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Air temperature optima of vegetation productivity across global biomes

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

56
57 Understanding how photosynthesis responds to warming has been a focus in plant research in recent
58 decades, and most of the existing knowledge comes from leaf-scale measurements¹⁻⁴. Most leaf-
59 scale temperature response curves show that photosynthetic capacity increases with temperature up
60 to an optimum temperature (T_{opt}^{leaf}), which typically occurs in the 30-40°C temperature range^{5,6}.
61 Above this optimum temperature, foliar photosynthetic capacity sharply declines as electron-
62 transport and Rubisco enzymatic capacities become impaired⁷. Field et al.⁸ first suggested that
63 ecosystem-scale optimum temperature (T_{opt}^{eco}) may differ from T_{opt}^{leaf} . At ecosystem scale, elevated
64 air temperatures do limit canopy photosynthesis by other processes than leaf carboxylation rates.
65 For instance, elevated air temperatures may accelerate leaf ageing and increase leaf thickness
66 (phenology; e.g. ref 9), and control stomatal closure, because a higher temperature usually comes
67 with a higher vapor pressure deficit (VPD)¹⁰. In a more extreme case, warming-induced water stress

68 could suppress canopy photosynthesis through partial hydraulic failure (hydraulics) by cavitation
69 (e.g. ref 11).

70
71 Empirical leaf-scale photosynthesis-temperature relationships¹² have been directly incorporated
72 into global ecosystem models, with variants to account for acclimation, i.e. a temporal adjustment
73 of optimum photosynthetic temperature to air temperature during growth^{5,13,14}. This direct scaling
74 of temperature responses from leaves to ecosystems partly determines model projections of Gross
75 Primary Productivity (GPP) and CO₂ uptake by terrestrial ecosystems in climatic scenarios.
76 Verifying the existence of T_{opt}^{eco} in real world ecosystems, defining its spatial distribution across
77 and within biomes and understanding the relationships between T_{opt}^{eco} , prevailing air temperature
78 and T_{opt}^{leaf} are important for evaluating models and understanding the impacts of various targets of
79 climatic warming targets on ecosystem productivity.

80
81 In this study, we formulate and test the following hypotheses: (i) T_{opt}^{eco} is higher for biomes where
82 air temperature during growth is warmer, (ii) T_{opt}^{eco} is lower than T_{opt}^{leaf} for any given ecosystem,
83 because the above mentioned limitations of stomatal conductance and phenology emerge before
84 temperature begins to impair foliar photosynthetic capacity, and (iii) tropical forests already operate
85 near a high T_{opt}^{eco} above which canopy photosynthesis may decrease with even moderate air
86 temperature warming^{15,16}. Here we defined T_{opt}^{eco} as the daytime air temperature at which GPP is
87 highest over a period of several years, thus T_{opt}^{eco} can be empirically determined from productivity
88 observations and proxies (see Methods).

89

90 **Results and discussion**

91 We first applied this approach on time series of daily GPP derived from CO₂ flux measurements at
92 153 globally distributed eddy covariance sites and found that a robust estimate of T_{opt}^{eco} could be
93 derived at 125 out of 153 sites (see Methods). T_{opt}^{eco} values derived from the FLUXNET data range
94 from 8.2°C to 35.8°C (Fig. 1a, Supplementary Table 1). Tropical sites have higher T_{opt}^{eco} values than
95 temperate and boreal sites (Supplementary Fig. 1), implying a dependence of T_{opt}^{eco} on background
96 climate. The FLUXNET multi-site analysis further indicates that across sites T_{opt}^{eco} values are
97 positively correlated with growing-season mean daily maximum air temperature ($T_{max\ gs}^{air}$, see
98 calculation in Methods) ($R=0.46$, $P<0.01$, t test), with a spatial linear regression slope of 0.61 °C
99 per °C across sites (Fig. 1a). Overall, these results confirm our first hypothesis stating that higher
100 T_{opt}^{eco} values occur where higher growth temperatures prevail, in support of findings of Baldocchi
101 et al.¹⁷ and Niu et al.¹⁸.

102
103 Since eddy covariance measurements do not have a continuous spatial coverage, we also used
104 satellite observations known to be highly correlated with photosynthetic activity¹⁹, that is, GPP
105 proxies. The first proxy used is the near-infrared reflectance of terrestrial vegetation (NIR_v, the
106 product of total-scene NIR reflectance (NIR_T) by the Normalized Difference Vegetation Index
107 (NDVI). NIR_v was proven to have a high temporal correlation with GPP at flux tower sites¹⁹.
108 Satellite observations of NIR_T and NDVI from the Terra Moderate Resolution Imaging
109 Spectroradiometer (MODIS) were used to calculate NIR_v for the period of 2001-2013 (see
110 Methods). NIR_v-derived T_{opt}^{eco} is comparable with that estimated from eddy covariance flux tower
111 measurements (Fig. 1b), which gives support to using the NIR_v proxy for a global mapping of
112 T_{opt}^{eco} . The average T_{opt}^{eco} over the global vegetated areas is estimated to be 23±6 °C (mean ± 1 SD)
113 with large spatial gradients in latitude. As shown in Fig. 1c, maximum values close to 30°C mainly

114 appear over tropical forests, savannas and drylands and minimum values near 10°C prevail at high-
115 latitudes and in mountainous regions (Fig. 1c). This spatial pattern of T_{opt}^{eco} is robust to the choice
116 of a particular climate forcing dataset, or to the method used to estimate T_{opt}^{eco} (Supplementary Fig.
117 2, see also Methods). Similar results are also found for other GPP proxies (vegetation greenness
118 (NDVI)²⁰, Enhanced Vegetation Index (EVI)²¹, sun-induced vegetation fluorescence (Sun-induced
119 Chlorophyll Fluorescence, SIF)²²), or when daily mean air temperature (T_{mean}^{air}) is used instead of
120 daily maximum air temperature (T_{max}^{air}) to calculate T_{opt}^{eco} (Supplementary Figs. 3-6, see also
121 Methods). Note that although the covariance between air temperature, atmospheric VPD and solar
122 radiation may confuse the direct effect of air temperature on vegetation productivity, we verified
123 that neither VPD nor radiation is the dominant factor determining the pattern of T_{opt}^{eco} at the global
124 scale (see Methods).

125
126 In order to test the second hypothesis, we compared satellite-derived T_{opt}^{eco} with T_{opt}^{leaf} from the
127 responses of maximum Rubisco-limited carboxylation rates (V_{cmax}) to temperature from leaf-scale
128 measurements for 36 species⁵. Note that the T_{opt}^{leaf} here refers to the temperature optima for leaf-
129 scale (gross) photosynthetic capacity rather than for leaf net photosynthesis, which equals gross
130 photosynthesis minus photorespiration and minus dark respiration (see more details in Methods).
131 We found that T_{opt}^{eco} is indeed lower than T_{opt}^{leaf} (Supplementary Fig. 7). This difference may
132 originate from that T_{opt}^{eco} is additionally limited by high VPD during hot and dry periods⁶ and by
133 soil-moisture deficits during extensive dry episodes²³, under real world conditions. Under
134 conditions of high temperature, atmospheric VPD increases while soil moisture decreases. Stomatal
135 conductance and hence carbon assimilation rates (GPP at ecosystem-scale) decrease to prevent
136 exceedingly low leaf water potentials and resulting plant tissue damage from cavitation²⁴. In

137 contrast, leaf-level photosynthesis measurements that determine the temperature response curve of
138 V_{cmax} are usually performed in absence of water stress through maintaining relatively low VPD
139 conditions (e.g. ref 25-30) unless the research objective is to investigate drought effect on leaf
140 photosynthetic parameters as the studies by Vaz et al.³¹ and Zhou et al.³². In addition, plant
141 phenology controls leaf age, vitality (photosynthetic rates) and foliar density (e.g. Leaf Area Index,
142 LAI)³³, and may therefore co-determine ecosystem-level temperature limitations and the optimum
143 temperature for canopy photosynthesis³⁴. It is also important to remark when comparing T_{opt}^{leaf} with
144 T_{opt}^{eco} that leaf-scale measurements are often limited to sunlit leaves, which could lead to a positive
145 bias of existing in-situ T_{opt}^{leaf} measurements. Furthermore, the tree species database used by Kattge
146 & Knorr⁵ from which T_{opt}^{leaf} data were collected does not include any tropical species. This may
147 explain why global models prescribed with T_{opt}^{leaf} give divergent results for tropical biomes.

148
149 The relationship between T_{opt}^{eco} and background climate is shown in Fig. 1d. The sampling of leaf-
150 scale studies does not provide consistent evidence about the dependence of T_{opt}^{leaf} on climate, with
151 positive correlations between T_{opt}^{leaf} and growing season air temperature in a set of studies^{1, 5, 35-37}
152 attributed to evolutionary adaptation³⁸, but no clear relationship between T_{opt}^{leaf} and growth
153 temperature³⁹⁻⁴¹. In contrast, T_{opt}^{eco} inferred from satellite GPP proxies in our study increases with
154 $T_{max\ gs}^{air}$ across the globe. In temperature-precipitation space, the spatial sensitivity of T_{opt}^{eco} to
155 $T_{max\ gs}^{air}$ (the slope of the linear regression between these two variables) is lower than 1 for any
156 precipitation bin (Fig. 1d), suggesting that spatial gradients of T_{opt}^{eco} are smaller than those of
157 $T_{max\ gs}^{air}$, possibly because hydraulic and phenological limitations further limit T_{opt}^{eco} across spatial
158 gradients. In fact, the spatial sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ generally increases with increasing mean

159 annual precipitation (Fig. 1d), even though T_{opt}^{eco} is not significantly correlated with precipitation
160 after controlling for the effect of $T_{max\ gs}^{air}$ (Fig. 1d). This thermal adaptation of T_{opt}^{eco} , suggested by
161 the positive spatial slope of the T_{opt}^{eco} -air temperature relation, is also observed across biomes. As
162 shown in Fig. 2, there is a significant positive correlation between T_{opt}^{eco} and $T_{max\ gs}^{air}$ with a slope
163 of 0.76 across different biomes. Among biomes, the largest mean T_{opt}^{eco} is found in tropical
164 evergreen broad-leaved forest (29 ± 3 °C), and the smallest mean T_{opt}^{eco} (13 ± 3 °C) in cold grasslands
165 covering the Tibetan Plateau (Fig. 2 and Supplementary Fig. 8).

166
167 Both model results and very limited observational studies suggest a decrease in canopy
168 photosynthesis of tropical forests at high temperature^{15, 42-45} which led us to formulate the third
169 hypothesis of tropical forests already operating at T_{opt}^{eco} being close to $T_{max\ gs}^{air}$ implying that canopy
170 photosynthesis may decrease in case of future warming^{15, 16}. This hypothesis is verified from the
171 data shown in Fig. 3 (see also Supplementary Fig. 9). T_{opt}^{eco} is indeed slightly (1.4 °C) lower than
172 $T_{max\ gs}^{air}$ over tropical evergreen forests, suggesting a small ‘safety margin’ for canopy
173 photosynthesis under future warming. Note that the “safety margin” could become larger than that
174 suggested by the air temperature data if leaf thermal regulation would acclimate to the warming air
175 temperature (see Methods). In contrast, arctic (north of 65°N) and boreal (50°N-65°N) ecosystems
176 exhibit substantially larger safety margins, i.e. a larger positive difference between T_{opt}^{eco} and
177 $T_{max\ gs}^{air}$ (Fig. 3a and Supplementary Fig. 9). Analysis of the 16-day averaged T_{max}^{air} distribution
178 during the period when T_{opt}^{eco} is observed further shows that the rank of T_{opt}^{eco} in the T_{max}^{air}
179 distribution is already near the highest quantile of T_{max}^{air} (>70%) for tropical evergreen forests
180 (Supplementary Fig. 10). Based on this result, one may expect that rising air temperature in the

181 future, irrespective of the indirect effect of increasing VPD, may limit or decrease vegetation
182 productivity in tropical forests, but not in temperate or boreal ecosystems.

183

184 Global terrestrial daily maximum air temperature is projected to rise by 1.9 °C under the RCP2.6
185 low warming climate scenario and by 5.6 °C under the RCP8.5 scenario by 2100⁴⁶. We compared
186 these $T_{max\ gs}^{air}$ projections with the present-day distribution of T_{opt}^{eco} with a focus on tropical
187 evergreen forests, where optimum temperature is currently just below the limit of $T_{max\ gs}^{air}$ (see
188 Methods; Fig. 3b and 3c). The key uncertainty in this discussion is, however, whether or not T_{opt}^{eco}
189 will acclimate and follow the increase in $T_{max\ gs}^{air}$. We therefore looked at possible acclimation from
190 time series of T_{opt}^{eco} retrieved from the Advanced Very High Resolution Radiometer (AVHRR)
191 NDVI, which spans the last 30 years and comprises almost a 1°C temperature range. NDVI-derived
192 T_{opt}^{eco} did not have a significant trend over the last three decades except for the northern lands (north
193 of 60°N) where warming is more pronounced⁴⁷ (Supplementary Fig. 11). This suggests that the
194 recent 1°C warming is not large enough to elicit an acclimation response from some ecosystems,
195 given decadal variability⁴⁸. Also the annual T_{opt}^{eco} derived from flux sites estimates of GPP did not
196 exhibit a positive trend and was not significantly correlated with annual variations of $T_{max\ gs}^{air}$,
197 although the flux time series are probably too short to properly evaluate trends of T_{opt}^{eco} related to
198 possible acclimation processes (Supplementary Fig. 12). Because we detected no indication for its
199 existence, we first assumed no acclimation in the comparison of future $T_{max\ gs}^{air}$ projections from
200 climate models with the current distribution of T_{opt}^{eco} . Under this assumption, the average $T_{max\ gs}^{air}$
201 of tropical evergreen forests will exceed the current value of T_{opt}^{eco} for RCP2.6 by 2.6°C, and by 5.7
202 °C for RCP8.5 (Fig. 3c). On the other hand, boreal and arctic biomes will still remain within the

203 safety margin, with T_{opt}^{eco} staying above $T_{max\ gs}^{air}$ except under the RCP8.5 high warming scenario
204 (Fig. 3b and Supplementary Fig. 13).

205
206 Despite the lack of in situ observational evidence for GPP acclimation to the ongoing warming
207 trend, we tested a simple future acclimation scenario based on the space-for-time substitution
208 approach⁴⁹ as applied in several studies using observed spatial gradients to hindcast temporal
209 changes^{50,51}. Here, we assume that temporal change of T_{opt}^{eco} will evolve proportionally to $T_{max\ gs}^{air}$,
210 following the spatial temperature sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ in Fig. 1d and the indirect effects
211 of temperature increase (e.g. by increasing VPD) are excluded. We took the differences in
212 precipitation levels into account, so that areas that become wetter also exhibit faster acclimation.
213 Even with this assumed acclimation law, $T_{max\ gs}^{air}$ will still surpass T_{opt}^{eco} by 1.7 °C under RCP2.6
214 and by 2.5 °C under RCP8.5 for tropical evergreen forests (Fig. 3c). Not accounting for
215 precipitation levels in the acclimation rates produced similar results (Supplementary Figs. 14 and
216 15).

217
218 Our global-scale analysis of T_{opt}^{eco} derived from globally distributed point measurements of eddy
219 covariance and space-borne observations of proxies of vegetation productivity is a first attempt to
220 diagnose the global distribution of ecosystem-scale temperature optima of photosynthesis. It should
221 be noted, however, that hypotheses about that thermal acclimation of T_{opt}^{eco} are still highly uncertain,
222 because ecosystem adjustments can lag substantially behind the rate of future warming, particularly
223 for forests. More studies using data sets with longer time spans are needed in the future in order to
224 more accurately detect eventual thermal acclimation of T_{opt}^{eco} . Furthermore, the acclimation of
225 plants to increasing atmospheric CO₂ concentration and to changes in other environmental factors

226 (e.g. VPD) was also not considered in the current analyses. Constraining the spatially observed
227 temperature sensitivity of T_{opt}^{eco} over time is a priority for future studies. Continuous monitoring and
228 dedicated manipulative experiments could improve our understanding of the features of T_{opt}^{eco} and
229 thermal acclimation in earth system models⁵².

230

231 **Methods**

232 **FLUXNET data** The half-hourly eddy-covariance Gross Primary Productivity (GPP) data were
233 obtained from FLUXNET datasets, and were quality-controlled, filtered against low turbulence,
234 and gap-filled using consistent methods, as described by Papale et al.⁵³. Only freely available
235 FLUXNET data were used in this study. All the half-hourly GPP data were aggregated into daily
236 accumulated GPP for further estimates of the optimal temperature for vegetation productivity.
237 Daily maximum air temperature (T_{max}^{air}) was determined as the maximum air temperature value
238 from all the half-hourly air temperature observations. We included only site-years with more than
239 80% of half-hourly data available. A total of 153 individual FLUXNET sites with 663 site-years of
240 GPP data were used in this study.

241

242 **Near-infrared reflectance of terrestrial vegetation** Badgley et al.¹⁹ have recently proposed a new
243 approach for estimating vegetation photosynthetic capacity by remote sensing, i.e. the near-infrared
244 reflectance (NIR) of terrestrial vegetation (NIR_V), which can differentiate between the confounding
245 effects of background brightness, leaf area and the distribution of photosynthetic capacity with
246 depth in canopies¹⁹. NIR_V is calculated as the product of total scene NIR reflectance (NIR_T) and
247 Normalized Difference Vegetation Index (NDVI)¹⁹. As a proxy of photosynthesis, NIR_V is
248 suggested to be strongly correlated with Solar-induced Chlorophyll Fluorescence (SIF), a direct

249 index of photons intercepted by chlorophyll, and shows higher correlation with observed GPP than
250 NDVI¹⁹. We used satellite-derived NIR_v to calculate and map the optimal air temperature for
251 vegetation productivity at an ecosystem scale (T_{opt}^{eco}). Following Badgley et al.¹⁹, we calculated 16-
252 day NIR_v for 2001-2013 as the product of Moderate Resolution Imaging Spectroradiometer
253 (MODIS) 16-day NIR reflectance and MODIS 16-day NDVI, both of which were derived from the
254 MOD13A2 Vegetation Index Product with a spatial resolution of 1 km. Only positive NIR_v values
255 were used in the analysis.

256

257 **Normalized Difference Vegetation Index** The Normalized Difference Vegetation Index (NDVI)
258 is a vegetation index defined as the ratio of the difference between NIR and red visible reflectance
259 to their sum, and is widely used to represent vegetation greenness⁵⁴. To account for uncertainties
260 from different satellite datasets, three independent NDVI datasets were utilized, including biweekly
261 NDVI data from Global Inventory Modeling and Mapping Studies (GIMMS) Advanced Very High
262 Resolution Radiometer (AVHRR), 16-day NDVI data from Terra Moderate Resolution Imaging
263 Spectroradiometer (MODIS) and 10-day NDVI data from Satellite Pour l'Observation de la Terre
264 Vegetation (SPOT Vegetation). The three NDVI datasets spanned the last three decades: 1982-
265 2009 for AVHRR NDVI datasets, 2000-2009 for MODIS NDVI datasets, and 1999-2009 for SPOT
266 NDVI datasets, with the spatial resolutions of 8 km, 1 km, and 1 km, respectively. All NDVI
267 datasets have been corrected to reduce the effects of volcanic aerosols, solar angle, and sensor
268 errors^{20,55,56}. Pixels with a mean annual NDVI>0.1 were defined as the vegetated area for each
269 dataset.

270

271 **Enhanced Vegetation Index** The Enhanced Vegetation Index (EVI) is another vegetation index
272 designed to enhance the vegetation signal by minimizing canopy-soil variations and to improve

273 sensitivity over dense vegetation conditions²¹, and is found to correlate well with estimated GPP
274 on a site-by-site basis⁵⁷. We used a 16-day EVI dataset for the period of 2000-2009 with a spatial
275 resolution of 1 km from the MOD12A1 Vegetation Index Product. Effects from aerosols, solar
276 angle and sensor error have all been corrected²¹.

277

278 **Sun-induced Chlorophyll Fluorescence** Chlorophylls in plant absorb shortwave radiation and
279 dissipate excess energy as light or heat. The longwave radiation re-emitted by chlorophylls is
280 referred to as chlorophyll fluorescence. Recent studies have reported that remotely sensed Sun-
281 induced Chlorophyll Fluorescence (SIF) could serve as an indicator of photosynthesis rate and it is
282 well correlated with model-simulated GPP⁵⁸. Following the previous studies^{58,59}, we retrieved SIF
283 from two different retrieval windows, 757 nm and 771 nm, as well as the two polarization states, S
284 and P using observation of Fourier Transform Spectrometer (FTS) on the Japanese Greenhouse
285 gases Observing SATellite (GOSAT)²⁰. These diverse SIF samples were then aggregated into
286 monthly gridded data at a spatial resolution of 2° from June 2009 to June 2012.

287

288 **Vegetation distribution** We used MODIS land cover with the classification scheme of the
289 International Geosphere-Biosphere Programme (IGBP). The MODIS IGBP land cover data were
290 derived from the MOD12Q1 Land Cover Science Data Product at a spatial resolution of 1 km and
291 an updated digital Köppen-Geiger world map of climatic classification⁶⁰. Within the vegetated area
292 defined by NDVI thresholds, the 17 land cover types were reclassified into 9 vegetation types,
293 namely evergreen needle-leaved forest (ENF), evergreen broad-leaved forest (EBF), deciduous
294 needle-leaved forest (DNF), deciduous broad-leaved forest (DBF), mixed forest (MF), savannas,
295 cropland, grassland and shrubland. Based on the main climates in the world Map of the Köppen-
296 Geiger climatic classification⁶⁰, grassland was further subdivided into temperate grasslands, boreal

297 and arctic tundra, and shrubland was further subdivided into temperate and boreal shrubland. The
298 grassland over the Tibetan Plateau was considered separately considering the fact that Tibetan
299 Plateau has an average altitude higher than 4000 m a.s.l.⁶¹, and thus an unique alpine climate. In
300 contrast to temperate grasslands / shrubland where water is major limiting factor for vegetation
301 productivity, alpine ecosystems on the Tibetan Plateau are mainly limited by thermal conditions⁶².

302
303 **Climate dataset** The gridded air temperature and precipitation data for the period of 1982-2013
304 were obtained from the CRU/NCEP 6-hourly dataset with a spatial resolution of 0.5°. Note that the
305 purpose of this study is to investigate the optimal air temperature for photosynthesis. Optimal leaf
306 temperature is also interesting but not addressed in this study because accurate canopy-integrated
307 measurements of leaf temperatures are not available at the eddy covariance sites and at global scale
308 as gridded datasets. For a discussion about calculation of temperature optimum from air
309 temperature and from surface temperature, we used the remotely sensed land surface temperature
310 (LST), which is inversed from infra-red emissivity measured by MODIS (MYD11A2 version 6).
311 This dataset had an original spatial resolution of 1 km, spanning from July 2002 to December 2014.
312 The error of MODIS LST product, which primarily stems from cloud contamination and emissivity
313 uncertainties, was reported to be less than 3°C⁶³. Generally, the occurrence time of $T_{max}^{surface}$ (2:00-
314 4:00 P.M.) is relatively close to the Aqua overpass time (1:30 P.M.); thus, we assumed that
315 $T_{max}^{surface}$ from MODIS-Aqua is comparable with the daily maximum leaf surface temperature
316 (T_{max}^{leaf}). Corresponding to the temporal resolutions of MODIS, AVHRR and SPOT datasets,
317 respectively, the 6-hourly climate data were aggregated into 16-day, biweekly, and 10-day values
318 before further analyses. Given the different spatial resolutions of satellite observations and climate
319 data, we simply extracted time series of daily maximum air temperature and precipitation from the

320 aggregated CRU/NCEP data for each pixel of the sets of remotely sensed data. The daily maximum
321 air temperature (T_{max}^{air}) of the growing season averaged over 2001-2013 was calculated as the
322 current mean growing-season daily maximum air temperature ($T_{max\ gs}^{air}$). Information on the
323 growing season was derived from the study by Zhu et al.⁶⁴, which was first determined from the
324 GIMMS Leaf Area Index data set (GIMMS LAI_{3g}) using a Savitzky-Golay filter and then refined
325 by excluding the ground-freeze period identified by the Freeze/Thaw Earth System Data Record
326 (see details in ref 64). We also documented the temperature thresholds at which the growing season
327 begins and ends for each year. Temperature thresholds were averaged over 2001-2013 for the onset
328 and end of the growing season, respectively. We also used WATCH Forcing Data Methodology to
329 ERA-Interim data with a temporal resolution of three hours (WFDEI)⁶⁵.

330
331 We also used climate projections for the end of the 21st century (2091-2100) using 20 models that
332 participated in the phase five of Coupled Model Intercomparison Project (CMIP5) under the
333 RCP2.6, RCP4.5 and RCP8.5 scenarios⁴⁶ to determine the impact of future warming on vegetation
334 productivity (see model list in Supplementary Table 2). Considering the mismatch between
335 CRU/NCEP datasets and outputs from General Circulation Models (GCMs) for current climate
336 conditions, we generated future temperature and precipitation maps by adding the relative changes
337 in GCM-derived climate projections to the current climate for each pixel. $T_{max\ gs}^{air}$ for the late 21st
338 century was estimated using the same temperature thresholds as for the current $T_{max\ gs}^{air}$. All GCM
339 projections were resampled to a resolution of 1° using first-order conservative interpolation
340 method⁶⁶.

341

342 **Analysis** We estimated local T_{opt}^{eco} by examining the temperature response curve of MODIS NIR_V.
343 Following Yuan et al.³⁷ and Niu et al.¹⁸, NIR_V time series throughout the entire monitoring period
344 and the corresponding temperature data were grouped into 1°C-temperature bins for each pixel
345 within vegetated areas, which were defined as regions with a mean annual NDVI value larger than
346 0.1. We used the 90% quantile of the NIR_V data as the response of NIR_V within each temperature
347 bin due to the potential influences of other environmental constraints like clouds and droughts. We
348 next calculated the running means of every three temperature bins to develop the temperature
349 response curve of NIR_V. The T_{opt}^{eco} was then determined from the response curve at which NIR_V
350 was maximized (Supplementary Fig. 16). Note that T_{opt}^{eco} may not be detected for some pixels where
351 the maximum NIR_V was only attained at either end of the response curve, accounting for 3.5% of
352 the vegetated areas. Only vegetated areas with detectable T_{opt}^{eco} were shown when mapping the
353 spatial pattern of T_{opt}^{eco} . The derivation of T_{opt}^{eco} is robust to the choice of a particular climate-forcing
354 dataset (Supplementary Fig. 2). Instead of using the temperature corresponding to the maximum
355 90th quantile NIR_V to calculate T_{opt}^{eco} , we also applied nonlinear regression of the photosynthetic
356 temperature response data (Eq.1) to estimate T_{opt}^{eco} , which produced similar results (Supplementary
357 Fig. 2):

$$358 \text{NIR}_{V(T)} = \text{NIR}_{V(OPT)} - b(T - T_{opt}^{eco})^2 \quad (\text{Eq.1})$$

359 where $\text{NIR}_{V(T)}$ is the NIR_V value at a daily maximum temperature T, b is a parameter describing
360 the spread of the parabola^{48,67}. T_{opt}^{eco} is the vertex of each fit and $\text{NIR}_{V(OPT)}$ is the NIR_V value at
361 T_{opt}^{eco} . Finally, we used daily mean air temperature (T_{mean}^{air}) instead of T_{max}^{air} to calculate T_{opt}^{eco} . In this
362 test, T_{opt}^{eco} derived from T_{mean}^{air} is smaller than T_{opt}^{eco} estimated from T_{max}^{air} , but the two variables were
363 strongly spatially correlated (Supplementary Fig. 6).

364

365 We investigated the relationship between T_{opt}^{eco} and climate variables by averaging T_{opt}^{eco} in the
366 climate space with 1-°C intervals of mean annual T_{max}^{air} averaged over the growing season ($T_{max\ gs}^{air}$)
367 and 100-mm intervals of mean annual precipitation (MAP) (Fig. 1d). For each MAP interval, we
368 calculated the ‘apparent’ spatial sensitivity of T_{opt}^{eco} in response to changes in $T_{max\ gs}^{air}$ using
369 bootstrapping method. We performed the linear regression analysis 1000 times by randomly
370 selecting a subset of 80% of the samples from pairs of T_{opt}^{eco} and $T_{max\ gs}^{air}$ within each MAP interval.
371 The mean and SD of the 1000 temperature sensitivity of T_{opt}^{eco} were subsequently estimated along
372 the MAP gradient.

373
374 Air temperature, atmospheric vapor pressure deficit (VPD) and solar radiation usually co-vary in
375 time and space, so that the empirical observation of spatial patterns of T_{opt}^{eco} in this study cannot be
376 unambiguously attributed to air temperature as a single explaining factor of T_{opt}^{eco} . Under conditions
377 of high temperature, atmospheric VPD increases, soil moisture decreases with a lag, stomatal
378 conductance and hence carbon assimilation rates (GPP at the ecosystem-scale) decrease to prevent
379 exceedingly low leaf water potentials and resulting plant tissue damage from cavitation²⁴. We show
380 that across climatic gradients T_{opt}^{eco} is systematically higher at high maximum air temperatures but
381 not systematically lower at high VPD conditions (Supplementary Fig. 17). Then we calculated the
382 variance inflation factor (VIF) between VPD and $T_{max\ gs}^{air}$ under each VPD bin in the regression
383 model of:

$$384 \quad T_{opt}^{eco} = k_0 + k_1 \times T_{max\ gs}^{air} + k_2 \times VPD \quad (\text{Eq.2})$$

385 As shown in Supplementary Figure 18, we observed that VIF value ranged only between 1.001 and
386 1.438, suggesting relatively low multicollinearity between VPD and temperature. Even so, to
387 examine whether VPD can substantially affect the relationship between T_{opt}^{eco} and $T_{max\ gs}^{air}$, we

388 further calculated the partial ('intrinsic') sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ in each grid point based on
389 the following bilinear regression:

$$390 T_{opt}^{eco} = k_0 + k_1 \times T_{max\ gs}^{air} + k_2 \times VPD + k_3 \times VPD \times T_{max\ gs}^{air} \text{ (Eq.3)}$$

391 where the partial sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ is defined as k_1 in Eq. 3 under each VPD bin. Then
392 we compared the partial sensitivity with the apparent sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ estimated using
393 abovementioned linear regression between T_{opt}^{eco} and $T_{max\ gs}^{air}$ for each VPD bin. As shown in
394 Supplementary Fig. 19, although the apparent sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ is generally lower than
395 the partial ('intrinsic') sensitivity of T_{opt}^{eco} to $T_{max\ gs}^{air}$ the apparent sensitivity to $T_{max\ gs}^{air}$ remains
396 positive even when VPD is taken into account excepted under very high VPD bins (higher than
397 ~4.5 kPa) representing less than 1% of the study area. These results indicate that the patterns of
398 T_{opt}^{eco} are not dominated by high VPD reducing canopy photosynthesis, as an indirect effect of
399 higher air temperature increasing VPD. Moreover, we also calculated the percentiles of downward
400 shortwave solar radiation (Rad) at the time of year when T_{opt}^{eco} is observed for the 16-day averaged
401 Rad distribution. As shown in Supplementary Fig. 20, the Rad value when T_{opt}^{eco} was retrieved from
402 global observations were below the 95th percentile in the 16-day Rad distribution for ~80% of the
403 study area, which is mainly in mid and low latitudes such as Africa, India, Australia, eastern Brazil
404 and southern and southwestern of North America. By comparison, for most part of boreal regions,
405 part of south China, southeastern US, as well as part of South America, the timing of T_{opt}^{eco} is
406 consistent the time of maximum solar radiation. This is because T_{opt}^{eco} in these regions generally
407 appears in summer, which is also the period when solar radiation displays its maximum during the
408 year.

409

410 The NIR_v-derived T_{opt}^{eco} was compared with T_{opt}^{eco} estimated using GPP data from 153 eddy
411 covariance sites. Flux-derived T_{opt}^{eco} was determined for each site-year with daily-accumulated GPP
412 and corresponding temperature data from flux tower observations, applying the same method to
413 estimate local T_{opt}^{eco} using NIR_v datasets. A robust estimate of T_{opt}^{eco} can be derived for 125 sites
414 (Supplementary Table 1). For each site, we calculated the mean and SD of T_{opt}^{eco} across different
415 years. Then, we extracted and averaged T_{opt}^{eco} values within a 3×3 pixel window around each site
416 from the NIR_v-derived T_{opt}^{eco} map, and calculated the SD of the nine T_{opt}^{eco} values within the window.
417 The relationship between NIR_v- and flux-derived T_{opt}^{eco} was reported using a least square linear
418 regression, and the statistical significance of the slope, or its p -value, given by Student's t test. The
419 results show that NIR_v-derived T_{opt}^{eco} is comparable with that estimated independently from
420 measurements of flux-tower eddy covariance (Fig. 1b).

421
422 We compared the spatial distribution of T_{opt}^{eco} derived from NIR_v with the one obtained from NDVI
423 datasets. Consistent spatial patterns of T_{opt}^{eco} are derived from each of the three NDVI datasets
424 (Supplementary Fig. 21). A global composite map of T_{opt}^{eco} (Supplementary Fig. 3) was then
425 generated by averaging over estimates derived from the three NDVI datasets. Given the
426 inconsistent spatial resolutions of the different products, we resampled T_{opt}^{eco} to a common grid of
427 8 km before averaging. T_{opt}^{eco} from NDVI datasets generally show a spatial pattern similar to that
428 from NIR_v, but with smaller NDVI-derived T_{opt}^{eco} values for central Australia and southern South
429 America (Supplementary Fig. 3). We compared the spatial distribution of T_{opt}^{eco} derived from NIR_v
430 with that from MODIS EVI data during 2001-2013, and found that the EVI derived T_{opt}^{eco} shows
431 very similar spatial pattern to that of NIR_v derived T_{opt}^{eco} (Supplementary Fig. 4). The distribution

432 of T_{opt}^{eco} derived from NIR_v and from GOSAT SIF datasets also have similar spatial patterns, even
433 though the NIR_v-derived T_{opt}^{eco} is higher in tropical regions, particularly in cultivated areas of
434 southeastern Brazil (Supplementary Fig. 5).

435
436 At leaf scale, the photosynthesis-temperature response is suggested to be primarily controlled by
437 three sets of processes, namely biochemical, respiratory and stomatal processes⁶⁸. Much of the
438 effort to date to understand variability in the leaf-level photosynthesis-temperature response has
439 focused on biochemical processes⁶⁸, with V_{cmax} and J_{max} being two major parameters controlling
440 the maximum rates of photosynthesis limited by CO₂ and light, respectively⁶⁹. Therefore, in this
441 study, we compared T_{opt}^{eco} derived using GPP proxies with leaf-scale optimal temperature of
442 maximum Rubisco-limited carboxylation rates (V_{cmax}), although GPP is in theory more comparable
443 to net photosynthesis, that is, leaf gross photosynthesis minus photorespiration and minus dark
444 respiration. Since photorespiration increases exponentially with temperature⁷⁰, the optimum
445 temperature of GPP (T_{opt}^{eco}) should, in theory, be lower than the optimal temperature of maximum
446 Rubisco-limited carboxylation rates (V_{cmax}). For this comparison to be made, we extracted and
447 averaged T_{opt}^{eco} values within a 3×3 pixel window from the NIR_v-derived T_{opt}^{eco} map around the
448 reported site location (longitude and latitude) of leaf-scale measurements. For leaf-scale
449 measurements without the information of site location, we calculated the average NIR_v-derived
450 T_{opt}^{eco} values across pixels with both the same growing season mean temperature and the same plant
451 functional type as the corresponding site.

452
453 T_{opt}^{eco} is different from T_{opt}^{leaf} not only because of respiratory process, but also because air
454 temperature can differ from leaf temperatures⁷¹, which are regulated by leaf traits affecting the leaf

455 energy balance⁷². Because, to our knowledge, global gridded monthly leaf temperature data are not
456 available, we use daily maximum land surface temperature ($T_{max}^{surface}$) from MODIS to calculate
457 $T_{opt_LST}^{eco}$ in order to illustrate the potential differences between $T_{opt_LST}^{eco}$ and T_{opt}^{eco} . As shown in
458 Supplementary Figure 22, the $T_{opt_LST}^{eco}$ is similar to T_{opt}^{eco} over tropical savannas. However, over
459 moist tropical forests $T_{opt_LST}^{eco}$ is lower than T_{opt}^{eco} , which can be explained by the lower daytime
460 surface temperature than air temperature as a result of strong evapotranspiration effects^{71,73}. This
461 ecosystem-dependent difference between $T_{opt_LST}^{eco}$ and T_{opt}^{eco} suggests that the leaf thermal
462 regulation mechanism through the physiological and morphological changes⁷² is an important
463 ecosystem process shaping spatial variations of T_{opt}^{eco} . In addition, if the difference between leaf
464 temperature and air temperature would become larger in response to warmer air temperatures (i.e.
465 if leaf thermal regulation acclimates to warmer temperature), the “safety margin” of tropical
466 ecosystems would become larger than the air temperature data are currently suggesting. However,
467 the long-term in-situ leaf temperature data required to test this hypothesis independently are
468 currently not available.

469
470 To account for potential changes in T_{opt}^{eco} under future warming, we estimated the acclimated T_{opt}^{eco}
471 for vegetation productivity by the end of the 21st century (2091-2100), using recent IPCC climate
472 projections⁴⁶. To this end, we applied the space-for-time substitution approach⁴⁹, assuming that that
473 temporally T_{opt}^{eco} will evolve proportionally to $T_{max\ gs}^{air}$ following the spatial temperature sensitivity
474 of T_{opt}^{eco} to $T_{max\ gs}^{air}$. Given the relatively large uncertainties of precipitation projections, we
475 considered two future precipitation scenarios. For the first scenario, we estimated acclimated T_{opt}^{eco}
476 pixel by pixel using the temperature sensitivity of T_{opt}^{eco} under the present MAP level, assuming that
477 MAP does not change between the end of the 21st century. For the second scenario, we accounted

478 for in MAP, and the acclimated T_{opt}^{eco} was calculated pixel by pixel using the temperature sensitivity
479 of T_{opt}^{eco} under the projected MAP level for 2091-2100. Acclimated T_{opt}^{eco} was averaged across the
480 GCMs under each scenario. Latitudinal variation of future T_{opt}^{eco} was derived by averaging within
481 1°-latitude bins from future T_{opt}^{eco} maps and then compared with that in future $T_{max\ gs}^{air}$ summarized
482 by latitude from future $T_{max\ gs}^{air}$ maps.

483

484 **Data Availability**

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

487

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671

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703

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705

706 **Figure legends**

707 **Fig. 1 | Distribution of ecosystem-scale optimal temperature (T_{opt}^{eco}) for vegetation productivity**
708 **derived from flux tower sites and satellite-based data for near-infrared reflectance of**
709 **vegetation (NIR_v).** **a**, Relationship between mean annual daily maximum air temperature during
710 the growing season ($T_{max\ gs}^{air}$) and T_{opt}^{eco} derived from daily measurements of photosynthesis across
711 eddy-covariance sites. Flux-derived $T_{max\ gs}^{air}$ and T_{opt}^{eco} were both obtained using observations from
712 flux towers. Error bars indicate \pm SD. The dotted gray line represents $y=x$ and the dot line in red is
713 $y=0.61x+10.65$, which is derived by linear regression with the statistical significance of the slope,
714 or its p -value, given by Student's t test. **b**, Relationship between T_{opt}^{eco} derived from flux data and
715 T_{opt}^{eco} derived from NIR_v data. For each site, we extracted and averaged T_{opt}^{eco} values within a 3×3
716 pixel window around the site from NIR_v-derived T_{opt}^{eco} map, and calculated the SD of the nine T_{opt}^{eco}
717 values within the window. Error bars indicate \pm SD. The dotted gray line represents $y=x$ and the dot
718 line in red is $y=0.74x+7.10$, which is derived by linear regression with the statistical significance
719 of the slope, or its p -value, given by Student's t test. **c**, Spatial distribution of T_{opt}^{eco} for vegetation
720 productivity (left panel), and T_{opt}^{eco} averaged by latitude (right panel). T_{opt}^{eco} is determined using
721 NIR_v data calculated based on satellite observations from Moderate Resolution Imaging
722 Spectroradiometer (MODIS). Note that only gridded pixels with annual mean NDVI value larger
723 than 0.1 and detectable T_{opt}^{eco} are shown here. Areas of tropical forests based on current vegetation
724 distribution are indicated by hatching. The circles on the map are colored according to the local
725 value of T_{opt}^{eco} retrieved from GPP at the location of each flux site. The solid line and shaded area
726 in the right panel indicate the mean and SD, respectively, of T_{opt}^{eco} summarized by latitude. **d**, T_{opt}^{eco}
727 in the climate space (left panel) and the temperature sensitivity of T_{opt}^{eco} along the precipitation
728 gradient (right panel). Each climate bin is defined by 1-°C intervals of $T_{max\ gs}^{air}$ and 100-mm

729 intervals of mean annual precipitation, based on current climate conditions averaged over 2001-
730 2013. The solid line in the right panel represents the temperature sensitivity of T_{opt}^{eco} along the
731 precipitation gradient, calculated as the slope of the linear regression between T_{opt}^{eco} and $T_{max\ gs}^{air}$ for
732 a given precipitation level. The shaded area indicates the SD of temperature sensitivity of T_{opt}^{eco}
733 estimated by bootstrapping.

734

735 **Fig. 2 | Relationship between mean annual daily maximum air temperature during the**
736 **growing season ($T_{max\ gs}^{air}$) and ecosystem-scale optimum temperature for vegetation**
737 **productivity (T_{opt}^{eco}) across vegetation types.** The error bars indicate the SDs of $T_{opt}^{eco}/T_{max\ gs}^{air}$ for
738 each vegetation type: ENF, evergreen needle-leaved forest; EBF, evergreen broad-leaved forest;
739 DNF, deciduous needle-leaved forest; DBF, deciduous broad-leaved forest; MF, mixed forest;
740 Shrub, closed and open shrublands. The light-gray dotted line represents $y=x$. The dark-gray dotted
741 line is $y=0.76x+6.48$ derived by linear regression with the slope value (estimated using Student's t
742 test) shown in the bottom right. The red dotted line is the flux tower derived slope (0.61) from Fig.
743 1a. The size of each symbol corresponds to the three categories (< 3%, 3%-10% and > 10%) of
744 occupied vegetated area on land. Error bars indicate \pm SD.

745

746 **Fig. 3 | Change with latitude in ecosystem-scale optimal temperature for vegetation productivity (T_{opt}^{eco}) and daily**
747 **maximum air temperature averaged over the growing season ($T_{max\ gs}^{air}$).** **a**, Current T_{opt}^{eco} versus current $T_{max\ gs}^{air}$; **b**,
748 Future T_{opt}^{eco} versus future $T_{max\ gs}^{air}$. Current T_{opt}^{eco} and $T_{max\ gs}^{air}$ are calculated using current temperature for 2001-2013,
749 whereas acclimated T_{opt}^{eco} and future $T_{max\ gs}^{air}$ are first calculated pixel by pixel using temperature for 2091-2100
750 projected by General Circulation Models (GCMs) under the RCP4.5 scenario and then averaged by latitude.
751 Acclimated T_{opt}^{eco} is determined based on the projected temperature and temperature sensitivity of T_{opt}^{eco} using the annual
752 precipitation level predicted for 2091-2100. The solid line and shaded area in each panel indicate the mean and SD,

753 respectively, of T_{opt}^{eco} or $T_{max\ gs}^{air}$ summarized by latitude. **c**, Future T_{opt}^{eco} versus future $T_{max\ gs}^{air}$ for tropical evergreen
754 forests. ** indicates that T_{opt}^{eco} is significantly lower than $T_{max\ gs}^{air}$ at $P < 0.01$ in a paired t-test. Error bars indicate $\pm SD$.