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

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Abstract. Terrestrial ecosystem respiration (Re) is the major source of CO₂ release and constitutes the second largest carbon flux between the biosphere and atmosphere. Therefore, climate-driven changes of Re may greatly impact on future atmospheric CO₂ 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 °C. In ecosystems with the MAT below this threshold, the maximum Re 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 °C, in addition to temperature, other driving forces, such as water availability and surface heat flux, became significant drivers of the maximum Re rates and respiration was a multifactor-driven process. The information derived from this study highlight the key role of temperature as main controlling factor of the maximum Re rates on a large fraction of the terrestrial biosphere, while other driving forces reduce the maximum Re 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 (CO₂) 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 (Re) is the major source of CO₂ 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 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., 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°C 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-term time scale. Mahecha et al. (2010) showed that $Q_{10}$ values of $R_e$ were independent of temperature and converged on a constant 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 and Seiler, 2004). Some micrometeorological factors can affect the assimilatory process of plants and therefore the substrate quantity 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 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 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
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 CO₂ concentration and atmospheric H₂O 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 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 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 CO₂ concentration (denoted by CO₂), atmospheric H₂O content (H₂O), 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 CO₂ 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 (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., CO₂, H₂O, G, H, LE, P, RH, and SWC). Following the procedure of Cade and Noon (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 \( \tau \) 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 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 $11 \pm 2.3{^\circ}C$. 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 $>11 \pm 2.3{^\circ}C$, 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 $\leq$ 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 $\leq$ 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 $R_e$ rates. In the ecosystems with MAT $\leq 11 \pm 2.3{^\circ}C$, 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$_2$O, LE, P, RH, and SWC (Table 1, Fig. 3c-j).

In sites with MAT $> 11 \pm 2.3{^\circ}C$ (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, H$_2$O, and SWC, and negatively correlated to H and LE. For the data of maximum realizable $R_e$ rates vs. LE, the quantile slopes at 90th, 95th and 99th percentiles were significantly different from zero (Table 2), but did not show consistently positive or negative relationships. Therefore, further quantile linear regressions at $\tau$ levels...
5.3 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°C, the mean $R_e$ rates were typically low and other micrometeorological factors rarely regulated the $R_e$ rates. In sites with MAT > 2.96°C, 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 primarily 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 $R_e$ 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°C) (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 patterns (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$_2$O content (water vapour) increase may accelerate respiratory process of terrestrial ecosystem (Wang et al., 2016). In addition, elevated H$_2$O 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$_2$O.

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 (or in high-latitude regions) is stronger than that at high temperatures (or in low-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 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 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) 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 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 (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.

Acknowledgments

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2007.


**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 99th quantile piecewise linear regression. The regression analysis identifies a turning point (i.e., the threshold) at the MAT of 11±2.3°C. An equation for the line quantifying the maximum realizable $R_e$ rates in ecosystems with MAT ≤ the threshold is $R_e = 0.19(MAT) + 2.49$. An equation for the line quantifying the maximum realizable $R_e$ rates in ecosystems with MAT > the threshold is $R_e = 0.07(MAT) + 3.81$. 

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Figure 2: Distributions of patterns 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) ≤ 11±2.3 °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$_2$O concentration (H$_2$O) ($n = 359$), (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, 5 and dot lines represent the 99th, 95th, and 90th linear quantiles, respectively.
Figure 4: Terrestrial ecosystem respiration \( (R_e) \) rates in the terrestrial ecosystems with mean annual air temperature \( (\text{MAT}) > 11 \pm 2.3 \, ^\circ \text{C} \) (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 \( \text{CO}_2 \) concentration \( (\text{CO}_2) \) \( (n = 156) \), (e) atmospheric \( \text{H}_2\text{O} \) concentration \( (\text{H}_2\text{O}) \) \( (n = 131) \), (f) latent heat flux \( (\text{LE}) \) \( (n = 188) \), (g) precipitation \( (P) \) \( (n = 176) \), (h) relative humidity \( (\text{RH}) \) \( (n = 177) \), (i) upper layer soil water content \( (\text{SWC}_1) \) \( (n = 115) \), and (j) lower layer soil water content \( (\text{SWC}_2) \) \( (n = 91) \). Solid, dash, and dot lines represent the 99th, 95th and 90th linear quantiles, respectively. In Fig. 4f, since the trends from the 99th, 95th and 90th linear quantiles were not consistent, the quantile linear regression at \( \tau \) levels of 10th – 80th was conducted to confirm the negative relationship between the maximum realizable \( R_e \) rates and \( \text{LE} \).
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 90th, 95th, and 99th quantiles on mean annual air temperatures (MAT) of terrestrial ecosystems below 11±2.3°C.

<table>
<thead>
<tr>
<th>Quantile</th>
<th>MAT</th>
<th>CO₂</th>
<th>G</th>
<th>H</th>
<th>H₂O</th>
<th>LE</th>
<th>P</th>
<th>RH</th>
<th>SWC₁</th>
<th>SWC₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>90th</td>
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<td>0.49</td>
<td>0.80</td>
<td>&lt;0.0001</td>
<td>0.64</td>
<td>0.003</td>
<td>0.06</td>
<td>0.05</td>
<td>0.18</td>
<td>0.80</td>
</tr>
<tr>
<td>95th</td>
<td>&lt;0.0001</td>
<td>0.25</td>
<td>0.98</td>
<td>&lt;0.0001</td>
<td>0.73</td>
<td>0.03</td>
<td>&lt;0.0001</td>
<td>0.22</td>
<td>0.15</td>
<td>0.73</td>
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<tr>
<td>99th</td>
<td>&lt;0.0001</td>
<td>0.67</td>
<td>&lt;0.0001</td>
<td>0.002</td>
<td>0.22</td>
<td>0.54</td>
<td>0.66</td>
<td>0.93</td>
<td>0.01</td>
<td>0.64</td>
</tr>
</tbody>
</table>

MAT is mean annual air temperature. Micrometeorological factors include CO₂: atmospheric CO₂ concentration, G: soil heat flux, H: sensible heat flux, H₂O: atmospheric H₂O content, LE: latent heat flux, P: precipitation, RH: relative humidity, SWC₁: upper layer soil water content, and SWC₂: 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 90th, 95th, and 99th quantiles on mean annual air temperatures (MAT) of terrestrial ecosystems above 11±2.3°C.

<table>
<thead>
<tr>
<th>Quantile</th>
<th>MAT</th>
<th>CO₂</th>
<th>G</th>
<th>H</th>
<th>H₂O</th>
<th>LE</th>
<th>P</th>
<th>RH</th>
<th>SWC₁</th>
<th>SWC₂</th>
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<tbody>
<tr>
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<td>0.01</td>
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<tr>
<td>95th</td>
<td>&lt;0.0001</td>
<td>0.98</td>
<td>0.56</td>
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<td>0.02</td>
<td>0.04</td>
<td>0.07</td>
<td>0.01</td>
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<tr>
<td>99th</td>
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<td>&lt;0.0001</td>
<td>0.03</td>
<td>0.03</td>
<td>&lt;0.0001</td>
<td>0.003</td>
<td>0.09</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
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