotheses?, Global Change Biol., 8, 999-1017, 2002.

Reynolds, L. L., Johnson, B. R., Pfeifer-Meister, L., and Bridgham, S. D.: Soil respiration response to climate change in Pacific Northwest prairies is mediated by a regional Mediterranean climate gradient, Global Change Biol., 21, 487-500, 2015.

Rodhe, H.: A comparison of the contribution of various gases to the greenhouse effect, Science, 248, 1217, 1990.

Rogers, A. and Humphries, S. W.: A mechanistic evaluation of photosynthetic acclimation at elevated CO_2, Global Change Biol., 6, 1005-1011, 2000.

Rustad, L. E., Huntington, T. G., and Boone, R. D.: Controls on soil respiration: Implications for climate change, Biogeochemistry, 48, 1-6, 2000.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., and Gcte, N.: A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming, Oecologia, 126, 543-562, 2001.

Sage, R. F. and Kubien, D. S.: The temperature response of C_3 and C_4 photosynthesis, Plant Cell Environ., 30, 1086-1106,

2007.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., February, E. C., Frost, P. G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H. T., Ringrose, S., Sea, W., Tews, J., Worden, J., and Zambatis, N.: Determinants of woody cover in African savannas, Nature, 438, 846-849, 2005.

Saxe, H., Cannell, M. G. R., Johnsen, Ø., Ryan, M. G., and Vourlitis, G.: Tree and forest functioning in response to global warming, New Phytol., 149, 369-399, 2001.

Schaefer, D. A., Feng, W., and Zou, X.: Plant carbon inputs and environmental factors strongly affect soil respiration in a subtropical forest of southwestern China, Soil Biol. Biochem., 41, 1000-1007, 2009.

Scheffer, M. and Carpenter, S. R.: Catastrophic regime shifts in ecosystems: linking theory to observation, Trends Ecol. Evol., 18, 648-656, 2003.

Schipper, L. A., Hobbs, J. K., Rutledge, S., and Arcus, V. L.: Thermodynamic theory explains the temperature optima of soil microbial processes and high Q_{10} values at low temperatures, Global Change Biol., 20, 3578-3586, 2014.

Seneweera, S. P., Ghannoum, O., and Conroy, J.: High vapour pressure deficit and low soil water availability enhance shoot growth responses of a C_4 grass (Panicum coloratum cv. Bambatsi) to CO_2 enrichment, Funct. Plant Biol., 25, 287-292, 1998.

Song, B., Niu, S., Luo, R., Luo, Y., Chen, J., Yu, G., Olejnik, J., Wohlfahrt, G., Kiely, G., Noormets, A., Montagnani, L., Cescatti, A., Magliulo, V., Law, B. E., Lund, M., Varlagin, A., Raschi, A., Peichl, M., Nilsson, M. B., and Merbold, L.: Divergent apparent temperature sensitivity of terrestrial ecosystem respiration, J. Plant Ecol-UK., 7, 419-428, 2014.

Suding, K. N., Gross, K. L., and Houseman, G. R.: Alternative states and positive feedbacks in restoration ecology, Trends Ecol. Evol., 19, 46-53, 2004.

Swann, A. L. S., Hoffman, F. M., Koven, C. D., and Randerson, J. T.: Plant responses to increasing CO_2 reduce estimates of climate impacts on drought severity, P. Natl. Acad. Sci. USA, 113, 10019-10024, 2016.

Tjoelker, M. G., Oleksyn, J., Reich, P. B., and Żytkowiak, R.: Coupling of respiration, nitrogen, and sugars underlies convergent temperature acclimation in Pinus banksiana across wide-ranging sites and populations, Global Change Biol., 14, 782-797, 2008.

Wang, W., Smith, J. A., Ramamurthy, P., Baeck, M. L., Bou-Zeid, E., and Scanlon, T. M.: On the correlation of water vapor and CO_2: Application to flux partitioning of evapotranspiration, Water Resour. Res., 52, 9452-9469, 2016.

Wiseman, P. E. and Seiler, J. R.: Soil CO_2 efflux across four age classes of plantation loblolly pine (Pinus taeda L.) on the Virginia Piedmont, Forest Ecol. Manag., 192, 297-311, 2004.

Xu, L., and D. D. Baldocchi (2004), Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California, Agr. Forest Meteorol., 123(1–2), 79-96.
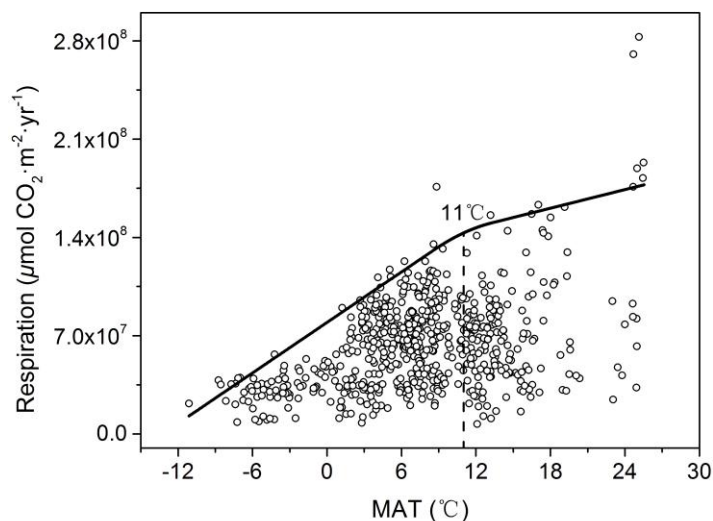
5 Xu, L., Baldocchi, D. D., and Tang, J.: How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature, Global Biogeochem. Cy., 18, GB4002, 2004.

Xu, M. and Qi, Y.: Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California, Global Change Biol., 7, 667-677, 2001.

Yvon-Durocher, G., Caffrey, J. M., Cescatti, A., Dossena, M., Giorgio, P. d., Gasol, J. M., Montoya, J. M., Pumpanen, J.,
10 Staehr, P. A., Trimmer, M., Woodward, G., and Allen, A. P.: Reconciling the temperature dependence of respiration across timescales and ecosystem types, Nature, 487, 472-476, 2012.

Zheng, Z., Yu, G., Fu, Y., Wang, Y., Sun, X., and Wang, Y.: Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: A trans-China based case study, Soil Biol. Biochem., 41, 1531-1540, 2009.

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Figure 1: Analysis of the terrestrial ecosystem respiration (R_e) rate as a function of mean annual air temperature (MAT) using data of 647 site-years across the globe. The maximum realizable R_e rates (i.e., the upper bound of R_e) are represented using the 99*th* quantile
20 piecewise linear regression. The regression analysis identifies a turning point (i.e., the threshold) at the MAT of 11±2.3℃. An equation for the line quantifying the maximum realizable R_e rates in ecosystems with MAT ≤ the threshold is $R_e = 0.19(\text{MAT}) + 2.49$. An equation for the line quantifying the maximum realizable R_e rates in ecosystems with MAT > the threshold is $R_e = 0.07(\text{MAT}) + 3.81$.
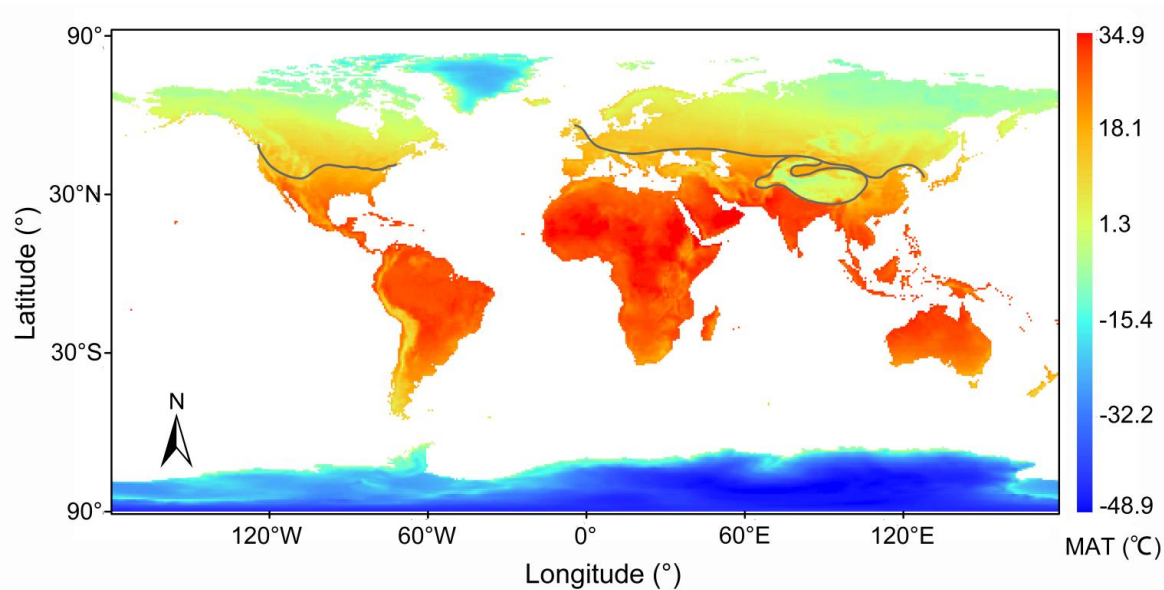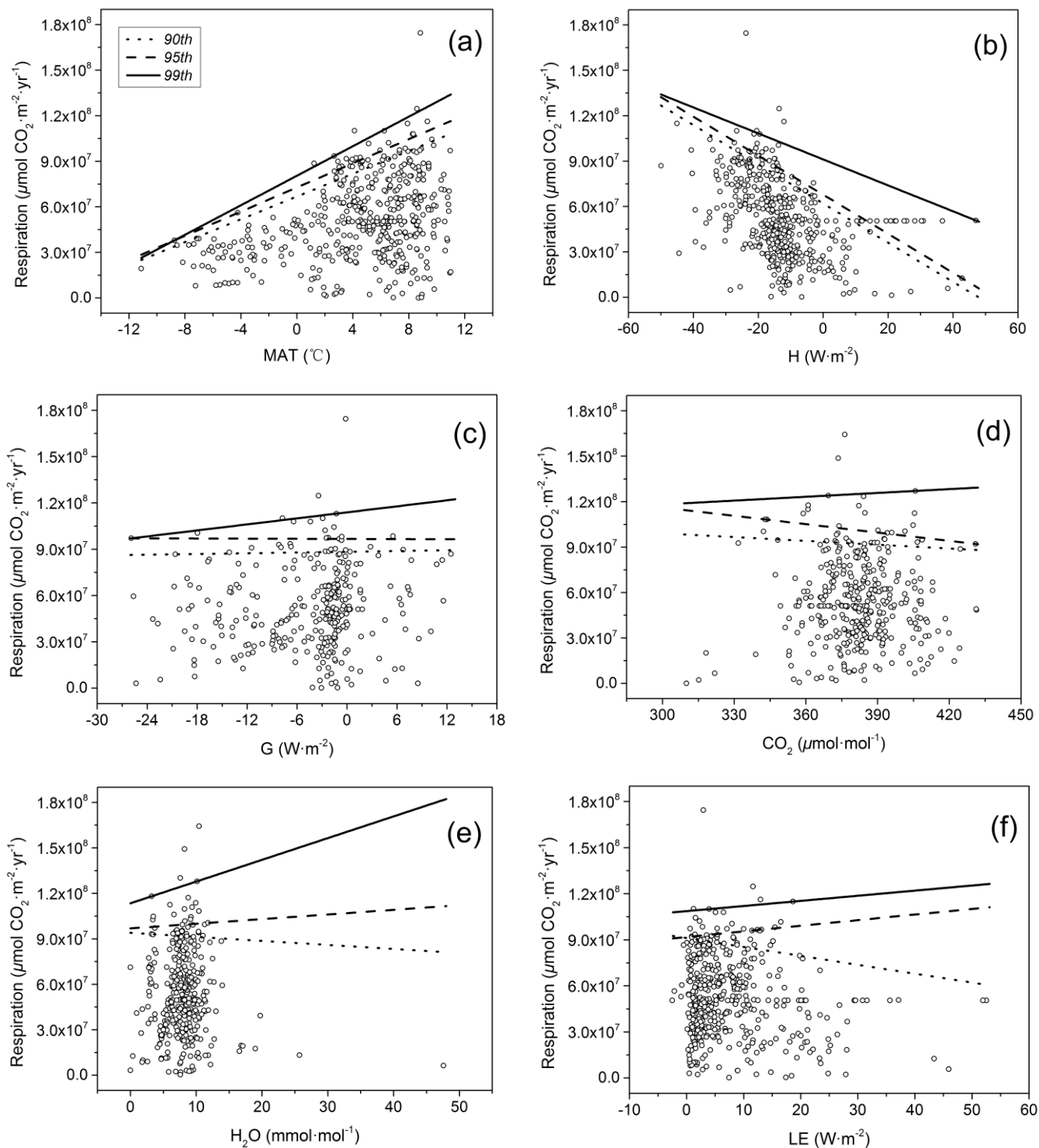
Figure 2: Distributions of patters of terrestrial ecosystem respiration (R_e)rate responses to temperature across the globe. The grey line denotes boundary of the patterns, and the data of MAT were from MERRA (Modern Era Retrospective-Analysis for Research and Application) with 5-year (from 2009-2013) mean values (https://gmao.gsfc.nasa.gov/reanalysis/MERRA/).
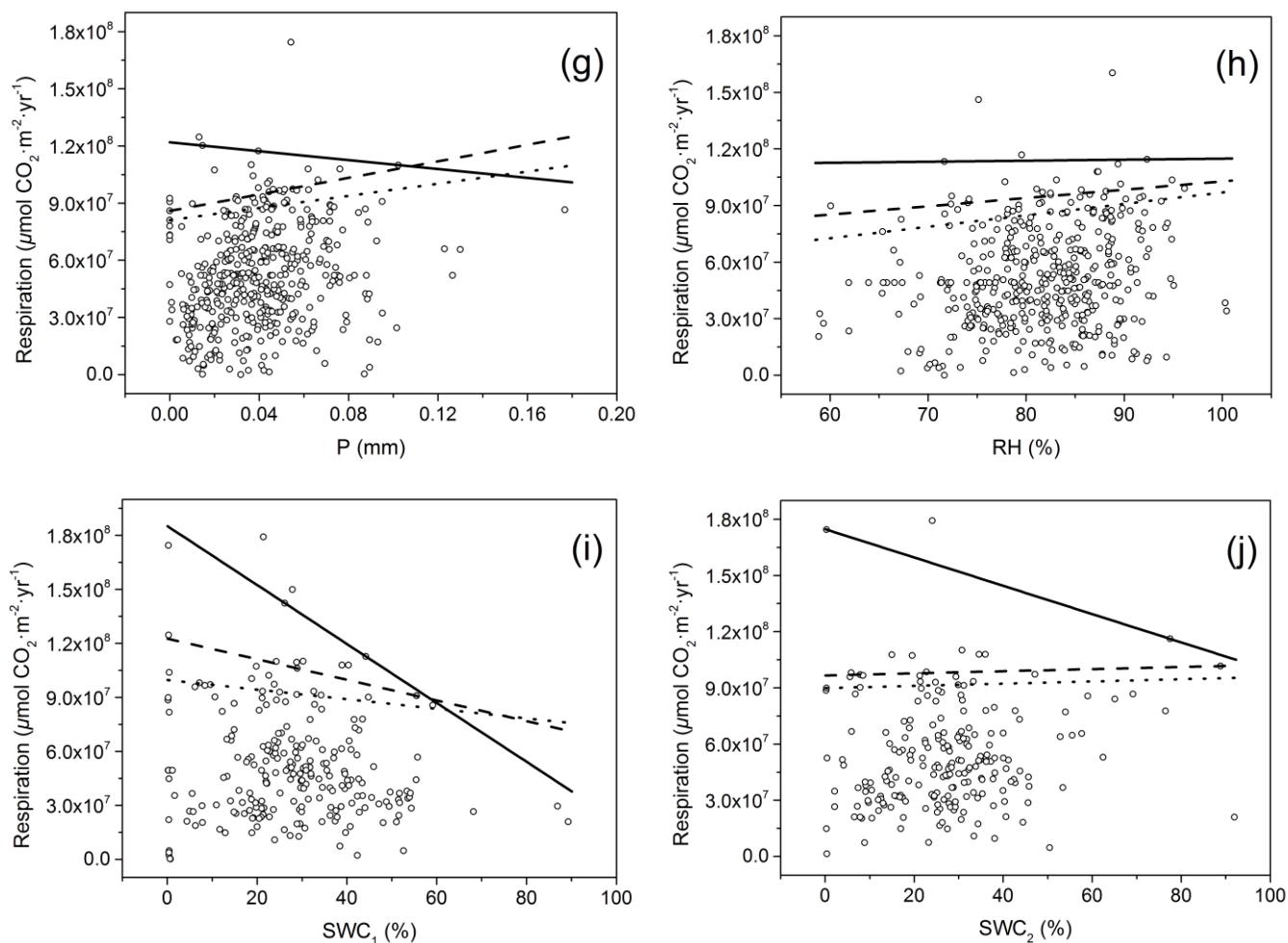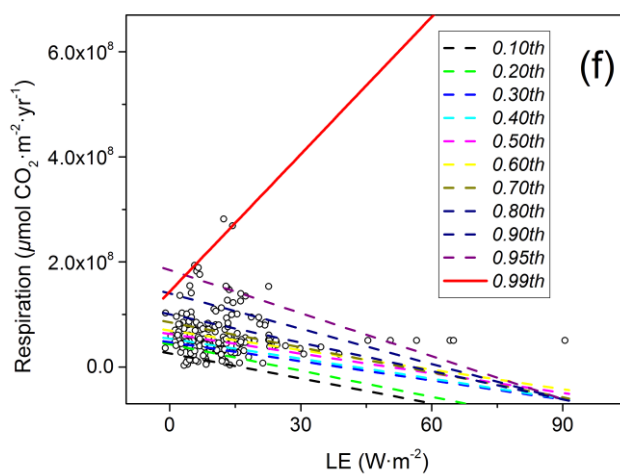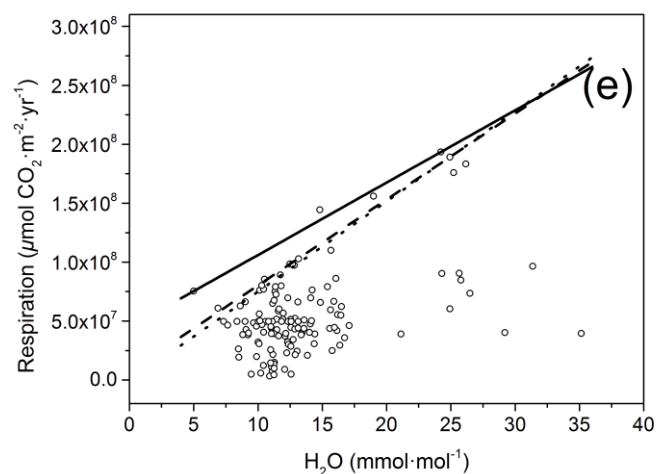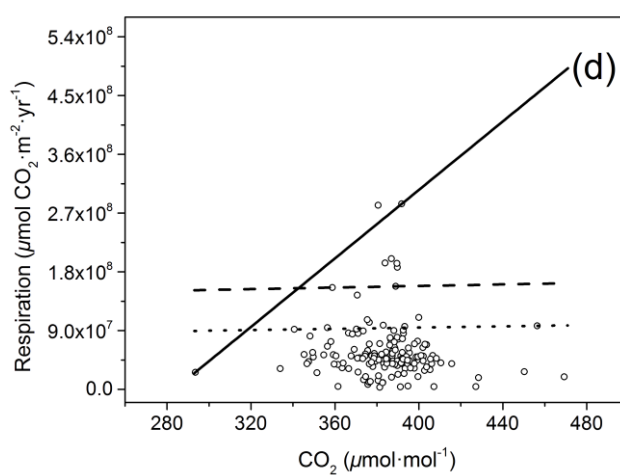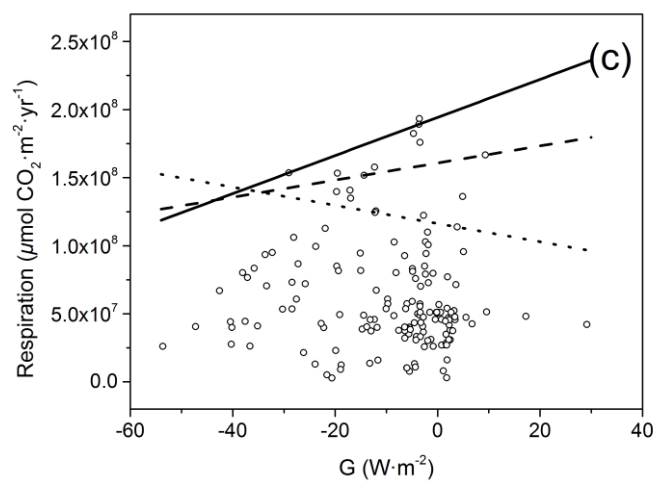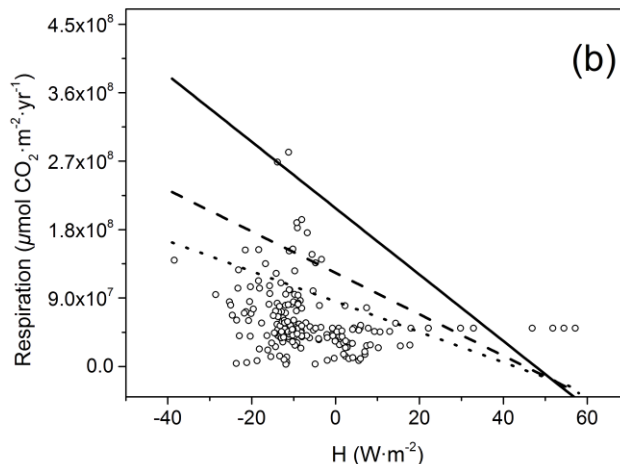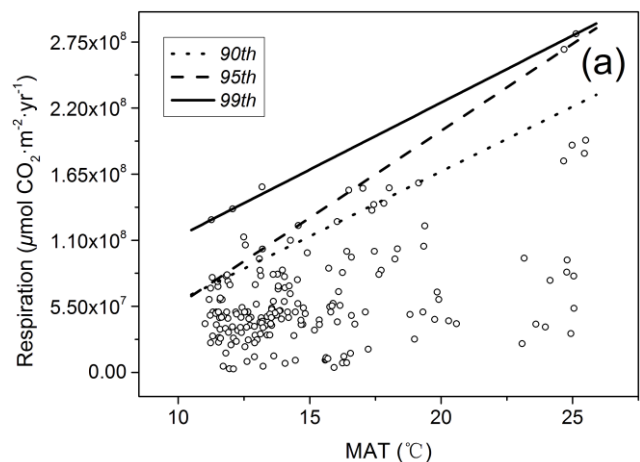
Figure 3: Terrestrial ecosystem respiration (R_e) rates in the terrestrial ecosystems with mean annual air temperature (MAT) $\leq 11\pm2.3\,^{\circ}C$ (i.e., in the high-latitude regions) as a function of some micrometeorological factors. Relationships between R_e rates and **(a)** MAT (n = 456), **(b)** sensible heat flux (H) (n = 451), **(c)** soil heat flux (G) (n = 311), **(d)** atmospheric CO_2 concentration (CO_2) (n = 374), **(e)** atmospheric H_2O concentration (H_2O) (n = 359), **(f)** latent heat flux (LE) (n = 449), **(g)** precipitation (P) (n = 432), **(h)** relative humidity (RH) (n = 435), **(i)** upper layer soil water content (SWC_1) (n = 234), and **(j)** lower layer soil water content (SWC_2) (n = 214). Solid, dash, and dot lines represent the 99*th*, 95*th*, and 90*th* linear quantiles, respectively.

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Figure 4: Terrestrial ecosystem respiration (R_e) rates in the terrestrial ecosystems with mean annual air temperature (MAT) > 11±2.3 ℃ (i.e., in lower-latitude regions) as a function of some micrometeorological factors. Relationships between R_e rates and **(a)** MAT (n = 191), **(b)** sensible heat flux (H) (n = 190), **(c)** soil heat flux (G) (n = 159), **(d)** atmospheric CO_2 concentration (CO_2) (n = 156), **(e)** atmospheric H_2O concentration (H_2O) (n = 131), **(f)** latent heat flux (LE) (n = 188), **(g)** precipitation (P) (n = 176), **(h)** relative humidity (RH) (n = 177), **(i)** upper layer soil water content (SWC_1) (n = 115), and **(j)** lower layer soil water content (SWC_2) (n = 91). Solid, dash, and dot lines represent the 99*th*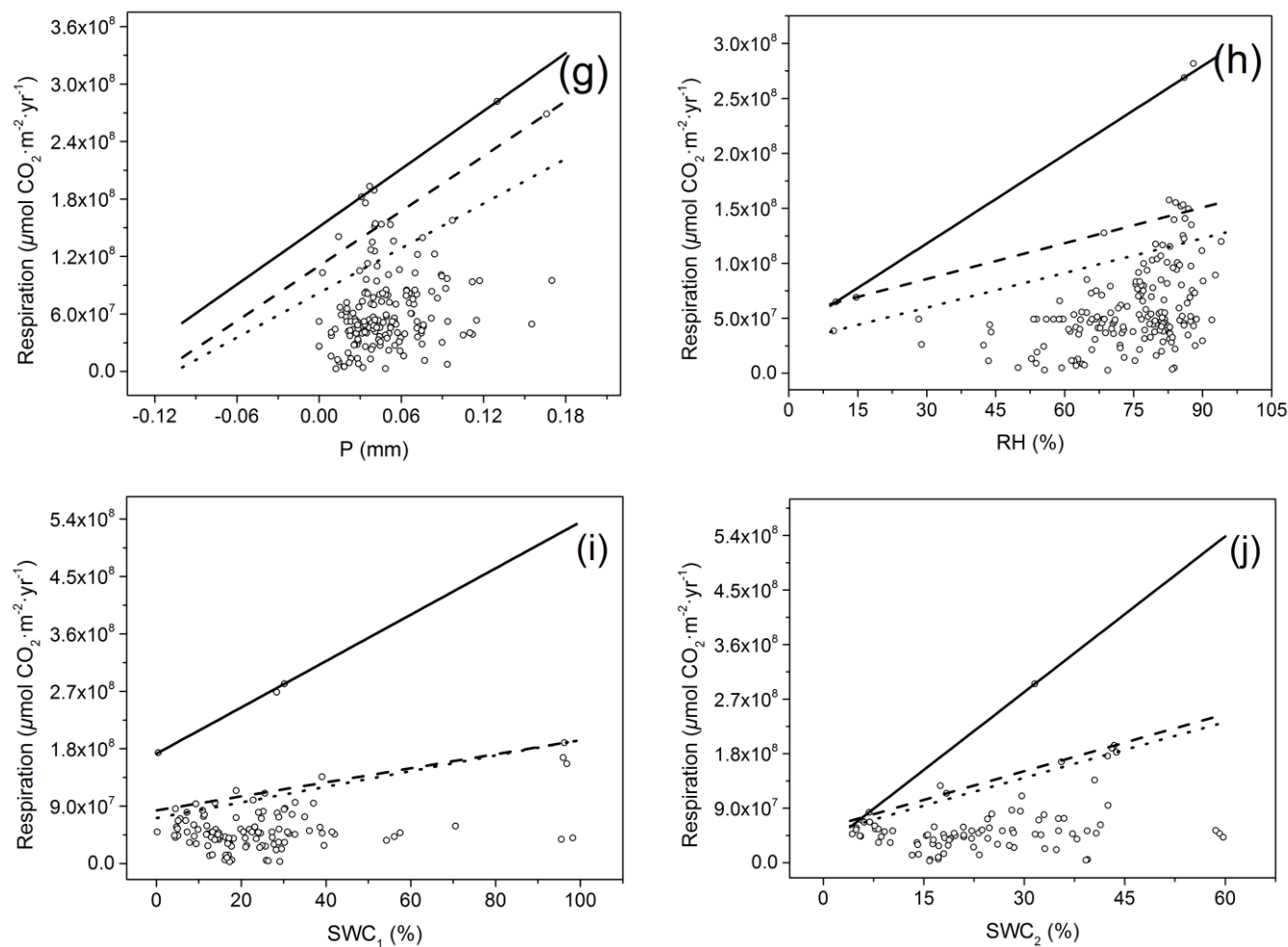, 95*th* and 90*th* linear quantiles, respectively. In Fig. 4f, since the trends from the 99*th*, 95*th* and 90*th* linear quantiles were not consistent, the quantile linear regression at τ levels of 10th – 80th was conducted to confirm the negative relationship between the maximum realizable R_e rates and LE.
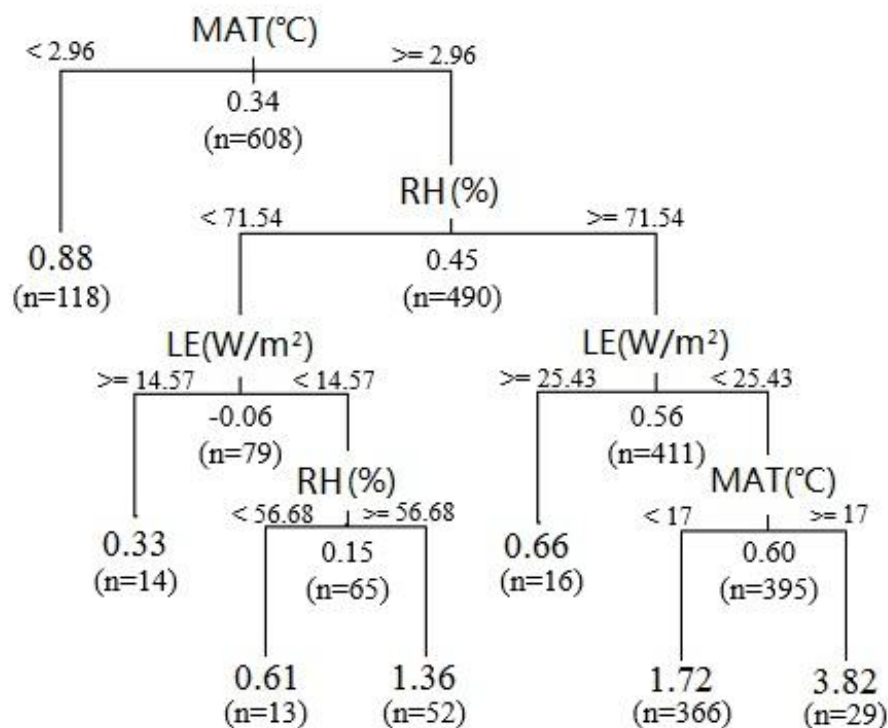
Figure 5: Regression tree showing generalized relationships between the mean R_e rates and the micrometeorological factors. The tree is divided into seven terminal nodes. Branches are labeled with criteria used to segregate data. Values in terminal nodes represent mean R_e rates of sites grouped within the cluster.

Table 1: *P* values of the null hypothesis test for quantile regression slopes in 90*th*, 95*th*, and 99*th* quantiles on mean annual air temperatures (MAT) of terrestrial ecosystems below $11 \pm 2.3\,℃$.

Quantile	MAT	CO_2	G	H	H_2O	LE	P	RH	SWC_1	SWC_2
90th	<0.0001	0.49	0.80	<0.0001	0.64	0.003	0.06	0.05	0.18	0.80
95th	<0.0001	0.25	0.98	<0.0001	0.73	0.03	<0.0001	0.22	0.15	0.73
99th	<0.0001	0.67	<0.0001	0.002	0.22	0.54	0.66	0.93	0.01	0.64

MAT is mean annual air temperature. Micrometeorological factors include CO_2: atmospheric CO_2 concentration, G: soil heat flux, H: sensible heat flux, H_2O: atmospheric H_2O content, LE: latent heat flux, P: precipitation, RH: relative humidity, SWC_1: upper layer soil water content, and SWC_2: lower layer soil water content. *P* < 0.05 indicates that quantile slope is significantly different from zero.

Table 2: *P* values of the null hypothesis test for quantile regression slopes in 90*th*, 95*th*, and 99*th* quantiles on mean annual air temperatures (MAT) of terrestrial ecosystems above $11 \pm 2.3\,℃$.

Quantile	MAT	CO_2	G	H	H_2O	LE	P	RH	SWC_1	SWC_2
90th	<0.0001	0.86	0.51	<0.0001	<0.0001	<0.0001	0.17	0.06	0.01	<0.0001
95th	<0.0001	0.98	0.56	0.03	0.03	0.02	0.04	0.07	0.01	<0.0001
99th	<0.0001	0.002	<0.0001	0.03	0.03	<0.0001	0.003	0.09	<0.0001	<0.0001