Air temperature optima of vegetation productivity across global biomes

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The global distribution of the optimum air temperature for ecosystem-level gross primary productivity (T_{opt}^{eco}) is poorly understood, despite its importance for ecosystem carbon uptake under future warming. We provide empirical evidence for the existence of such an optimum, using measurements of in situ eddy covariance and satellite-derived proxies, and report its global distribution. T_{opt}^{eco} is consistently lower than the physiological optimum temperature of leaf-level photosynthetic capacity, which typically exceeds 30 °C. The global average T_{opt}^{eco} is estimated to be 23 ± 6 °C, with warmer regions having higher T_{opt}^{eco} values than colder regions. In tropical forests in particular, T_{opt}^{eco} is close to growing-season air temperature and is projected to fall below it under all scenarios of future climate, suggesting a limited safe operating space for these ecosystems under future warming.

Understanding how photosynthesis responds to warming has been a focus in plant research in recent decades, and most of the existing knowledge comes from leaf-scale measurements1–3. Most leaf-scale temperature response curves show that photosynthetic capacity increases with temperature up to an optimum temperature (T_{opt}^{leaf}), which typically occurs in the 30–40 °C temperature range4–6. Above this optimum temperature, foliar photosynthetic capacity sharply declines as electron-transport and Rubisco enzymatic capacities become impaired4. Field et al.4 suggested that ecosystem-scale optimum temperature T_{opt}^{eco} may differ from T_{opt}^{leaf} at the ecosystem scale, elevated air temperatures do limit canopy photosynthesis by processes other than leaf carbon oxidation rates. For instance, elevated air temperatures may accelerate leaf ageing and increase leaf thickness (phenology; for example, ref. 7) and control stomatal closure because a higher temperature usually comes with increase leaf thickness (phenology; for example, ref. 9) and control stomatal closure because a higher temperature usually comes with increase leaf thickness (phenology; for example, ref. 9). Empirical leaf-scale photosynthesis–temperature relationships12 have been directly incorporated into global ecosystem models, with variants to account for acclimation, that is, a temporal adjustment of optimum photosynthetic temperature to air temperature during growth13,14. This direct scaling of temperature responses from leaves to ecosystems partly determines model projections of gross primary productivity (GPP) and CO₂ uptake by terrestrial ecosystems in climatic scenarios. Verifying the existence of T_{opt}^{eco} in real-world ecosystems, defining its spatial distribution across and within biomes, and understanding the relationships between T_{opt}^{eco}, prevailing air temperature and T_{opt}^{leaf} are important for evaluating models and understanding the impacts of various climatic warming targets on ecosystem productivity.

In this study, we formulate and test the following hypotheses: (1) T_{opt}^{eco} is higher for biomes when air temperature during growth is warmer, (2) T_{opt}^{eco} is lower than T_{opt}^{leaf} for any given ecosystem because the limitations mentioned earlier of stomatal conductance and phenology emerge before temperature begins to impair foliar photosynthetic capacity, and (3) tropical forests already operate near a high T_{opt}^{leaf} above which canopy photosynthesis may decrease with even moderate air temperature warming15,16. Here, we defined T_{opt}^{eco} as the daytime air temperature at which GPP is highest over a period of several years, and thus T_{opt}^{eco} can be empirically determined from productivity observations and proxies (see Methods).

Results and discussion
We first applied this approach on time series of daily GPP derived from CO₂ flux measurements at 153 globally distributed eddy covariance sites and found that a robust estimate of T_{opt}^{eco} could be derived

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at 125 out of 153 sites (see Methods). \( T_{\text{eco}}^{\text{opt}} \) values derived from the FLUXNET data range from 8.2 °C to 35.8 °C (Fig. 1a, Supplementary Table 1). Tropical sites have higher \( T_{\text{eco}}^{\text{opt}} \) values than temperate and boreal sites (Supplementary Fig. 1), implying a dependency of \( T_{\text{eco}}^{\text{opt}} \) on background climate. The FLUXNET multi-site analysis further indicates that \( T_{\text{eco}}^{\text{opt}} \) values across sites are positively correlated with daily maximum air temperature averaged over the growing season \( (T_{\text{max}}^{\text{air}}) \) (see calculation in Methods) \((R = 0.46, P < 0.01, t\text{-test})\), with a spatial linear regression slope of 0.61 °C per °C across sites (Fig. 1a). Overall, these results confirm our first hypothesis, which stated that higher \( T_{\text{eco}}^{\text{opt}} \) values occur when higher growth temperatures prevail, in support of findings in refs. 3,14.

Since eddy covariance measurements do not have a continuous spatial coverage, we also used satellite observations known to be highly correlated with photosynthetic activity\(^8\), that is, GPP proxies. The first proxy used is \( NIR_{v} \), the product of total scene NIR reflectance (\( NIR_{v} \)) by the NDVI. \( NIR_{v} \) was proven to have a high temporal correlation with GPP at flux-tower sites\(^9\). Satellite observations of \( NIR_{v} \) and NDVI from the terra MODIS were used to calculate \( NIR_{v} \) between 2001 and 2013 (see Methods). \( NIR_{v}\)-derived \( T_{\text{opt}}^{\text{leaf}} \) is comparable to that estimated from eddy covariance flux-tower measurements (Fig. 1b), which gives support to using the \( NIR_{v} \) proxy for a global mapping of \( T_{\text{opt}}^{\text{leaf}} \). The average \( T_{\text{opt}}^{\text{leaf}} \) over the global vegetated areas is estimated to be 23 ± 6 °C (mean ± 1 s.d.) with large spatial gradients in latitude. As shown in Fig. 1c, maximum values close to 30 °C mainly appear over tropical forests, savannas and drylands and minimum values near 10 °C prevail at high latitudes and in mountainous regions (Fig. 1c). This spatial pattern of \( T_{\text{opt}}^{\text{leaf}} \) is robust to the choice of a particular climate-forcing dataset or to the method used to estimate \( T_{\text{opt}}^{\text{leaf}} \) (Supplementary Fig. 2, see also Methods). Similar results are also found for other GPP proxies (vegetation greenness (NDVI)\(^9\), Enhanced Vegetation Index (EVII)\(^9\), solar-induced vegetation fluorescence (solar-induced chlorophyll fluorescence, SIF)\(^9\)), or when daily mean air temperature \( (T_{\text{mean}}^{\text{air}}) \) is used instead of daily maximum air temperature \( (T_{\text{max}}^{\text{air}}) \) to calculate \( T_{\text{opt}}^{\text{leaf}} \) (Supplementary Figs. 3–6; see also Methods). Note that although the covariance between air temperature, atmospheric VPD and solar radiation may confuse the direct effect of air temperature on vegetation productivity, we verified that neither VPD nor radiation is the dominant factor determining the pattern of \( T_{\text{eco}}^{\text{opt}} \) at the global scale (see Methods).

To test the second hypothesis, we compared satellite-derived \( T_{\text{eco}}^{\text{opt}} \) with \( T_{\text{leaf}}^{\text{opt}} \) from the responses of maximum Rubisco-limited carbonation rates \( (V_{\text{cmax}}) \) to temperature from leaf-scale measurements for 36 species\(^5\). Note that the \( T_{\text{leaf}}^{\text{opt}} \) here refers to the temperature optima for leaf-scale (gross) photosynthetic capacity rather than for leaf net photosynthesis, which equals gross photosynthesis minus photorespiration and minus dark respiration (for more details, see Methods).

We found that \( T_{\text{eco}}^{\text{opt}} \) is lower than \( T_{\text{leaf}}^{\text{opt}} \) (Supplementary Fig. 7). This difference may originate from \( T_{\text{eco}}^{\text{opt}} \) being additionally limited by high VPD during hot and dry periods\(^3\) and by soil-moisture deficits during extensive dry episodes\(^2\), under real-world conditions. Under conditions of high temperature, atmospheric VPD increases while soil moisture decreases. Stomatal conductance, and hence carbon assimilation rates (GPP at ecosystem scale), decrease to prevent exceedingly low leaf-water potentials and any resulting plant tissue damage from cavitation\(^4\). In contrast, leaf-level photosynthesis measurements that determine the temperature response curve of \( V_{\text{cmax}} \) are usually performed in absence of water stress by maintaining relatively low VPD conditions (for example, refs. 25–29), unless the research objective is to investigate drought effect on leaf photosynthetic parameters (as in refs. 3,15). In addition, plant phenology controls leaf age, vitality (photosynthetic rates) and foliar density (for example, Leaf Area Index, LAI)\(^3\), and may therefore co-determine ecosystem-level temperature limitations and the optimum temperature for canopy photosynthesis\(^5\). It is also important to note when comparing \( T_{\text{opt}}^{\text{leaf}} \) with \( T_{\text{opt}}^{\text{eco}} \) that leaf-scale measurements are often limited to sunlit leaves, which could lead to a positive bias of existing in situ \( T_{\text{opt}}^{\text{leaf}} \) measurements. Furthermore, the tree species database used by Kattge and Knorr\(^5\) from which \( T_{\text{opt}}^{\text{leaf}} \) data were collected does not include any tropical species. This may explain why global models prescribed with \( T_{\text{opt}}^{\text{leaf}} \) give divergent results for tropical biomes.

The relationship between \( T_{\text{eco}}^{\text{opt}} \) and background climate is shown in Fig. 1d. The sampling of leaf-scale studies does not provide consistent evidence about the dependence of \( T_{\text{opt}}^{\text{leaf}} \) on climate, and there are positive correlations between \( T_{\text{opt}}^{\text{leaf}} \) and growing-season air temperature in a set of studies\(^3,10–14\) attributed to evolutionary adaptation\(^15\), but no clear relationship between \( T_{\text{opt}}^{\text{leaf}} \) and growth temperature\(^14\). In contrast, \( T_{\text{opt}}^{\text{eco}} \) inferred from satellite GPP proxies in our study increases with \( T_{\text{max}}^{\text{air}} \) across the globe. In temperature–precipitation space, the spatial sensitivity of \( T_{\text{opt}}^{\text{eco}} \) to \( T_{\text{max}}^{\text{air}} \) (the slope of the linear regression between these two variables) is lower than 1 for any precipitation bin (Fig. 1d), suggesting that spatial gradients of \( T_{\text{opt}}^{\text{eco}} \) are smaller than those of \( T_{\text{max}}^{\text{air}} \), possibly because hydraulic and phenological limitations further limit \( T_{\text{opt}}^{\text{eco}} \) across spatial gradients. In fact, the spatial sensitivity of \( T_{\text{opt}}^{\text{eco}} \) to \( T_{\text{max}}^{\text{air}} \) generally increases with increasing mean annual precipitation (Fig. 1d), even though \( T_{\text{eco}}^{\text{opt}} \) is not significantly correlated with precipitation after control for the effect of \( T_{\text{max}}^{\text{air}} \) (Fig. 1d). This thermal adaptation of \( T_{\text{opt}}^{\text{eco}} \) suggested by the positive spatial slope of the \( T_{\text{eco}}^{\text{opt}} \)-temperature relation, is also observed across biases. As shown in Fig. 2, there
is a significant positive correlation between $T_{\text{eco}}^{\text{opt}}$ and $T_{\text{maxgs}}^{\text{air}}$ with a slope of 0.76 across different biomes. Among biomes, the largest mean $T_{\text{eco}}^{\text{opt}}$ is found in tropical evergreen broadleaved forest (EBF) ($29 \pm 3^\circ C$), and the smallest mean $T_{\text{eco}}^{\text{opt}}$ ($13 \pm 3^\circ C$) in cold grasslands covering the Tibetan Plateau (Fig. 2 and Supplementary Fig. 8).

Results from both model simulations and very limited observational studies suggest a decrease in canopy photosynthesis of tropical forests at high temperature\textsuperscript{15,42–45}, which led us to formulate the third hypothesis of tropical forests already operating at $T_{\text{eco}}^{\text{opt}}$ close to $T_{\text{maxgs}}^{\text{air}}$, implying that canopy photosynthesis may decrease under future warming\textsuperscript{15,36}. This hypothesis is verified from the data shown in Fig. 3 (see also Supplementary Fig. 9). $T_{\text{eco}}^{\text{opt}}$ is indeed slightly lower (1.4 °C) than $T_{\text{maxgs}}^{\text{air}}$ over tropical evergreen forests, suggesting a small safety margin for canopy photosynthesis under future warming. Note that the safety margin could become larger than that suggested by the air temperature data if leaf thermal regulation acclimatises to the warming air temperature (see Methods). In contrast, arctic (north of 65° N) and boreal (50° N–65° N) ecosystems exhibit substantially larger safety margins, that is, a larger positive difference between $T_{\text{eco}}^{\text{opt}}$ and $T_{\text{maxgs}}^{\text{air}}$.
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Change with latitude in $T_{\text{opt}}$ and $T_{\text{max,gs}}$. a. Current $T_{\text{opt}}$ versus current $T_{\text{max,gs}}$. b. Future $T_{\text{opt}}$ versus future $T_{\text{max,gs}}$. Current $T_{\text{opt}}$ and $T_{\text{max,gs}}$ are calculated using current temperature for 2001–2013, whereas acclimated $T_{\text{opt}}$ and future $T_{\text{max,gs}}$ are first calculated pixel by pixel using temperature for 2091–2100, projected by general circulation models (GCM) under the RCP4.5 scenario and then averaged by latitude. Acclimated $T_{\text{opt}}$ is determined based on the projected temperature and temperature sensitivity of $T_{\text{opt}}$ using the annual precipitation level predicted for 2091–2100. The solid line and shaded area in each panel indicate the mean and s.d., respectively, of $T_{\text{opt}}$ or $T_{\text{max,gs}}$ summarized by latitude. c. Future $T_{\text{opt}}$ versus future $T_{\text{max,gs}}$ for tropical evergreen forests. ** indicates that $T_{\text{opt}}$ is significantly lower than $T_{\text{max,gs}}$ at $P<0.01$ in a paired t-test. Error bars indicate ± s.d.

Fig. 2 | Relationship between $T_{\text{air max,gs}}$ and $T_{\text{eco,opt}}$ across vegetation types. The error bars indicate the s.d. of $T_{\text{eco,opt}}/T_{\text{air max,gs}}$ for each vegetation type: ENF, evergreen needle-leaved forest; EBF, evergreen broad-leaved forest; DNF, deciduous needle-leaved forest; DBF, deciduous broad-leaved forest; MF, mixed forest; Shrub, closed and open shrublands. The light grey dotted line represents y = x. The dark-grey dotted line is y = 0.76x + 6.48 derived by linear regression, with the slope value (estimated using Student’s t-test) shown in the bottom right. The red dotted line is the flux-tower-derived slope (0.61) from Fig. 1a. The size of each symbol corresponds to the three categories (<3%, 3–10% and >10%) of occupied vegetated area on land.

Fig. 3 | Change with latitude in $T_{\text{opt}}$ and $T_{\text{max,gs}}$. a. Current $T_{\text{opt}}$ versus current $T_{\text{max,gs}}$. b. Future $T_{\text{opt}}$ versus future $T_{\text{max,gs}}$. Current $T_{\text{opt}}$ and $T_{\text{max,gs}}$ are calculated using current temperature for 2001–2013, whereas acclimated $T_{\text{opt}}$ and future $T_{\text{max,gs}}$ are first calculated pixel by pixel using temperature for 2091–2100, projected by general circulation models (GCM) under the RCP4.5 scenario and then averaged by latitude. Acclimated $T_{\text{opt}}$ is determined based on the projected temperature and temperature sensitivity of $T_{\text{opt}}$ using the annual precipitation level predicted for 2091–2100. The solid line and shaded area in each panel indicate the mean and s.d., respectively, of $T_{\text{opt}}$ or $T_{\text{max,gs}}$ summarized by latitude. c. Future $T_{\text{opt}}$ versus future $T_{\text{max,gs}}$ for tropical evergreen forests. ** indicates that $T_{\text{opt}}$ is significantly lower than $T_{\text{max,gs}}$ at $P<0.01$ in a paired t-test. Error bars indicate ± s.d.
precipitation levels into account, so that areas that become wetter also exhibit faster acclimation. Even with this assumed acclimation law, $T_{\text{air}}^{\text{opt}}$ will still surpass $T_{\text{eco}}^{\text{opt}}$ by 1.7°C under RCP2.6 and by 2.5°C under RCP8.5 for tropical evergreen forests (Fig. 3c). Not accounting for precipitation levels in the acclimation rates produced similar results (Supplementary Figs. 14 and 15).

Our global-scale analysis of $T_{\text{eco}}^{\text{opt}}$ derived from globally distributed point measurements of eddy covariance and space-borne observations of proxies of vegetation productivity is an attempt to diagnose the global distribution of ecosystem-scale temperature optima of photosynthesis. It should be noted, however, that hypotheses about thermal acclimation of $T_{\text{eco}}^{\text{opt}}$ are still highly uncertain because ecosystem adjustments can lag substantially behind the rate of future warming, particularly for forests. More studies using datasets with longer time spans are needed in the future to more accurately detect eventual thermal acclimation of $T_{\text{eco}}^{\text{opt}}$. Furthermore, the acclimation of plants to increasing atmospheric CO$_2$ concentration and to changes in other environmental factors (for example, VPD) was also not considered in the current analyses. Constraining the spatially observed temperature sensitivity of $T_{\text{opt}}$ over time is a priority for future studies. Continuous monitoring and dedicated manipulative experiments could improve our understanding on the features of $T_{\text{eco}}^{\text{opt}}$ and thermal acclimation in earth system models.

Methods

**FLUXNET data.** The half-hourly eddy covariance GPP data were obtained from FLUXNET datasets, and were quality-controlled, filtered against low turbulence, and gap-filled using consistent methods, as described in ref. 21. Only freely available FLUXNET data were used in this study. All the half-hourly GPP data were aggregated into daily-accumulated GPP for further estimates of the optimal temperature for vegetation productivity. Daily maximum air temperature ($T_{\text{air}}^{\text{max}}$) was determined as the maximum air temperature value from all the half-hourly air temperature observations. We observed only site-years with more than 80% of half-hourly data available. A total of 153 individual FLUXNET sites with 663 site-years of GPP data were used in this study.

**NIR.** An approach was recently proposed for estimating vegetation photosynthetic capacity by remote sensing, that is, the NIR, which can differentiate between the confounding effects of background brightness, leaf area and the distribution of photosynthetic capacity with depth in canopies. NIR, is calculated as the product of NIR, and NDVI. As a proxy of photosynthesis, NIR is suggested to be strongly correlated with solar-induced chlorophyll fluorescence (SIF), a direct index of photosynthetic efficiency of chlorophyll, and shows higher correlation with observed GPP than NDVI. We used satellite-derived NIR, to calculate and map the optimal air temperature for vegetation productivity at an ecosystem scale ($T_{\text{eco}}^{\text{opt}}$). Following ref. 21, we calculated 16-day NIR, for 2001–2013 as the product of MODIS 16-day NIR reflectance and MODIS 16-day NDVI, both of which were derived from the MOD13A2 Vegetation Index Product with a spatial resolution of 1 km. Only positive NIR, values were used in the analysis.

**NDVI.** The NDVI is a vegetation index defined as the ratio of the difference between NIR and red visible reflectance to their sum, and is widely used to represent vegetation greenness. To account for uncertainties from different satellite datasets, three independent NDVI datasets were used, including bi-weekly NDVI data from Global Inventory Modeling and Mapping Studies (GIMMS) AVHRR, 16-day NDVI data from Terra MODIS and 10-day NDVI data from Satellite Pour l’Observation de la Terre Vegetation (SPOT Vegetation). The three NDVI datasets spanned three decades: 1982–2009 for AVHRR NDVI datasets, 2000–2009 for MODIS NDVI datasets and 1999–2009 for SPOT NDVI datasets, with the spatial resolutions of 8 km, 1 km, and 1 km, respectively. All NDVI datasets have been corrected to reduce the effects of volcanic aerosols, solar angle and sensor errors. Pixels with a mean annual NDVI $>0.1$ were defined as the vegetated area for each dataset.

**EVI.** EVI is another vegetation index designed to enhance the vegetation signal by minimizing canopy–soil variations and to improve sensitivity over dense vegetation conditions, and is found to correlate well with estimated GPP on a site-by-site basis. We used a 16-day EVI dataset for 2000–2009 with a spatial resolution of 1 km from the MOD12A1 Vegetation Index Product. Effects from aerosols, solar angle and sensor error have all been corrected.

**SIF.** Chlorophylls in plants absorb short-wave radiation and dissipates excess energy as light or heat. The long-wave radiation re-emitted by chlorophylls is referred as chlorophyll fluorescence. Recent studies have reported that remotely sensed SIF could serve as an indicator of photosynthesis rate and it is correlated with model-simulated GPP. Following previous studies, we retrieved SIF from two different retrieval windows, 755 nm and 771 nm, as well as two polarization states, S and P, using a Fourier transform spectrometer on the Japanese Greenhouse gases Observing SATellite (GOSAT). These diverse SIF samples were then aggregated into monthly gridded data at a spatial resolution of 2° from June 2009 to June 2012.

**Vegetation distribution.** We used MODIS land cover with the classification scheme of the International Geosphere–Biosphere Programme (IGBP). The MODIS IGBP land cover data were derived from the MOD12Q1 Land Cover Science Data Product at a spatial resolution of 1 km and an updated digital Köppen–Geiger world map of climatic classification. Within the vegetated area defined by NDVI thresholds, the 17 land cover types were reclassified into five vegetation types: ENF, EBE, DNF, DBF, MF, savannas, cropland, grassland and shrubland. Based on the main climates in the world map of the Köppen–Geiger climatic classification, grassland was further subdivided into temperate grasslands, boreal and arctic tundra, and shrubland was further subdivided into temperate and boreal shrubland. The grassland over the Tibetan Plateau was considered separately because the Tibetan Plateau has an average altitude higher than 4,000 m above sea level, and thus a unique alpine climate. In contrast to temperate grasslands and shrubland, where water is a major limiting factor for vegetation productivity, alpine ecosystems on the Tibetan Plateau are mainly limited by thermal conditions.

**Climate dataset.** The gridded air temperature and precipitation data for 1982 to 2013 were obtained from the Climatic Research Unit/National Centers for Environmental Protection (CRU/NCEP) 6-hourly dataset with a spatial resolution of 0.5°. Note that the purpose of this study is to investigate the optimal air temperature for photosynthesis. Optimal leaf temperature is also of interest; however, it was not addressed in this study because accurate observed measurements of leaf temperatures are not available at the eddy covariance sites and at a global scale as gridded datasets. For a discussion about calculation of temperature optimum from air temperature and from surface temperature, we used remotely sensed land surface temperature (LST), which is inverted from infrared reflectance measured by MODIS (MYD11A2 version 6). This dataset had an original spatial resolution of 1 km, spanning from July 2002 to December 2014. The error of the MODIS LST product, which primarily stems from cloud contamination and emissivity uncertainties, was reported to be less than 3°C. Generally, the occurrence time of $T_{\text{max}}$ (14:00–16:00) is relatively close to the Aqua overpass time (13:30), and thus we assumed that $T_{\text{max}}$ from MODIS–Aqua is comparable with the daily maximum leaf surface temperature ($T_{\text{max}}^{\text{leaf}}$) corresponding to the temporal resolutions of MODIS, AVHRR and SPOT datasets, the 6-hourly climate data were aggregated into 16-day, biweekly and 10-day values, respectively, before further analyses. Given the different spatial resolutions of satellite observations and climate data, we extracted time series of daily maximum air temperature and precipitation from the aggregated CRU/NCEP data for each vegetation state and temporal resolution. The daily maximum air temperature ($T_{\text{air}}^{\text{max}}$) of the growing season averaged from 2001 to 2013 was calculated as the current mean growing-season daily maximum air temperature ($T_{\text{air}}^{\text{max}}$). Information on the growing season was derived from the study by ref. 47, which was determined from the GIMMS Leaf Area Index dataset (GIMMS LAI, using a Savitzky–Golay filter) and then refined by excluding the ground-freeze period identified by the freeze/thaw earth system data record (see details in ref. 36). We also documented the temperature thresholds at which the growing season begins and ends for each year. Temperature thresholds were averaged from 2001 to 2013 for the onset and end of the growing season, respectively. We also applied Water and Global Change(WATCH) Forcing Data (WFD) methodology to ERA-interim (WFDEI) data with a temporal resolution of 3 hours.

We used climate projections for the end of the twenty-first century (2091–2100) using 20 models that participated in the phase five of coupled model intercomparison project (CMIP5) under the RCP2.6, RCP4.5 and RCP8.5 scenarios to determine the impact of future warming on vegetation productivity (see model list in Supplement Table 2). Considering the mismatch between CRU/NCEP datasets and outputs from GCM for current climate conditions, we generated future temperature and precipitation maps by adding the relative changes in GCM-derived climate projections to the current climate for each pixel. $T_{\text{max}}^{\text{opt}}$ for the late twenty-first century was estimated using the same temperature thresholds as for the current $T_{\text{max}}^{\text{opt}}$. All GCM projections were resampled to a 3-hourly resolution.
to develop the temperature response curve of NIR. The $T_{Evo}$ was determined from the response curve at which NIR was maximized (Supplementary Fig. 16). Note that $T_{Evo}$ may not be detected for some pixels where the maximum NIR was only attained at either end of the response curve, accounting for 3.5% of the vegetated areas. Only vegetated areas with detectable $T_{Evo}$ were shown when mapping the spatial pattern of $T_{Evo}$. The derivation of $T_{Evo}$ is robust to the choice of a particular climate-forcing dataset (Supplementary Fig. 2). Instead of using the temperature corresponding to the maximum 90th quantile NIR, to calculate $T_{opt}$ we also applied nonlinear regression of the photosynthetic temperature response data (equation (1)) to estimate $T_{Evo}$, which produced similar results (Supplementary Fig. 2):

$$NI_{R}(T) = NI_{R}(OPT) - k(T - T_{Evo})$$

where $NI_{R}(OPT)$ is the NIR value at a daily maximum temperature $T$ and $b$ is a parameter describing the spread of the parabola. $T_{Evo}$ is the vertex of the each fit and $NI_{R}(OPT)$ is the the NIR value at $T_{Evo}$. Finally, we used daily mean air temperature ($T_{air}$) instead of $T_{opt}$ to calculate $T_{Evo}$. In this test, $T_{Evo}$ derived from $T_{air}$ is smaller than $T_{Evo}$ estimated from $T_{opt}$, but the two variables were strongly spatially correlated (Supplementary Fig. 6).

We investigated the relationship between $T_{Evo}$ and climate variables by averaging $T_{opt}$ in the climate space with 1 °C intervals of mean annual $T_{max}$ averaged over the growing season ($T_{max}^{g}$) and 100 mm intervals of mean annual precipitation (MAP) (Fig. 10). For each MAP interval, we calculated the apparent spatial sensitivity of $T_{Evo}$ in response to changes in $T_{opt}$ using bootstrapping method. We performed the linear regression analysis 1,000 times by randomly selecting a subset of 80% of the samples from pairs of $T_{Evo}$ and $T_{max}^{g}$ within each MAP interval. The mean and s.d. of the temperature sensitivity of $T_{Evo}$ were subsequently estimated along the MAP gradient.

We calculated the variance inflation factor (VIF) between $T_{opt}$ and $T_{max}^{g}$, under each VIF bin in the regression model of:

$$T_{Evo} = k_{0} + k_{1} \times T_{max}^{g} + k_{2} \times V_{PD} + k_{3} \times V_{PD} \times T_{max}^{g}$$

where $k_{0}$ and $k_{1}$ are the apparent sensitivity of $T_{Evo}$ to $T_{max}^{g}$ and $V_{PD}$, respectively, with a constant term $k_{2}$. As shown in Supplementary Fig. 18, we observed that the VIF value ranged only between 1.001 and 1.438, suggesting relatively low multicollinearity between $T_{opt}$ and $T_{max}^{g}$. However, we also observed that a larger spatial scale of $T_{Evo}$ decreased to prevent exceedingly low leaf-water potentials and resulting plant tissue damage from cavitation. We show that across climatic gradients $T_{Evo}$ is systematically higher at high maximum air temperatures, but not systematically lower at high VPD conditions (Supplementary Fig. 17). We then calculated the variance inflation factor (VIF) between $T_{opt}$ and $T_{max}^{g}$, under each VIF bin in the regression model of:

$$T_{Evo} = k_{0} + k_{1} \times T_{max}^{g} + k_{2} \times V_{PD} + k_{3} \times V_{PD} \times T_{max}^{g}$$

where the partial sensitivity of $T_{Evo}$ to $T_{max}^{g}$ is defined as $k_{1}$ in equation (3) under each VIF bin. We then compared the partial sensitivity with the apparent sensitivity of $T_{opt}$ to $T_{max}^{g}$ estimated using the previously mentioned linear regression between $T_{opt}$ and $T_{max}^{g}$ for each VIF bin. As shown in Supplementary Fig. 19, although the apparent sensitivity of $T_{opt}$ to $T_{max}^{g}$ is generally lower than the partial (intrinsical) sensitivity of $T_{Evo}$ to $T_{max}^{g}$, the apparent sensitivity to $T_{air}$ remains positive, even when VPD is taken into account, except under very high VPD bins (higher than ~4.5 kPa) representing less than 1% of the study area. These results indicate that the patterns of $T_{opt}$ are not dominated by high VPD reducing canopy photosynthesis as an indirect effect of higher air temperature increasing VPD. Moreover, we also observed a pronounced forward-shade wave radiation (Rad) at the time of year when $T_{Evo}$ is observed for the 16-day averaged Rad distribution. As shown in Supplementary Fig. 20, the Rad value when $T_{Evo}$ was retrieved from global observations was below the 95th percentile in the 16-day Rad distribution for ~80% of the study area, which is mainly in mid and low latitudes, such as Africa, India, Australia, eastern Brazil, and the south and southwest of North America. By comparison, for most boreal regions in parts of northern China, southeast US, as well as in parts of South America, the timing of $T_{Evo}$ is consistent with the time of maximum solar radiation. This is because $T_{Evo}$ in these regions generally appears in summer, which is also the period when solar radiation is at its maximum during the year.

The NIR-derived $T_{Evo}$ was compared with $T_{Evo}$ estimated using GPP data from 153 eddy covariance sites. Flux-derived $T_{Evo}$ was determined for each site-year with daily-accumulated GPP and corresponding temperature data from flux-tower observations. The same method to estimate local $T_{Evo}$ using NIR, datasets was applied. A robust estimate of $T_{Evo}$ can be derived for 125 sites (Supplementary Table 1). For each site, we calculated the mean and s.d. of $T_{Evo}$ across different years. We then extracted and averaged $T_{Evo}$ values within a 3 x 3 pixel window around each site from the NIR-derived $T_{Evo}$ map, and calculated the the nine $T_{Evo}$ values within the window. The relationship between NIR- and flux-derived $T_{Evo}$ was reported using a least-square linear regression and the statistical significance of the slope, or its P-value, by given Student’s t-test. The results show that NIR-derived $T_{Evo}$ is comparable to that estimated independently from measurements of flux-tower eddy covariance (Fig. 15). We compared the spatial distribution derived from NIR, with the one obtained from NDVI datasets. Consistent spatial patterns of $T_{Evo}$ are derived from each of the three NDVI datasets (Supplementary Fig. 21). A global composite map of $T_{Evo}$ (Supplementary Fig. 3) was then generated by averaging estimates derived from the three NDVI datasets. Given the inconsistent spatial resolutions of the different products, we resampled $T_{Evo}$ to a common grid of 8 km before averaging. $T_{Evo}$ from NDVI datasets generally show a spatial pattern similar to that from NIR, but with smaller NDVI-derived $T_{Evo}$ values for central and southern South America (Supplementary Fig. 3). We compared the spatial distribution of $T_{Evo}$ derived from NIR, with that from MODIS EVI data between 2001 and 2013, and found that the EVI-derived $T_{Evo}$ showed very similar spatial pattern to that of NIR-derived $T_{Evo}$ (Supplementary Fig. 4). The distribution of $T_{Evo}$ derived from NIR, and from GOSAT SIF datasets also have similar spatial patterns, even though the NIR-derived $T_{Evo}$ is higher in tropical regions, particularly in cultivated areas of southeast Brazil (Supplementary Fig. 5).

At leaf scale, the photosynthesis–temperature response is suggested to be primarily controlled by three sets of processes: biochemical, respiratory and stomatal processes. Much of the effort to date to understand variability in the leaf-level photosynthesis–temperature response has focused on biochemical processes. Since photorespiration increases exponentially with temperature, the optimum temperature of GPP ($T_{opt}$) should be lower than the optimal temperature of $V_{max}$. For this comparison to be made, we extracted and averaged $T_{Evo}$ values within a 3 x 3 pixel window from the NIR-derived $T_{Evo}$ map around the reported site location (longitude and latitude) of leaf-scale measurements. For leaf-scale measurements with the information of site location, no $T_{Evo}$ derived $T_{Evo}$ values across pixels with both the same growing season mean temperature and the same plant functional type as the corresponding site. $T_{Evo}$ is different from $T_{leaf}$ not only because of respiratory process, but also because air temperature can differ from leaf temperatures, which are regulated by leaf traits affecting the leaf energy balance. Because, to our knowledge, global gridded monthly leaf temperature data are not available, we used daily maximum LST ($T_{opt}$) from MODIS to calculate $T_{Evo}$, to illustrate the potential differences between $T_{Evo}$ and $T_{SLST}$. As shown in Supplementary Fig. 22, the $T_{Evo}$ is similar to $T_{SLST}$ over tropical savannas. However, over most tropical forests $T_{opt}$ is lower than $T_{SLST}$, which can be explained by the lower daytime surface temperature than air temperature as a result of strong evapotranspiration effect. This ecosystem-dependent difference between $T_{opt}$ and $T_{SLST}$ suggests that the leaf thermal regulation mechanism through the physiological and morphological changes is an important ecosystem process that shapes spatial variations of $T_{Evo}$. In addition, if the difference between leaf temperature and air temperature increases in response to warmer air temperatures (that is, if leaf thermal regulation acclimates to warmer temperature), the safety margin of tropical ecosystems would increase more than the air temperature, data optimistically suggests. However, the long-term in situ leaf temperature data required to test this hypothesis independently are currently not available.

To account for potential changes in $T_{opt}$ under future warming, we estimated the acclimated $T_{opt}$ for vegetation productivity by the end of the twenty-first century (2091–2100) using recent IPCC climate projections. To this end, we applied the space-for-time substitution approach, assuming that temporally constant climate conditions are representative of the future climate. The acclimated $T_{opt}$ was calculated using $T_{opt}$ estimated from different climate change scenarios. We compared the spatial distribution of $T_{Evo}$ under the projected MAP level for 2091–2100. Acclimated $T_{Evo}$ was averaged across the GCMs under each scenario. Latitudinal variation of future $T_{Evo}$ was derived by averaging within 1°-latitude bins from future $T_{Evo}$ maps and then compared to future $T_{opt}$ maps summarized by latitude from future $T_{opt}$ maps.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.
Data availability

All data are available in the main text or the supplementary information. All computer codes used in this study can be provided by the corresponding author upon reasonable request.

Received: 4 October 2018; Accepted: 5 February 2019;
Published online: 11 March 2019

References


Nature Ecology & Evolution


Acknowledgements

This study was supported by the Strategic Priority Research Program (A) of the Chinese Academy of Sciences (Grant No. XDA20050101), the National Natural Science Foundation of China (41530528) and the National Key R&D Program of China (2017YFA0604702). This work used eddy covariance data acquired by the FLUXNET community and in particular by the following networks: AmeriFlux (US Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program (DE- FG02-04ER63917 and DE-FG02-04ER6391)), AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada (supported by CFCAS, NSERC, BOCAP, Environment Canada and NRCan), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia and USCCCE. We acknowledge the financial support to the eddy covariance data harmonization provided by CarboEuropeIP, FAO-GTOS-CO, iLEAPS, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, Universitat Laval and Environment Canada, and the US Department of Energy and the database development and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California Berkeley and University of Virginia.

Author contributions

S. Piao designed the research, M. H. performed the analysis, S. Piao drafted the paper. All authors contributed to the interpretation of the results and the text.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-0838-x.

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- Clearly defined error bars
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Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

- **Data collection**: No software was used to collect data.
- **Data analysis**: The analyses and mapping were both performed using MATLAB (R2017b). Details were reported in Analysis section of the Method.

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## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

<table>
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<th>Study description</th>
<th>We provide empirical evidence for the existence of the optimum air temperature of ecosystem-level gross primary productivity, using measurements of in-situ eddy covariance and satellite-derived proxies, and report its global distribution.</th>
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<tr>
<td>Research sample</td>
<td>The half-hourly eddy-covariance Gross Primary Productivity data were obtained from FLUXNET datasets. A total of 153 individual FLUXNET sites with 663 site-years of GPP data were used in this study. We also used an ensemble of global remote sensing observations. Details can be seen in the Methods section.</td>
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<td>Data exclusions</td>
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<td>Blinding</td>
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Did the study involve field work?  [ ] Yes  [x] No

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## Reporting for specific materials, systems and methods

### Materials & experimental systems

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### Methods

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