

# Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms

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## Summary

- It is well established that individual organisms can acclimate and adapt to temperature to optimize their functioning. However, thermal optimization of ecosystems, as an assemblage of organisms, has not been examined at broad spatial and temporal scales.
- Here, we compiled data from 169 globally distributed sites of eddy covariance and quantified the temperature response functions of net ecosystem exchange (NEE), an ecosystem-level property, to determine whether NEE shows thermal optimality and to explore the underlying mechanisms.
- We found that the temperature response of NEE followed a peak curve, with the optimum temperature (corresponding to the maximum magnitude of NEE) being positively correlated with annual mean temperature over years and across sites. Shifts of the optimum temperature of NEE were mostly a result of temperature acclimation of gross primary productivity (upward shift of optimum temperature) rather than changes in the temperature sensitivity of ecosystem respiration.
- Ecosystem-level thermal optimality is a newly revealed ecosystem property, presumably reflecting associated evolutionary adaptation of organisms within ecosystems, and has the potential to significantly regulate ecosystem–climate change feedbacks. The thermal optimality of NEE has implications for understanding fundamental properties of ecosystems in changing environments and benchmarking global models.

## Introduction

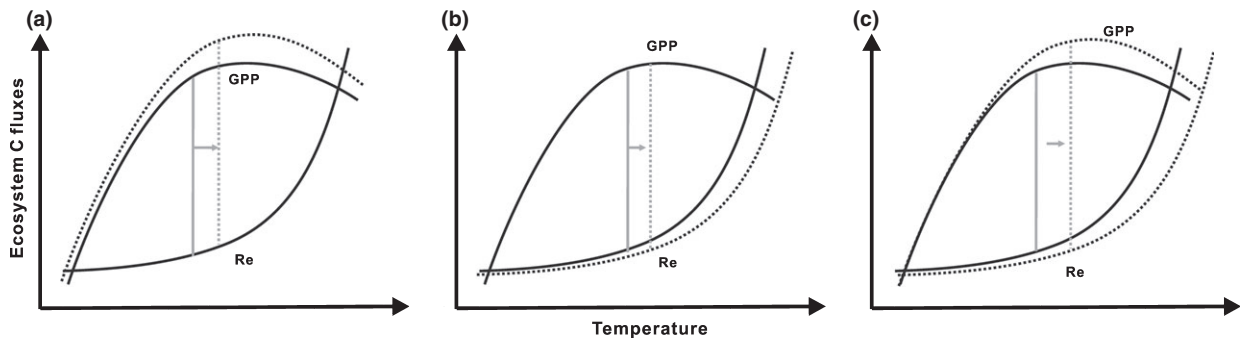
Ecosystems are represented in most Earth system models in order to simulate the responses and feedbacks of land processes to climate change (Chapin *et al.*, 2002; Friedlingstein *et al.*, 2006). Virtually all ecosystem carbon cycle models use temperature response functions that have been developed from our understanding of biochemical processes of enzymes and/or physiological processes of leaf photosynthesis and organic matter decomposition (Enquist *et al.*, 2003; Friedlingstein *et al.*, 2006) because we lack essential knowledge about ecosystem-level responses to temperature change.

The integrated response of ecosystem processes to temperature change is influenced by the responses of its constituents, including plants, animals, microbes, and their interactions. It is well documented that plants (Mooney *et al.*, 1978; Berry & Bjorkman, 1980; Atkin & Tjoelker, 2003), animals (Parmesan, 2006), and microbes (Bradford *et al.*, 2008) acclimate and/or adapt to prevailing environmental conditions in a way that can optimize their functioning under varying temperatures, which is collectively termed optimality (Parker & Maynard Smith, 1990). Thus, we hypothesize that the integrated response of an ecosystem, as an assemblage of interacting organisms, might also demonstrate thermal optimality under temperature change (Loreau, 2010). Nevertheless, thermal optimality at the ecosystem level has not yet been carefully examined.

Net ecosystem exchange (NEE) of carbon dioxides is an ecosystem process that reflects the balance of gross primary productivity (GPP) and ecosystem respiration ( $R_c$ ), and is often used to approximate net ecosystem productivity (NEP =  $-NEE$ ) (Chapin *et al.*, 2006). Previous studies have shown that plant photosynthesis and GPP can acclimate to temperature change via an increase in optimum temperature in a warmer environment

(Mooney *et al.*, 1978; Baldocchi *et al.*, 2001; Niu *et al.*, 2008). It has also been documented that  $R_c$  responds exponentially to temperature as long as there is no soil water limitation (Law *et al.*, 1999), and its temperature sensitivity ( $Q_{10}$ ) decreases in a warmer environment, a process also described as temperature acclimation (Lloyd & Taylor, 1994; Luo *et al.*, 2001; Tjoelker *et al.*, 2008; Piao *et al.*, 2010). The temperature acclimation of either GPP or  $R_c$  can lead to changes in the temperature response of NEP. As illustrated in the conceptual Fig. 1, if GPP acclimates to temperature by increasing its optimum temperature in a warmer environment while  $R_c$  stays unchanged (Fig. 1a), the optimum temperature of NEP at the maximum differences between GPP and  $R_c$  may also shift upward. Alternatively, if  $R_c$  acclimates to temperature with decreasing  $Q_{10}$  at higher temperature, while GPP stays unchanged (Fig. 1b), the optimum temperature of NEE will also increase. If both GPP and  $R_c$  acclimate, the optimum temperature of NEE will likely increase more than that in the previously described two conditions (Fig. 1c). A recent study suggests thermal adaptation of NEE based on a positive relationship between the optimum temperature of NEE and the average summer temperature across space (Yuan *et al.*, 2011). Still, we do not know yet which of these possible processes contributes to the shift of optimum temperature of NEE, and whether or not the optimum temperature of NEE shifts over time.

With the advent of eddy-covariance measurements of NEE, together with detailed meteorological variables (Baldocchi *et al.*, 2001), it has become possible to characterize the ecosystem-level temperature response. In this study, we quantified temperature responses of NEE to determine whether NEE exhibits thermal optimality over time and space, and we further explored the underlying mechanisms. Here, we define acclimation as short-term reversible adjustments of NEE over time and



**Fig. 1** Conceptual figure for the shifts of optimum temperature of net ecosystem productivity (NEP;  $NEP = -NEE$  (net ecosystem exchange)) as a result of the changes in optimum temperature of gross primary productivity (GPP) or the temperature sensitivity of respiration. (a) Here it is assumed that in a warmer year or at a warmer site, the optimum temperature of NEP shifts higher owing to a shift of optimum temperature of GPP. In (b) it is assumed that the shifts in the optimum temperature of NEP are the result of the temperature acclimation of  $R_e$  (decrease of  $Q_{10}$ ). In (c) it is assumed that the optimum temperature of NEP shifts higher owing to acclimation of both GPP and  $R_e$ . The dashed curves represent the temperature response curve in a warmer year or at a warmer site. The vertical lines refer to the maximum NEP.

adaptation as geographical changes which are the result of long-term genetic and species compositional changes in ecosystems and the physiological adjustment of those organisms to the prevailing environment. The thermal optimum of NEE and its acclimation and adaptation together are described as thermal optimality. Thermal optimality of whole ecosystem carbon exchange is here assumed to represent ensemble responses of multiple temperature optima of productivity, metabolic, and decomposition processes among organisms within the ecosystem.

## Materials and Methods

### Site information and data analysis

Ecosystem carbon fluxes and meteorological data used in this analysis were taken from standardized files from the North America Carbon Program (NACP), AmeriFlux, CARBOEUROPE, and the FLUXNET-LaThuile datasets. These data have been quality-controlled and gap-filled using consistent methods (Papale *et al.*, 2006; Moffat *et al.*, 2007). We analyzed only those sites that have at least 1 yr of complete meteorological data because we needed to calculate mean annual temperature, precipitation and solar radiation. In total, 169 sites with 818 site-years were used to investigate the optimum temperature of NEE ( $T_{opt}^{NEE}$ ). The sites included eight major terrestrial biomes: deciduous broadleaf forests (DBF), mixed forests (MF), evergreen needleleaf forests (ENF), grasslands (GRA), evergreen broadleaf forests (EBF), wetlands (WET), savanna (SAV) and shrubs (SHR) (Supporting Information, Table S1, Fig. S1). The climatic zones of the sites included the polar tundra arctic, continental temperate, subtropical Mediterranean, and tropical areas. The quality-controlled and gap-filled database, including eddy-covariance fluxes of  $CO_2$  (NEE), GPP and  $R_e$ , were used together with solar radiation, air temperature, and precipitation in this study.

We used daily accumulated NEE rather than half-hourly values to obtain the temperature response curve with the intention of avoiding diurnal variations caused by asynchrony between cyclic

changes in photosynthesis and respiration. Daily values, which integrate diurnal cycles of photosynthesis and respiration, are more robust than hourly values in reflecting ecosystem responses to temperature over the season. Hourly data during a few h near midday were used to test the robustness of the temperature response functions of NEE as discussed in the supplementary materials.

For each site or year, temperatures were binned in 1°C daily temperature. The daily air temperature and NEE were averaged in each temperature bin to quantify the temperature response of NEE. In practice, the running mean of every three temperature bins was calculated, and the value  $T_{opt}^{NEE}$ , at which the maximum carbon uptake was attained, was determined from the curve relating NEE with temperature. The robustness of the parabolic pattern of NEE response to temperature was analyzed as shown in the supplementary materials (Figs S2–S7). We used the same method of calculating  $T_{opt}^{NEE}$  to estimate the optimum temperature of GPP ( $T_{opt}^{GPP}$ ).

To determine the temperature dependence of  $R_e$ , we fitted the daily mean temperature and  $R_e$  data to a modified Van't Hoff equation:  $R_e = R_b e^{bT}$  (Lloyd & Taylor, 1994). The parameter  $b$  determines temperature sensitivity of respiration ( $Q_{10}$ ) and can be expressed in terms of the  $Q_{10}$  coefficient as  $b = \ln(Q_{10})/10$ . Although there are other types of  $R_e$  acclimation, for example, changes in absolute  $R_e$  rates with a constant  $Q_{10}$  (type II), and functional switches in both absolute  $R_e$  and  $Q_{10}$  (type III) (Atkin & Tjoelker, 2003; Bradford *et al.*, 2008), we only assessed type I acclimation (changes in  $Q_{10}$ ) in this study as a result of the limitation of eddy flux data to address the other two types.

### Uncertainty assessment

The bootstrapping method, which is a statistical technique based on building a sampling distribution by resampling from the dataset, was used to estimate the uncertainty of each optimum temperature (Banks *et al.*, 2010). We constructed a number of resamplings of the observed dataset (of equal size to the observed

dataset), each of which was obtained by random sampling with replacement from the original datasets. We estimated one optimal temperature from each resampled dataset. This was done 5000 times to obtain 5000 optimum temperatures, from which we computed a mean and standard deviation of  $T_{\text{opt}}^{\text{NEE}}$ , as well as the distribution of statistics for each site or year (Fig. S8). The same methods were used to obtain the mean and standard deviation of  $T_{\text{opt}}^{\text{GPP}}$  and  $Q_{10}$ .

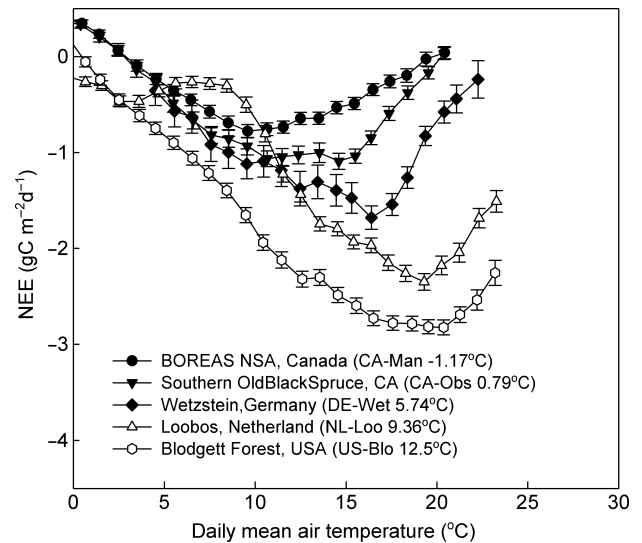
### Statistical analysis

To examine the potential thermal acclimation of  $T_{\text{opt}}^{\text{NEE}}$  and the underlying mechanisms, we analyzed the relationship of  $T_{\text{opt}}^{\text{NEE}}$  with environmental factors and with  $T_{\text{opt}}^{\text{GPP}}$  and  $Q_{10}$  across the years within each site and across all site-years at 12 sites with >10 yr of data. Because each site has relatively few yr of data, we used standardized residual analysis to remove outliers by using a magnitude of  $\pm 2.0$  to omit points from the regression. One outlier was removed from each of IT-Ren (Renon, Italy, 2007) and Ru-Fyo (Fyodorovskoye, Russia, 2006). To examine the potential thermal adaptation of  $T_{\text{opt}}^{\text{NEE}}$ , we used linear regression to analyze the relationship of  $T_{\text{opt}}^{\text{NEE}}$  with environmental factors and with  $T_{\text{opt}}^{\text{GPP}}$  and  $Q_{10}$  across all the 169 sites. All the regression analyses were performed using SPSS 11.0 for Windows (SPSS Inc., Chicago, IL, USA).

### Results

We used results from the five sites (Fig. 2) to illustrate the general pattern of peak-curve temperature responses of NEE with the optimum temperature shifting over different temperature zones (from cold to warm). NEE increased (i.e. became more negative) with temperature in the lower temperature range to reach a maximum, and then declined (became less negative) as temperature increased further (Fig. 2). The temperature responses of NEE were caused by the relative changes in GPP and  $R_c$ . At low temperatures, GPP increased more than  $R_c$  for a unit of temperature change. Nevertheless, at higher temperatures,  $R_c$  increased further with temperature (without water limitation), while GPP leveled off or even decreased (Fig. S9). As a consequence, there was always a well-defined  $T_{\text{opt}}^{\text{NEE}}$ , at which NEE attained the maximum value (Fig. 2).

Twelve sites with measurements longer than 10 yr in our database were examined to illustrate interannual shifts of  $T_{\text{opt}}^{\text{NEE}}$ . In comparison with the values obtained in the average year,  $T_{\text{opt}}^{\text{NEE}}$  shifted to a higher temperature in warmer years at each site (Fig. 3). Across all years,  $T_{\text{opt}}^{\text{NEE}}$  tended to increase with annual mean air temperature at all sites, although this was statistically significant only at some sites (Fig. 4a). Across all years of the 12 sites, annual air temperature explained 35% of the changes in  $T_{\text{opt}}^{\text{NEE}}$ . Solar radiation had no significant relationship with  $T_{\text{opt}}^{\text{NEE}}$  across years within any site or across all site-years ( $P > 0.05$ , Fig. 4b). Although there was no significant relationship of  $T_{\text{opt}}^{\text{NEE}}$  with precipitation across the years within any site ( $P = 0.11\text{--}0.97$ ), we found that across all site-years, precipitation explained 23% of the



**Fig. 2** The general pattern of peak-curve temperature response of net ecosystem exchange (NEE) at five representative sites over different temperature zones (mean annual temperature ranges from  $-1.17$  to  $12.5^\circ\text{C}$ ). At all five sites, net ecosystem  $\text{CO}_2$  uptake (negative NEE) increased with temperature in the low range, reached a maximum, and then declined in the high range.

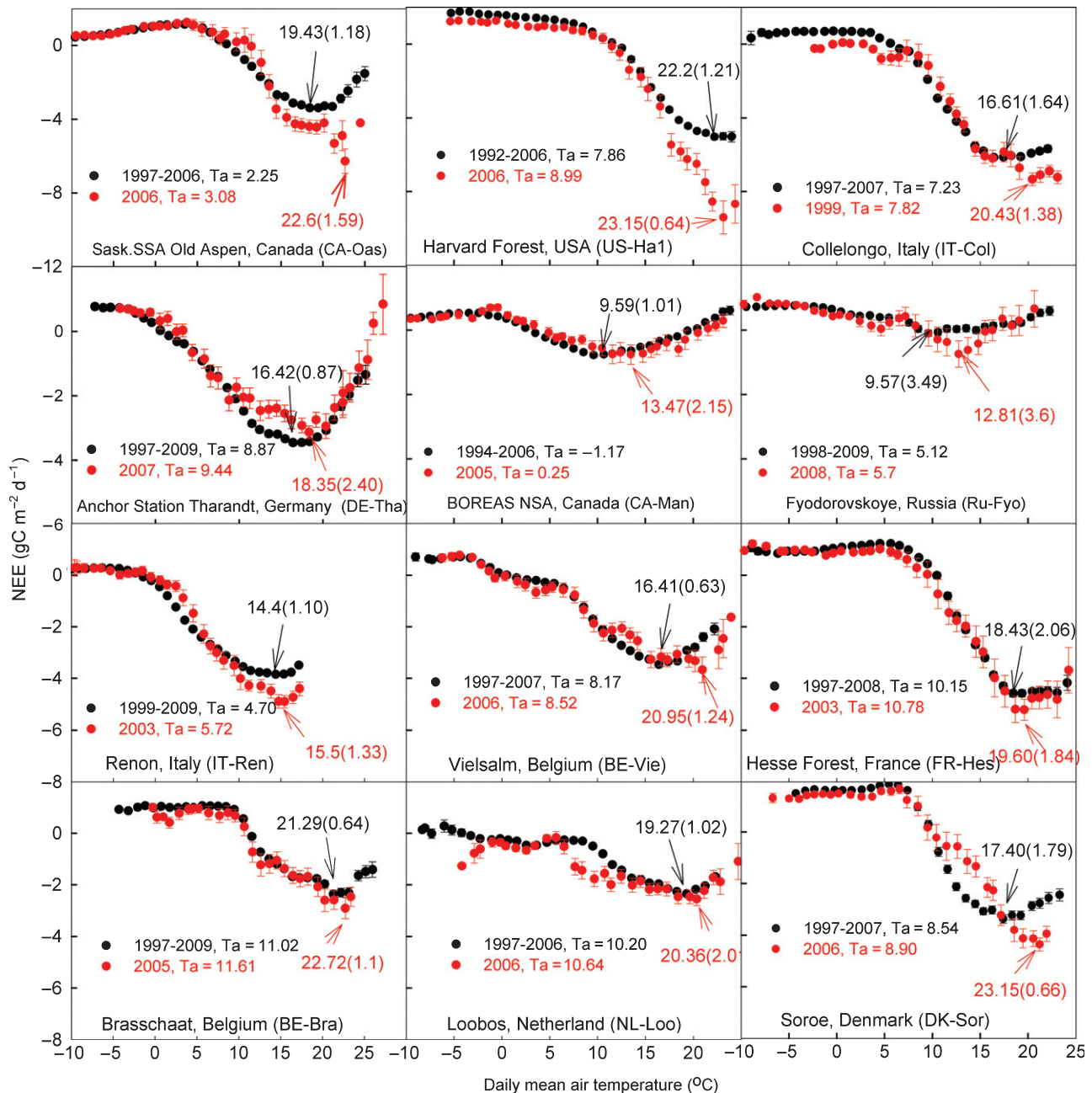
changes in  $T_{\text{opt}}^{\text{NEE}}$  ( $P < 0.01$ , Fig. 4c). Multiple (stepwise) regression analysis showed that air temperature and precipitation together explained 39% of changes in  $T_{\text{opt}}^{\text{NEE}}$ , while temperature and precipitation alone explained 31 and 8%, respectively, of the changes in  $T_{\text{opt}}^{\text{NEE}}$ , suggesting that temperature was the main factor regulating the shifts of  $T_{\text{opt}}^{\text{NEE}}$  across site-years.

Across all site-years,  $T_{\text{opt}}^{\text{NEE}}$  was correlated positively with  $T_{\text{opt}}^{\text{GPP}}$ , but negatively with  $Q_{10}$  (Fig. 5). Multiple regression analysis showed that  $T_{\text{opt}}^{\text{GPP}}$  and  $Q_{10}$  together explained 36% of the changes in  $T_{\text{opt}}^{\text{NEE}}$ , but the contribution of  $T_{\text{opt}}^{\text{GPP}}$  was greater (29%) than  $Q_{10}$  (7%). The optimum temperature of GPP ( $T_{\text{opt}}^{\text{GPP}}$ ) was positively related to mean annual air temperature across the site-years at the Canadian sites and at the other 10 sites (Fig. S10a). Solar radiation and precipitation contributed little to the shifts of  $T_{\text{opt}}^{\text{GPP}}$ . Changes in  $Q_{10}$  correlated negatively with temperature and precipitation, but were not related to the changes in solar radiation (Fig. S10).

Globally,  $T_{\text{opt}}^{\text{NEE}}$  was higher at warmer than at cold sites, leading to a positive relationship between  $T_{\text{opt}}^{\text{NEE}}$  and annual mean air temperature regardless of climate zone (Fig. 6a). Mean annual precipitation and solar radiation together only explained 5% of the changes in  $T_{\text{opt}}^{\text{NEE}}$  based on multiple regression analysis. Across all sites,  $T_{\text{opt}}^{\text{NEE}}$  had a positive linear relationship with  $T_{\text{opt}}^{\text{GPP}}$ , but no significant relationship with  $Q_{10}$  (Fig. 6b,c).

### Discussion

We found an universal peak-curve pattern of NEE in response to temperature, a phenomenon which was first reported in a high-elevation subalpine forest (Huxman *et al.*, 2003). The peak pattern of the temperature response curve could be explained by relative

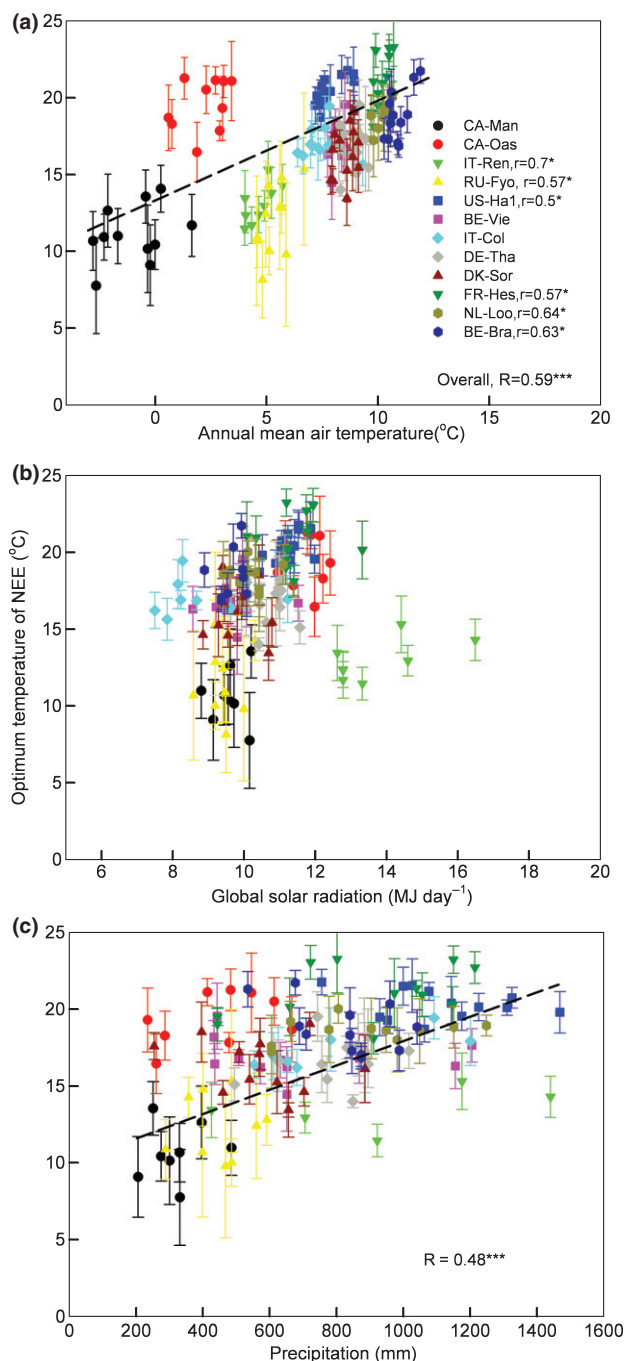


**Fig. 3** Shift of the optimum temperature of net ecosystem exchange (NEE) to a higher value in a warmer year compared with the average of all studied years at the 12 sites with > 10 yr of data length. Black closed circles, average over all years; red closed circles, represent a warmer year (mean ± 1 SD).  $T_a$  is annual mean temperature. The numbers labeled in the figures are the optimum temperatures of NEE and their standard deviation.

changes in GPP and  $R_c$ . The increase in carbon uptake at low temperature resulted from a relatively larger increase in GPP than  $R_c$  for a given change in temperature. The decrease of carbon uptake at higher temperatures resulted from the continuous increase in  $R_c$  against the leveling-off or decline of GPP (Figs 1, S9).

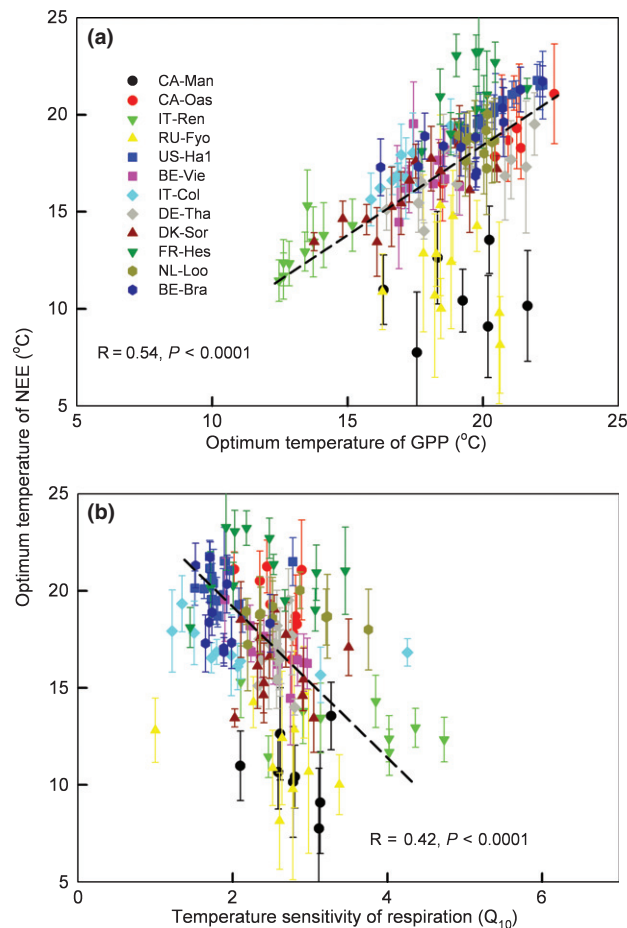
Shifts of  $T_{opt}^{NEE}$  across years were primarily caused by temperature (Fig. 4), suggesting thermal acclimation at interannual scales. The upward trend of  $T_{opt}^{NEE}$  with increasing temperature was largely the result of the shifts of optimum temperature in photosynthesis (Fig. 5), which has been well documented at plant level (Mooney *et al.*, 1978; Berry & Bjorkman, 1980; Niu

*et al.*, 2008; Gunderson *et al.*, 2010) and primarily results from increased electron transport capacity and/or greater heat stability of Rubisco (Sage & Kubien, 2007). In addition, extended growing seasons, increased nitrogen mineralization, and enhanced root growth (Penuelas & Filella, 2001; Churkina *et al.*, 2005; Luo *et al.*, 2009) may also have contributed to the increased  $CO_2$  uptake under higher temperatures, leading to the upward shift in the optimum temperature of GPP in warmer years (Fig. S10a). For example, fine roots in boreal ecosystems are more active in warmer years, allowing greater access to water and nutrients (Jarvis & Linder, 2000; Pregitzer *et al.*, 2000). Although respiration



**Fig. 4** The relationship between optimum temperature of net ecosystem exchange (NEE; mean  $\pm$  SD) and annual mean air temperature (a), global solar radiation (b) and precipitation (c) at the 12 sites with > 10 yr of data. \* and \*\*\* indicate that the relationship was significant at the  $P < 0.1$  and 0.001 levels, respectively. Site abbreviations and names are as follows: CA-Man, BOREAS NSA, Canada; CA-Oas, Sask.SSA Old Aspen, Canada; IT-Ren, Renon, Italy; Ru-Fyo, Fyodorovskoye, Russia; US-Ha1, Harvard Forest, USA; BE-Vie, Vielsalm, Belgium; IT-Col, Collelongo, Italy; DE-Tha, Anchor Station Tharandt, Germany; DK-Sor, Soroe, Denmark; FR-Hes, Hesse Forest, France; NL-Loo, Loobos, Netherlands; and BE-Bra, Brasschaat, Belgium.

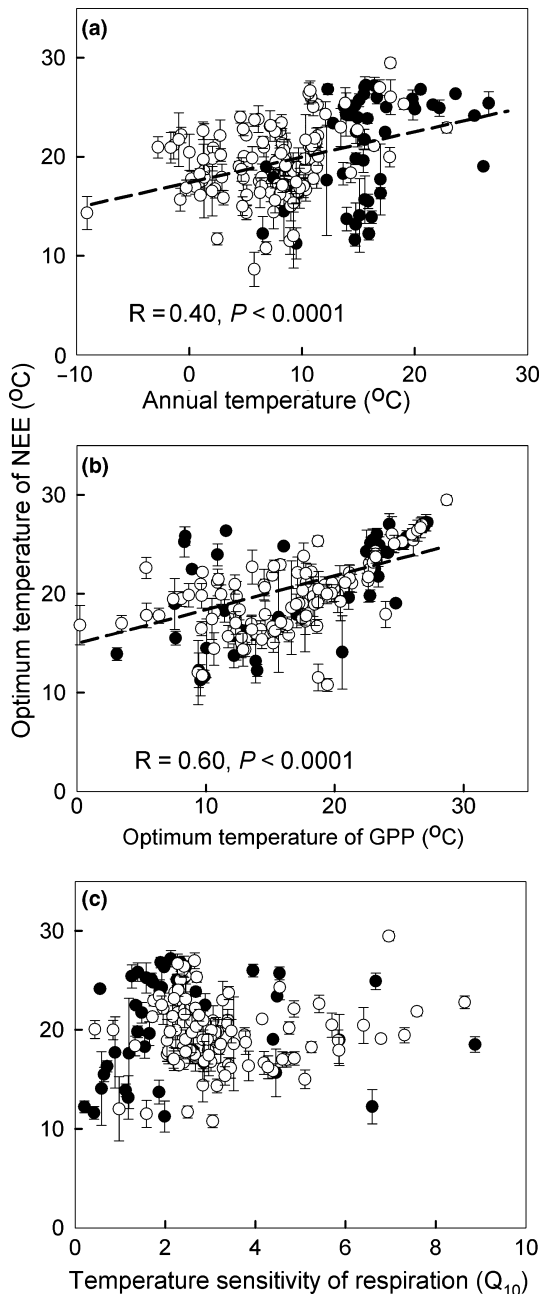
normally increases with temperature, water stress and respiratory acclimation during high temperatures can offset or reverse the direct temperature effect (Luo *et al.*, 2001; Irvine *et al.*, 2008;



**Fig. 5** The relationship of optimum temperature of net ecosystem exchange (NEE) to optimum temperature of gross primary productivity (GPP) (a) and temperature sensitivity of respiration ( $Q_{10}$ ) (b) across the site-years at the 12 sites with > 10 yr of data.

Scott *et al.*, 2009). Increases in GPP overcompensated for any respiration increases at higher temperature, leading to the upward shift of  $T_{opt}^{NEE}$  in warmer years. The relative roles of these processes may vary at different sites, leading to site-specific responses of  $T_{opt}^{NEE}$  to temperature (Fig. 4). Thus, the mechanisms underlying thermal optimization of NEE across temporal scales most likely vary among sites and require further investigation.

Shifts of  $T_{opt}^{NEE}$  with annual mean air temperature across space are consistent with previous studies on geographical shifts of optimum temperature of GPP and NEE with summer or growing season temperatures (Baldocchi *et al.*, 2001; Yuan *et al.*, 2011), also suggesting thermal adaptation of NEE. Such spatial shifts in  $T_{opt}^{NEE}$  likely result from processes at several hierarchical scales and may involve adaptive changes of various organisms. At the ecosystem level, thermal adaptation of NEE likely reflects associated changes in the structure and function of plant, animal, and microbial communities, which are likely the result of both long-term genetic changes and physiological adjustment to the prevailing environment (Diaz *et al.*, 2001; Janssens *et al.*, 2001; Knohl *et al.*, 2005; Larsen *et al.*, 2007). At the community level, species competition may also be a very important determinant of the changes in  $T_{opt}^{NEE}$ . The universal existence of  $T_{opt}^{NEE}$  and its



**Fig. 6** The relationship of optimum temperature of net ecosystem exchange (NEE; means  $\pm$  SD) to annual mean air temperature (a), optimum temperature of gross primary productivity (GPP) (b), and temperature sensitivity of respiration ( $Q_{10}$ ) (c) in tropical and subtropical areas (closed circles) and temperate and boreal areas (open circles) across all 169 sites.

acclimation and adaptation to temporal and spatial temperature changes strongly suggest thermal optimality of NEE. Compared with previous studies (Baldocchi *et al.*, 2001; Yuan *et al.*, 2011), this study holistically reveals the thermal optimality of NEE via acclimation and adaptation and withstands more rigorous uncertainty analysis. A particularly novel point found here is the identification of the relative roles of photosynthesis and respiration. The shifts of  $T_{\text{opt}}^{\text{NEE}}$  are mostly attributable to changes in GPP rather than in  $R_c$ . Although respiration has been documented to

be the main determinant of intraregional forest carbon balance variation (Valentini *et al.*, 2000), our study clearly showed that the temperature response of GPP overrides  $R_c$  in determining thermal optimality of NEE. According to Atkin & Tjoelker (2003) and Bradford *et al.* (2008), changes in  $Q_{10}$  as used in this study only reflect type I acclimation. However, if the type II and type III acclimation occur, the upward shift of  $T_{\text{opt}}^{\text{NEE}}$  in a warmer environment can also happen. Owing to the limitations of eddy flux data, we can only address type I acclimation in this study. This might cause partial assessment on  $R_c$  acclimation.

Thermal acclimation/adaptation of NEE, in conjunction with the adaptation of GPP (Baldocchi *et al.*, 2001) and plant and soil respiration (Atkin & Tjoelker, 2003; Bradford *et al.*, 2008), will influence the long-term responses and feedback of ecosystem carbon storage to global temperature changes. Shifts of  $T_{\text{opt}}^{\text{NEE}}$  with interannual variations in temperature may dampen short-term temperature effects on ecosystem carbon balances and could contribute to a lower apparent sensitivity of global ecosystem carbon uptake to temperature than to rainfall (Tian *et al.*, 1998; Angert *et al.*, 2005). These shifting thermal optima with temperature over time and space may lower the sensitivity of the carbon cycle feedback to future climate warming (Frank *et al.*, 2010; Mahecha *et al.*, 2010).

The observed patterns of thermal optimality over time and space represent a useful benchmark for evaluating the capability of Earth system models (Randerson *et al.*, 2009; Frank *et al.*, 2010). Benchmarking against these observed sensitivities is not sufficient to validate models but represents an important first step in assessing model capabilities on centennial time scales (Randerson *et al.*, 2009; Frank *et al.*, 2010). Models that replicate short-term patterns of ecosystem optimization are not guaranteed to succeed on longer timescales. However, models that do not replicate these observed temperature sensitivities will almost certainly fail to simulate biosphere and carbon cycle responses to climate change accurately. Further research is needed to explore whether land process models can reproduce this thermally optimal pattern across space and time.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Global map of site distribution.

**Figs S2–S7** Robustness test of the parabolic temperature response curves of NEE.

**Fig. S8** Uncertainty test for  $T_{\text{opt}}^{\text{NEE}}$  using bootstrapping methods.

**Fig. S9** Examples of temperature response curves of NEE, GPP and  $R_c$  in the average vs warmer years.

**Fig. S10** Relationship of  $T_{\text{opt}}^{\text{GPP}}$  and  $Q_{10}$  with environmental factors.

**Table S1** Site information

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