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4 Global evidence for the acclimation of ecosystem photosynthesis to light

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15

## 16 **Abstract**

17 Photosynthesis responds quickly to changes in light, increasing with incoming photosynthetic  
18 photon flux density (PPFD) until leaves become light saturated. This instantaneous response to  
19 PPFD, which is widely studied and incorporated into models of photosynthesis, is overlaid on  
20 non-instantaneous photosynthetic changes resulting from the acclimation of plants to average  
21 PPFD over intermediate timescales of a week to months ( $\overline{\text{PPFD}}$ ). Such photosynthetic light  
22 acclimation is not typically incorporated into models, due to the lack of observational constraints.  
23 Here, we use eddy covariance observations from globally distributed and automated sensor  
24 networks, along with photosynthesis estimates from 9 terrestrial biosphere models (TBMs) to  
25 quantify and assess photosynthetic acclimation to light in natural environments. In addition, we  
26 use recent theoretical developments to incorporate light acclimation in a TBM. Our results show  
27 widespread light acclimation of ecosystem photosynthesis. On average, a  $1 \mu\text{mol m}^{-2} \text{s}^{-1}$  increase

28 in  $\overline{\text{PPFD}}_{10}$  (10-day average PPFD) leads to a  $0.031 \pm 0.013 \mu\text{mol C m}^{-2} \text{ s}^{-1}$  increase in maximum  
29 photosynthetic assimilation rate ( $A_{\text{max}}$ ), with croplands having a stronger acclimation rate than  
30 grasslands and forests. Our analysis shows that the TBMs examined either neglect or  
31 substantially underestimate light acclimation. By updating a TBM to include photosynthetic  
32 acclimation, successfully reproducing the  $\overline{\text{PPFD}}_{10}$ - $A_{\text{max}}$  relationship, we provide a robust method  
33 for the incorporation of photosynthetic light acclimation in future models.

34

## 35 **Main**

36 Global photosynthesis is the largest carbon flux in the global carbon cycle <sup>1</sup>, removing CO<sub>2</sub> from  
37 the atmosphere and thus contributing to climate change mitigation. The amount of carbon  
38 assimilated by photosynthesis is dependent on the short- and long-term responses of vegetation  
39 to a range of climate factors, in particular incoming solar irradiance, about half of which is  
40 photosynthetically active photons <sup>2</sup>. The intensity of incoming photosynthetic active photons is  
41 described by photosynthetic photon flux density (PPFD; unit:  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ). PPFD is  
42 utilized by leaves in a fast biochemical process that converts photonic energy into biochemical  
43 energy to drive the Calvin-Benson cycle and ultimately fix CO<sub>2</sub> into starches and sugars that are  
44 used to maintain metabolism and grow biomass <sup>3</sup>. The relationship between the instantaneous  
45 rate of photosynthesis ( $A$ ) and PPFD has been well documented using light response curves, in  
46 which  $A$  generally increases with PPFD and plateaus at maximum  $A$  ( $A_{\text{max}}$ ) when leaves become  
47 light saturated <sup>4</sup>.

48

49 The well documented light response curves, and the understanding of leaf biochemical processes  
50 generated from them, form the basis of many terrestrial biosphere models (TBMs), the principle

51 tools used to estimate the terrestrial carbon cycle<sup>5</sup>. In such models, however, PPFD only  
52 influences instantaneous rates of photosynthetic carbon assimilation. This approach is at odds  
53 with results from field experiments, which show that, over intermediate timescales of a week to  
54 months, plants also respond to increasing PPFD by increasing  $A_{\max}$ <sup>6-10</sup>. Experimental  
55 observations consistently show that leaves exposed to higher average levels of PPFD over  
56 intermediate timescales ( $\overline{\text{PPFD}}$ ) tend to have larger  $A_{\max}$ . For example, leaf-level  $A_{\max}$  can  
57 increase from less than  $5 \mu\text{mol C m}^{-2} \text{s}^{-1}$  to more than  $15 \mu\text{mol C m}^{-2} \text{s}^{-1}$  while autumn  $\overline{\text{PPFD}}$   
58 increases from approximately  $50 \mu\text{mol photon m}^{-2} \text{s}^{-1}$  to  $600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ <sup>6</sup>. This strategic  
59 adjustment to  $\overline{\text{PPFD}}$  improves plant light-use efficiency, a process known as photosynthetic light  
60 acclimation, to further increase the magnitude of instantaneous  $A$ .

61  
62 Historically, studies have investigated photosynthetic light acclimation at the leaf scale and for  
63 limited species in controlled experiments, providing an incomplete picture of the existence,  
64 degree and pattern of photosynthetic light acclimation in natural ecosystems. Additionally, many  
65 studies have found that the within-canopy gradient of leaf-level photosynthetic capacity is  
66 optimized to follow the within canopy light profile<sup>11,12</sup>, indicating that leaf-level light  
67 acclimation underlies the ecosystem-scale photosynthetic activity. However, the connection  
68 between leaf and ecosystem light acclimation has remained elusive, as direct evidence of  
69 ecosystem-scale light acclimation is lacking, as is an effective method to simulate acclimation.  
70 Hence, photosynthetic light acclimation is ignored in state-of-the-art TBMs<sup>13</sup>. Globally  
71 distributed observations of ecosystem carbon fluxes based on the eddy-covariance technique<sup>14,15</sup>,  
72 and the resulting estimates of ecosystem gross primary productivity<sup>16</sup>, offer a unique opportunity  
73 to examine the degree of photosynthetic light acclimation in natural ecosystems. In tandem,

74 recent theoretical developments, in particular the coordination hypothesis, which suggests that  
75 plant photosynthesis acclimates at intermediate timescales of weeks to months<sup>17-21</sup>, provide a  
76 potential approach to incorporate the process of photosynthetic light acclimation into TBMs.

77

78 Here, we use globally distributed eddy covariance measurements from more than a hundred sites  
79 to examine ecosystem scale photosynthetic light acclimation. We estimate ecosystem  $A_{\max}$  using  
80 a light response curve approach<sup>16</sup> across all sites, and characterize the ecosystem light  
81 acclimation rate ( $\gamma_A$ ) as the sensitivity of  $A_{\max}$  to  $\overline{\text{PPFD}}_{10}$  (i.e. 10-day average PPFD). The  
82 objectives of this study are to examine whether and to what degree ecosystem photosynthetic  
83 light acclimation (i.e. positive  $\gamma_A$ ) occurs, to understand the distribution of  $\gamma_A$  along  
84 environmental and ecological gradients, to evaluate TBMs using  $\gamma_A$  inferred from observations,  
85 and to develop and test an approach to incorporate photosynthetic light acclimation into TBMs.

86

## 87 **Results and Discussion**

88 We derived ecosystem  $A_{\max}$  from half-hourly net ecosystem carbon exchange measured at eddy  
89 covariance sites covering a wide range of variation in  $A_{\max}$  and environmental factors. Multiple  
90 environmental factors co-vary with PPFD on intermediate timescales, in particular daytime air  
91 temperature ( $T_{\text{air}}$ ) and vegetation foliage densities (indicated by fraction of absorbed  
92 photosynthetic active radiation; fAPAR; unitless). In order to remove the influence of extraneous  
93 environmental variability, we grouped the derived  $A_{\max}$  and observed  $\overline{\text{PPFD}}_{10}$  into bins by their  
94 corresponding fAPAR and  $T_{\text{air}}$  (see Methods) and then quantified  $\gamma_A$  within each bin (Fig.1). In  
95 addition to removing extraneous influences on the derived photosynthetic light acclimation, this  
96 also allowed us to examine light acclimation across environmental gradients. We detected

97 positive  $\gamma_A$  in 85% of the bins studied, suggesting a widespread existence of photosynthetic light  
98 acclimation under natural conditions (Fig. 1a). 59.8% of those positive  $\overline{\text{PPFD}}_{10}$ - $A_{\text{max}}$  correlations  
99 were statistically significant ( $p < 0.1$ ; 48.1% for  $p < 0.05$ ). Our analysis found an average  $\gamma_A$  of  
100  $0.031 \pm 0.013 \text{ mol mol}^{-1}$  ( $\mu\text{mol C m}^{-2} \text{ s}^{-1}$  per  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ; mean  $\pm$  s.d.) for the significant  
101 acclimation cases ( $p < 0.1$ ). Changes in the length of the time windows we used to detect light  
102 acclimation did not affect our results (Extended Data Fig. 1). We used a linear regression of  $A_{\text{max}}$   
103 to  $\overline{\text{PPFD}}_{10}$  to derive  $\gamma_A$  (Fig. 1b) as it was commonly adopted by previous leaf-level experiments  
104 <sup>6,9</sup>, though we acknowledge cases where  $A_{\text{max}}$  responded to  $\overline{\text{PPFD}}$  non-linearly <sup>8,10</sup>. The  
105 ecosystem  $\gamma_A$  ( $0.031 \pm 0.013 \text{ mol mol}^{-1}$ ) we derived from the eddy covariance data was  
106 comparable to the leaf-level  $\gamma_A$  ( $0.027 \pm 0.016 \text{ mol mol}^{-1}$ ) we collated from previous studies (Fig.  
107 1c; Supplementary Table 1). It should be noted that ecosystem  $\gamma_A$  is the slope of the regression of  
108 canopy  $A_{\text{max}}$  ( $\mu\text{mol C m}^{-2}$  ground surface area  $\text{s}^{-1}$ ) to  $\overline{\text{PPFD}}_{10}$  ( $\mu\text{mol photon m}^{-2}$  ground surface  
109 area  $\text{s}^{-1}$ ), while leaf  $\gamma_A$  is the slope of the regression of leaf  $A_{\text{max}}$  ( $\mu\text{mol C m}^{-2}$  leaf area  $\text{s}^{-1}$ ) to  
110  $\overline{\text{PPFD}}_{10}$  ( $\mu\text{mol photon m}^{-2}$  ground surface area  $\text{s}^{-1}$ ), meaning that ecosystem  $\gamma_A$  is equal to the  
111 sum of  $\gamma_A$  of all leaves in a canopy divided by total leaf area (a.k.a. the average leaf  $\gamma_A$ ). The  
112 ecosystem  $\gamma_A$  we derived is therefore comparable to published leaf-level  $\gamma_A$  (Fig. 1c). We note  
113 that using an  $A_{\text{max}}$  standardized to a PPFD of  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  resulted in a somewhat lower  $\gamma_A$   
114 of  $0.025 \pm 0.012 \text{ mol mol}^{-1}$  (Extended Data Fig. 2).

115

116 Although we show light acclimation is related to light intensity (i.e.  $\overline{\text{PPFD}}_{10}$ ), some studies  
117 suggested photoperiod <sup>22</sup> and the total amount of photons <sup>10</sup> received by vegetation can cause  
118 changes in  $A_{\text{max}}$ . We assessed the dependence of  $A_{\text{max}}$  on photoperiod (the number of daytime  
119 hours in a day; unit: hours) and total photons ( $\text{mol m}^{-2} \text{ day}^{-1}$ ) of the same 10-day windows, and

120 found positive  $\gamma_A$  in more than 80% of the bins in both cases (Extended Data Fig. 3). The  
121 patterns of  $\gamma_A$  we derived from the regressions of  $A_{\max}$  to photoperiod and total photons were  
122 very similar to what we obtained when using  $\overline{\text{PPFD}}_{10}$  (Fig. 1a), potentially caused by the strong  
123 correlations between three light metrics. In this study, we used  $\overline{\text{PPFD}}_{10}$  as the primary predictor  
124 in order to compare with theoretical acclimation predictions of the response of  $A_{\max}$  to light  
125 intensity.

126

127 We further examined several potential drivers to explain the changes in ecosystem  $\gamma_A$ . First, we  
128 found that ecosystem  $\gamma_A$  (the average  $\gamma_A$  of bins with significant ( $p < 0.1$ ) light acclimation) was  
129 relatively insensitive to fAPAR between 0.4 to 0.6, as  $\gamma_A$  stabilized at  $0.028 \pm 0.011 \text{ mol mol}^{-1}$   
130 (Fig. 2a). However, for dense canopies where  $\text{fAPAR} > 0.6$ ,  $\gamma_A$  significantly increased with  
131 fAPAR to  $0.041 \pm 0.015 \text{ mol mol}^{-1}$  ( $p < 0.05$ ; Fig. 2a; Extended Data Fig. 1). Considering that  
132 ecosystem  $\gamma_A$  indicates the average leaf  $\gamma_A$  within a canopy, and that shaded leaves constitute an  
133 increasingly larger portion of a canopy as fAPAR increases (Extended Data Fig. 4)<sup>23</sup>, our results  
134 indicate that shaded leaves acclimate to light faster than sunlit leaves. This suggests a nonlinear  
135 and gradually saturating response of  $A_{\max}$  to  $\overline{\text{PPFD}}$ , which has been proposed by a meta-  
136 analysis<sup>10</sup> though some studies suggested otherwise<sup>6,8</sup>. Meanwhile, the changes in fAPAR did  
137 not influence the detectability of light acclimation (i.e. the ratio of the number of the bins where  
138  $\gamma_A > 0$  and  $p < 0.1$  to the total number of bins) using our method, as the detectability stabilized at  
139 60%.

140

141 We found that the detectability of light acclimation changed as a function of  $T_{\text{air}}$ , with  
142 detectability declining from almost 100% to 0% when  $T_{\text{air}}$  either increased or decreased from

143 around 10 °C to the higher or lower end of the temperature range (Fig. 2b). The decreased  
144 detectability of acclimation at low temperature could potentially be caused by photoinhibition, a  
145 light-induced process that damages photosystem II and downregulates  $A_{\max}$ <sup>24</sup> and consequently  
146 influences  $\gamma_A$ . Several studies have found that the effect of photoinhibition is particular evident at  
147 low temperature<sup>25-27</sup>, though there are conflicting reports over the temperature dependence of  
148 photoinhibition<sup>28</sup>. In addition, we found that the decreased detectability of light acclimation  
149 under high temperature was related to the effect of vapor pressure deficit (VPD) on stomatal  
150 conductance (Fig. 2d). Stomatal aperture is inversely related to VPD<sup>29,30</sup>, and stomatal closure  
151 could reduce  $A_{\max}$  and hence influence  $\gamma_A$ . Note however that our data pre-filtering criteria  
152 removed most periods with moderate to high VPD (see Methods section 3), in order to minimize  
153 the VPD effect on  $\gamma_A$ . For those bins with significant ( $p < 0.1$ ) light acclimation,  $\gamma_A$  was  $0.033 \pm$   
154  $0.017 \text{ mol mol}^{-1}$  for  $T_{\text{air}} < 10 \text{ °C}$ ,  $0.027 \pm 0.010 \text{ mol mol}^{-1}$  for  $T_{\text{air}}$  between 10 °C and 20 °C, and  
155  $0.039 \pm 0.013 \text{ mol mol}^{-1}$  for  $T_{\text{air}} > 20 \text{ °C}$ . (Fig. 2b; Extended Data Fig. 1). The significantly  
156 higher  $\gamma_A$  ( $t$ -test,  $p < 0.05$ ) under warmer conditions is consistent with some previous reports<sup>31,32</sup>,  
157 though a lack of experimental observations on the temperature dependence of light acclimation  
158 precludes a mechanistic explanation. We also noted that the higher percentage of data pairs from  
159 cropland and broadleaf forests (Extended Data Fig. 5), which had a higher acclimation rate (Fig.  
160 2c), might explain the higher  $\gamma_A$  we found under warm conditions.

161  
162  $\gamma_A$  varied by plant functional type (PFT) (Fig. 2c; Extended Data Fig. 6), with croplands (CRO)  
163 having the largest acclimation rate around  $0.073 \pm 0.117 \text{ mol mol}^{-1}$ , followed by evergreen  
164 broadleaf forests (EBF;  $0.052 \pm 0.058 \text{ mol mol}^{-1}$ ), deciduous broadleaf forests (DBF;  $0.049 \pm$   
165  $0.077 \text{ mol mol}^{-1}$ ), grasslands (GRA;  $0.045 \pm 0.042 \text{ mol mol}^{-1}$ ), mixed forests (MF;  $0.034 \pm 0.059$

166 mol mol<sup>-1</sup>) and evergreen needleleaf forests (ENF;  $0.032 \pm 0.043$  mol mol<sup>-1</sup>).  $\gamma_A$  from CRO was  
167 significantly larger than  $\gamma_A$  of the others (*t*-test,  $p < 0.05$ ). This variation in  $\gamma_A$  reflects a  
168 difference in the photosynthetic plasticity between PFTs, with some studies attributing the inter-  
169 species variations in photosynthetic plasticity to successional stages<sup>33</sup> and nutrient use strategies  
170<sup>34</sup>. The inter-PFT variation in  $\gamma_A$  is potentially related to nitrogen use efficiency (NUE), which  
171 could influence  $A_{\max}$ <sup>35</sup>. The rank ordering of  $\gamma_A$  we observed for each PFT (CRO > DBF = EBF >  
172 ENF) (Fig. 2c), was similar to the rank ordering of NUE reported based on the global TRY plant  
173 trait database<sup>36</sup>. We note that some bins had negative  $\gamma_A$ , though most of the negative  $\gamma_A$  were  
174 not statistically significant (Extended Data Fig. 6). Uncertainties in  $\gamma_A$ , as well as the occurrences  
175 of negative  $\gamma_A$ , can be caused by some light properties (i.e. spectral quality<sup>37</sup> and light  
176 fluctuations<sup>38,39</sup>) and biological factors (i.e. leaf age<sup>40</sup>) that are known to impact light acclimation  
177 but not considered here. We also note that most negative  $\gamma_A$  values corresponded to bins with few  
178 data pairs (i.e. only 6 – 60 pairs per bin) available to constrain the  $A_{\max} - \overline{\text{PPFD}}_{10}$  relationship  
179 (Extended Data Fig. 5 and 7).

180

181 We further tested nine TBMs (Supplementary Table 3) to assess the degree of  $\gamma_A$  in their  
182 simulations (Fig. 3a). We found that none of the models captured the observed distribution of  $\gamma_A$ ,  
183 with five models showing positive but underestimated  $\gamma_A$  (BEPS  $0.011 \pm 0.021$  mol mol<sup>-1</sup>; CN-  
184 CLASS  $0.007 \pm 0.030$  mol mol<sup>-1</sup>; ECOSYS  $0.023 \pm 0.025$  mol mol<sup>-1</sup>; SiBCASA  $0.006 \pm 0.017$   
185 mol mol<sup>-1</sup>; SSiB2  $0.004 \pm 0.010$  mol mol<sup>-1</sup>) and four models showing zero or negative mean  $\gamma_A$   
186 (Can-IBIS  $-0.011 \pm 0.008$  mol mol<sup>-1</sup>; ORCHIDEE  $-0.010 \pm 0.016$  mol mol<sup>-1</sup>; SiB  $-0.007 \pm 0.016$   
187 mol mol<sup>-1</sup>; TECO  $-0.029 \pm 0.021$  mol mol<sup>-1</sup>). Non-zero  $\gamma_A$  in models that do not explicitly  
188 account for acclimation can potentially arise due to a prescribed variation in the maximum

189 carboxylation rate ( $V_{c_{max}}$ ), which influences simulated  $A_{max}$  under light saturation conditions <sup>36</sup>.  
190 However,  $V_{c_{max}}$  variation in the examined TBMs is dependent on either biomass allocation <sup>41</sup>, or  
191 soil nutrient limitation and optimized water use <sup>42</sup>, or a simple scaling factor <sup>43</sup>, rather than the  
192 direct acclimation of  $A_{max}$  to  $\overline{PPFD}_{10}$ . These empirical methods are often generalized from local  
193 studies and prone to estimating biased  $\gamma_A$  when extrapolated to large scales (Fig. 3a), highlighting  
194 a need to explicitly consider the  $\overline{PPFD}_{10}$  -  $A_{max}$  relationship in TBMs.

195  
196 Recent theoretical advances provide an opportunity to implement photosynthetic light  
197 acclimation from the first principles of photosynthesis. Here, we tested an approach that predicts  
198 the responses of  $V_{c_{max}}$  to multiple environmental factors from first principles <sup>19</sup>, and which can  
199 be used to predict the acclimation of  $A_{max}$  to light. The model was developed based on the  
200 coordination hypothesis which suggests that the light and dark reactions of photosynthesis are  
201 coordinated to optimize light use efficiency <sup>17-21</sup> (see Methods). We incorporated this optimality  
202 model in one of the TBMs investigated, BEPS <sup>44,45</sup>, and found that  $\gamma_A$  significantly improved (*t*-  
203 test,  $p < 0.05$ ) from  $0.011 \pm 0.021$  mol mol<sup>-1</sup> in the original BEPS to  $0.023 \pm 0.014$  mol mol<sup>-1</sup> in  
204 the updated BEPS (BEPS-opt) (Fig. 3b). The improvement in  $\gamma_A$  resulted in a 5.2% increase in  
205 the intra-annual variation in estimated gross primary productivity (GPP) and a 28.9% increase (*t*-  
206 test,  $p < 0.05$ ) in the inter-annual variation in estimated GPP, which were closer to the variations  
207 in GPP we derived from eddy covariance observations (Fig. 3c, d).

208  
209 Photosynthetic light acclimation is a key feature of plants that leads to spatial and temporal  
210 changes in global photosynthesis and ecosystem carbon uptake. In this study, we analyzed a  
211 database of eddy covariance observations and found widespread photosynthetic light acclimation.

212 The global average acclimation rate detected was  $0.031 \pm 0.013 \text{ mol mol}^{-1}$  ( $p < 0.1$ ), which is  
213 comparable to the previously reported leaf-level acclimation rate. The acclimation rate of  
214 croplands was observed to be stronger than that of forests and grasslands. The observed light  
215 acclimation was independent of changes in canopy leaf area for sparse canopies but increase with  
216 foliage amount for dense canopies, potentially suggesting shaded leaves acclimate faster to light  
217 than sunlit leaves. Low temperature reduced the detectability of light acclimation potentially due  
218 to photoinhibition, and high temperature did so by increasing VPD and the resulting stomatal  
219 closure. Nine state-of-the-art TBMs we tested failed to accurately reproduce the magnitude of  
220 light acclimation we observed. By incorporating a recently developed optimality model in a  
221 TBM, we constrained the associated uncertainty and successfully reproduced the magnitude of  
222 observed light acclimation. Together, these results suggest that the long-observed acclimation of  
223 photosynthesis to light at the leaf scale is also prevalent at the ecosystem scale, and provide an  
224 effective approach for its incorporation into land surface models.

225

226

## 227 **Methods**

### 228 **1. Derivation of $A_{\max}$ from eddy covariance measurements**

229 We used eddy covariance observations of carbon exchange between ecosystems and the  
230 atmosphere provided in the standard FLUXNET2015 Tier 1 dataset<sup>46</sup>. It provides half-hourly  
231 and hourly net carbon flux ( $F_c$ ) and their concurrent meteorological records for 166 sites from  
232 different regional networks (Supplementary Table 2). We used gap-filled meteorological records  
233 including incoming solar radiation (SW\_IN\_F), air temperature (TA\_F) and vapor pressure

234 deficit (VPD<sub>F</sub>) to derive the seasonal varying  $A_{\max}$  of eddy covariance sites from non-gap-filled  
235  $F_c$  measurements.

236  $F_c$  is the balance of CO<sub>2</sub> taken up by photosynthesis and released by respiration. In the process of  
237 partitioning  $F_c$  into an ecosystem photosynthesis and respiration term using the daytime  
238 partitioning method<sup>16,47</sup>, a key step is to fit  $F_c$  with a light response curve (LRC):

$$239 \quad F_c = \frac{\alpha\beta R_g}{\alpha R_g + \beta} + \gamma \quad (1)$$

240 where  $\alpha$  ( $\mu\text{mol J}^{-1}$ ) is the canopy-scale quantum yield,  $\beta$  is the maximum rate of CO<sub>2</sub> uptake of  
241 the canopy under saturating light levels ( $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ ), which is equivalent to  $A_{\max}$ .  $R_g$  is  
242 the global radiation and  $\gamma$  is the ecosystem respiration term. The impact of VPD on  $\beta$  is  
243 considered by requiring that  $\beta$  decreases exponentially with the increase of VPD when VPD  
244 exceeds a threshold (VPD<sub>0</sub>).

$$245 \quad \beta = \begin{cases} \beta_0 \exp(-k(\text{VPD} - \text{VPD}_0)), & \text{VPD} > \text{VPD}_0 \\ \beta_0, & \text{VPD} \leq \text{VPD}_0 \end{cases} \quad (2)$$

246 where  $\beta_0$  and  $k$  are fitted parameters and VPD<sub>0</sub> is 10 hPa<sup>47</sup>.

247 To account for the seasonal variation in  $A_{\max}$ , we applied the equations above to a short time  
248 window (2-14 days) of  $F_c$  depending on the availability of flux measurements (Extended Data  
249 Fig. 8), and assumed every day in the same time window has the same daily  $A_{\max}$ . We retrieved  
250 the daily  $A_{\max}$  of these 166 sites by implementing equations (1) and (2) using the REddyProc R  
251 package (<https://github.com/bgctw/REddyProc>), and we found the majority of the fitted LRCs  
252 were robust for  $A_{\max}$  retrievals (Extended Data Fig. 9).

253 After obtaining daily  $A_{\max}$ , we calculated the average  $A_{\max}$  for every adjacent and non-  
254 overlapped 10-day window for each site.  $\overline{\text{PPFD}}_{10}$  and  $T_{\text{air}}$  are the averages of the daytime PPFD

255 and daytime air temperature within the same 10-day window. fAPAR in each 10-day window  
256 was acquired by interpolating the 8-day MODIS fAPAR time series (MOD15A2H) at each site.

257

## 258 **2. Derivation of $A_{\max}$ from the estimates of terrestrial biosphere models**

259 The North America Carbon Program (NACP) site-level interim synthesis is a model-data  
260 comparison aimed at discerning the impact of different model structures on carbon flux estimates.

261 The program data repository (<https://daac.ornl.gov/NACP/>) provides access to the estimates of

262 Gross Primary Productivity (GPP) from 22 TBMs and their corresponding meteorological

263 records at 41 eddy covariance sites located in US and Canada (Supplementary Table 4)<sup>48</sup>. To

264 obtain the  $A_{\max}$  of these sites from the TBMs estimates, we used hourly estimates of GPP<sup>49</sup>

265 along with hourly meteorological records (PPFD, air temperature, VPD) and MODIS fAPAR

266 obtained from the NACP repository<sup>50</sup>, and fitted the LRC to these hourly GPP and

267 meteorological variables (Equation 1). Since we used GPP as the  $F_c$  term in equation (1) in this

268 step, the respiration term ( $\gamma$ ) was fixed at 0. Because GPP estimates from models are temporally

269 continuous, we applied this LRC to a time window of 10 days directly to get an  $A_{\max}$  for every

270 10 days.  $\overline{\text{PPFD}}_{10}$  and  $T_{\text{air}}$  are the averages of the daytime PPFD and air temperature within the

271 same 10-day window. We retrieved  $A_{\max}$  from modelled GPP for all 22 TBMs in NACP using

272 equations (1) and (2) (<https://github.com/lxzswr/simpleLRC>). However, in this study we only

273 included the nine TBMs that had hourly GPP estimates at more than 20 sites in order to derive

274 enough  $\gamma_A$  samples for our analysis (Extended Data Fig. 10 and Supplementary Table 3).

275 In addition, we used the boreal ecosystem productivity simulator (BEPS) – one of the nine TBMs

276 in NACP – to test the possibility of incorporating an optimality model (see section 4 of the

277 Methods) in TBMs to improve the simulation of light acclimation. BEPS is a two-leaf enzyme

278 kinetic model that has been extensively validated against measured carbon and water fluxes over  
279 different biomes<sup>51,52</sup> and its parameterization and structure is described in detail elsewhere<sup>53,54</sup>.

280

### 281 **3. Calculation of the photosynthetic light acclimation rate ( $\gamma_A$ )**

282 Following the derivation of seasonal varying  $A_{\max}$  from eddy covariance measurements and  
283 TBM estimates, we analyzed the relationship between  $A_{\max}$  and its corresponding  $\overline{\text{PPFD}}_{10}$  and  
284 defined  $\gamma_A$  as the rate of light acclimation of photosynthesis. Since fAPAR and  $T_{\text{air}}$  also change  
285 across the season and might influence the variations of  $A_{\max}$ , it is necessary to remove the effects  
286 of fAPAR and  $T_{\text{air}}$  on  $A_{\max}$  to identify the  $\overline{\text{PPFD}}_{10}$ - $A_{\max}$  relationship. To do so, we grouped the  
287  $A_{\max}$  and  $\overline{\text{PPFD}}_{10}$  pairs into bins, with each bin confined to a narrow interval of fAPAR and  $T_{\text{air}}$ .  
288 We used an interval of fAPAR of 0.02 and an interval of  $T_{\text{air}}$  of 1 °C. Then, in each bin, we  
289 regressed  $A_{\max}$  against  $\overline{\text{PPFD}}_{10}$  to obtain  $\gamma_A$ . The specific intervals of fAPAR and  $T_{\text{air}}$  were  
290 chosen to ensure the number of the pairs of  $\overline{\text{PPFD}}_{10}$  and  $A_{\max}$  was large enough for a regression  
291 analysis and small enough to assume fAPAR and  $T_{\text{air}}$  were nearly constant within each bin. In  
292 addition, water stress (i.e. high VPD, low soil water content) may also influence the variations of  
293  $A_{\max}$ <sup>55,56</sup>, so we used a strict threshold to remove the drought-affected data points using the 10-  
294 day average of the ratio of actual evapotranspiration (ET) to potential ET ( $\alpha$ ), which has been  
295 suggested as an effective indicator of soil moisture stress on photosynthesis<sup>56</sup>. We calculated  $\alpha$   
296 using the actual ET measured by eddy covariance and the potential ET calculated from the  
297 Priestley-Taylor equation<sup>57</sup>. We excluded days with  $\alpha \leq 0.8$  as they were deemed water-  
298 stressed. In addition to applying this threshold, we also removed shrubland and savanna sites as  
299 they are sensitive to water stress. After the removal, the average VPD for all  $\overline{\text{PPFD}}_{10}$ - $A_{\max}$  pairs  
300 was  $0.47 \pm 0.43$  kPa, or 90% of the data pairs had VPD < 1 kPa. We ended up with 26985 pairs

301 of  $A_{\max}$  and  $\overline{\text{PPFD}}_{10}$  in total from 118 sites. The regression of  $A_{\max}$  and  $\overline{\text{PPFD}}_{10}$  was carried out  
302 for each bin only if there were at least 20 pairs of  $A_{\max}$  and  $\overline{\text{PPFD}}_{10}$  in it (900 bins in total;  
303 Extended Data Fig. 7) for cross-sites analysis and at least 5 pairs for PFT-specific analysis. Since  
304 every site on average only had 229 pairs of  $A_{\max}$  and  $\overline{\text{PPFD}}_{10}$ , we were not able to bin these pairs  
305 at each site and calculate  $\gamma_A$  for each site specifically. For the derivation of  $A_{\max}$  and  $\gamma_A$  from  
306 TBMs estimated fluxes, we followed the same procedures as used for the flux observations. We  
307 also derived  $A$  standardized to a PPFD of  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $A_{2000}$ ) from the fitted light response  
308 curves (Equation 1) to study light acclimation as the response of  $A_{2000}$  to  $\overline{\text{PPFD}}_{10}$  and presented  
309 the results in Extended Data Fig. 2. However, for the convenience of incorporating light  
310 acclimation in TBMs and providing a consistent benchmark for future model-data comparisons,  
311 we presented the results in the main text using  $A_{\max}$ .

312

#### 313 **4. The optimality model for $V_{c_{\max}25}$**

314 The maximum carboxylation rate ( $V_{c_{\max}}$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is often used to represent the activity of  
315 the photosynthetic enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) in light  
316 saturated leaves, meaning the increase of  $A_{\max}$  to  $\overline{\text{PPFD}}$  is related to an increase of  $V_{c_{\max}}$  to  
317  $\overline{\text{PPFD}}$ . A recent study developed an optimality model for  $V_{c_{\max}}$ <sup>19</sup> based on the coordination  
318 hypothesis<sup>21</sup> and the least-cost hypothesis<sup>17</sup> to estimate leaf  $V_{c_{\max}}$  using various climate  
319 variables including  $\overline{\text{PPFD}}$ . This optimality model therefore provides an approach to include the  
320 impact of  $\overline{\text{PPFD}}$  on  $A_{\max}$  in TBMs.

321 According to the classic Farquhar biochemical model<sup>58</sup>, the photosynthetic rate,  $A$ , is limited by  
322 either  $V_{c_{\max}}$ , or by the electron transport rate for the regeneration of ribulose-1,5,-bisphosphate  
323 (RuBP;  $J$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The two processes are represented by equations (3) and (4), respectively:

324  $A_c = Vc_{max} \frac{C_i - \Gamma^*}{C_i + K}$  (3)

325  $A_j = \left(\frac{J}{4}\right) \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*}$  (4)

326 where  $C_i$  is the intercellular  $\text{CO}_2$  concentration (Pa),  $\Gamma^*$  is the  $\text{CO}_2$  compensation point (Pa) in  
 327 the absence of mitochondrial respiration, and  $K$  (Pa) is estimated as:

328  $K = K_c \left(1 + \frac{O_i}{K_o}\right)$  (5)

329 where  $K_c$  and  $K_o$  are Michaelis-Menten coefficients of Rubisco activity for  $\text{CO}_2$  and  $\text{O}_2$  (Pa), and  
 330  $O_i$  is the intercellular  $\text{O}_2$  concentration (Pa).  $K$  and  $\Gamma^*$  are temperature dependent variables and  
 331 the calculation of them is introduced in detail by Smith et al.<sup>19</sup>.  $J$  is dependent on a response  
 332 curve of the incident photosynthetically active photon flux density ( $I$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), converging  
 333 at the maximum electron transport rate ( $J_{max}$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ):

334  $\theta J^2 - (\varphi I + J_{max})J + \varphi I J_{max} = 0$  (6)

335 where  $\theta$  is the curvature of the light response curve and assumed to be 0.85, and  $\varphi$  is the  
 336 maximum quantum yield of photosynthetic electron transport fixed at  $0.257 \text{ mol mol}^{-1}$ .

337 Combining equations (4) and (6) gives:

338  $A_j = \varphi I \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} \left(\frac{\varpi^*}{8\theta}\right)$  (7)

339 where  $\varpi^*$  is derived from the following two equations:

340  $\varpi^* = 1 + \varpi - \sqrt{(1 + \varpi)^2 - 4\theta\varpi}$  (8)

341  $\varpi = -(1 - 2\theta) + \sqrt{(1 - \theta) \left(\frac{1}{\frac{4c}{m}(1 - \theta\frac{4c}{m})} - 4\theta\right)}$  (9)

342 For the calculation of  $\varpi$ ,  $c$  was assumed to be a constant at  $0.053$ <sup>19</sup>, and  $m$  is  $\frac{C_i - \Gamma^*}{C_i + 2\Gamma^*}$ . According  
 343 to the coordination hypothesis, photosynthesis under typical daytime conditions is close to the

344 point where Rubisco-limited and electron transport-limited rate are equal, meaning  $A_c = A_j$ .

345 Therefore, by combining equation (3) and (7), we get:

$$346 \quad Vc_{max} = \varphi I \frac{C_i + K}{C_i + 2\Gamma^*} \left( \frac{\varpi^*}{8\theta} \right) \quad (10)$$

347 This equation implies that  $Vc_{max}$  adjusts to incident light levels over intermediate timescales, as  $I$   
348 is equivalent to  $\overline{PPFD}$ . Following the least-cost hypothesis,  $C_i$  is sustained at an optimal level to  
349 minimize the carbon cost of water use<sup>17</sup>:

$$350 \quad \frac{C_i}{C_a} = \frac{\Gamma^*}{C_a} + \left( 1 - \frac{\Gamma^*}{C_a} \right) \frac{\xi}{\xi + \sqrt{VPD}} \quad (11)$$

$$351 \quad \xi = \sqrt{\beta \frac{K + \Gamma^*}{1.6\eta^*}} \quad (12)$$

352 where  $\xi$  defines the sensitivity of  $C_i/C_a$  to VPD and  $\beta$  is a constant 146. More details about the  
353 calculation of  $C_i$  are introduced in Smith et al.<sup>19</sup>.

354 In this study, we used 10-day average climate variables acquired from the meteorological  
355 measurements of eddy covariance sites, including  $\overline{PPFD}$ ,  $T_{air}$ , VPD to drive the optimality model  
356 to get the 10-day  $Vc_{max}$ , normalized  $Vc_{max}$  from growing temperature to 25 °C ( $Vc_{max25}$ ) and then  
357 linearly interpolated 10-day  $Vc_{max25}$  to daily values to drive BEPS.

358 Note that the optimality model provides us with  $Vc_{max}$  at the growing temperature. We  
359 normalized  $Vc_{max}$  to 25 °C using a modified Arrhenius temperature response function<sup>59</sup> used in  
360 BEPS following equation (13):

$$361 \quad Vc_{max} = Vc_{max25} \exp[H_a(T_l - T_{ref})/(T_{ref}RT_l)] \frac{1 + \exp(\frac{T_{ref}\Delta S - H_d}{T_{ref}R})}{1 + \exp(\frac{T_l\Delta S - H_d}{T_lR})} \quad (13)$$

362 where  $T_l$  is the growing temperature of leaf in Kelvin,  $T_{ref}$  is the reference temperature of  $Vc_{max25}$   
363 (298.15K),  $H_a$  is the activation energy for carboxylation (55000 J mol<sup>-1</sup>),  $H_d$  is the deactivation

364 energy ( $200000 \text{ J mol}^{-1}$ ),  $\Delta S$  is an entropy term ( $663.1 \text{ J mol}^{-1} \text{ K}^{-1}$ ) and  $R$  is the universal gas  
365 constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ).

366

### 367 **Data Availability**

368 This study used openly available eddy covariance measurements provided by FLUXNET2015  
369 Tier 1 dataset (<https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>), and the North America  
370 Carbon Program site-level interim synthesis data downloaded from <https://daac.ornl.gov/NACP/>.  
371 The MODIS fAPAR time series (MOD15A2H) for eddy covariance sites were acquired from  
372 <https://lpdaac.usgs.gov/tools/appears>.

373

### 374 **Code Availability**

375 The code to derive maximum ecosystem photosynthetic rate from eddy covariance  
376 measurements is available at <https://github.com/bgctw/REddyProc>; the code of the optimality  
377 model for  $V_{c_{\max}}$  is available at [https://github.com/SmithEcophysLab/optimal\\_vcmax\\_R](https://github.com/SmithEcophysLab/optimal_vcmax_R); the  
378 code of the Boreal Ecosystem Productivity Simulator is available at [https://github.com/JChen-  
379 UToronto/BEPS\\_hourly\\_site\\_4.02](https://github.com/JChen-UToronto/BEPS_hourly_site_4.02).

380

381

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399 the writing; T.F.K. contributed to the writing.

400 The authors declare no conflict of interest.

401

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556

557 **Fig. 1 | The relationships between the maximum photosynthetic rate ( $A_{\max}$ ) of ecosystems**  
558 **and 10-day average PPFD ( $\overline{\text{PPFD}}_{10}$ ).** (a) the rate of photosynthetic light acclimation ( $\gamma_A$ ; mol  
559 mol<sup>-1</sup>;  $\mu\text{mol C m}^{-2} \text{ s}^{-1}$  per  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ) under different vegetation densities (indicated by  
560 fraction of absorbed PAR; fAPAR) and daytime air temperature ( $T_{\text{air}}$ ), and the black dots indicate  
561 where there is a significant ( $p < 0.1$ ) linear correlation between  $\overline{\text{PPFD}}_{10}$  and  $A_{\max}$ .  $A_{\max}$  and  
562  $\overline{\text{PPFD}}_{10}$  pairs are grouped by fAPAR and  $T_{\text{air}}$ , where the interval of fAPAR is 0.02 and the  
563 interval of  $T_{\text{air}}$  is 1 °C. Only bins with at least 20 pairs of  $A_{\max}$  and  $\overline{\text{PPFD}}_{10}$  are plotted. (b)  
564 several exemplary and significant ( $p < 0.05$ ) responses of  $A_{\max}$  to  $\overline{\text{PPFD}}_{10}$  under different fAPAR  
565 and  $T_{\text{air}}$ . The shadings indicate 95% confidence interval of the linear regressions. (c) The  
566 comparison between ecosystem  $\gamma_A$  derived from flux data and published leaf-level  $\gamma_A$ . For each  
567 box, the cross indicates the mean, the center line indicates the median, the box indicates the  
568 upper and lower quartiles and the whiskers indicate the 5th and 95th percentiles of the data.

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572 **Fig. 2 | Ecosystem photosynthetic light acclimation rate ( $\gamma_A$ ) changes with (a) vegetation**  
573 **densities (fAPAR), (b) daytime temperature ( $T_{\text{air}}$ ), (c) plant functional types (PFTs) and (d)**  
574 **vapor pressure deficit (VPD).** The shadings in (a) and (b) indicate one standard deviation of  $\gamma_A$   
575 ( $n > 5$ ;  $n$  is the number of bins with significant  $\gamma_A$  ( $p < 0.1$ )) for each fAPAR and  $T_{\text{air}}$ , the red  
576 lines indicate the detectability of photosynthetic light acclimation (i.e.  $n$  divided by the total  
577 number of bins). (c)  $\gamma_A$  of each PFT. For each box, the cross indicates the mean, the center line  
578 indicates the median, the box indicates the upper and lower quartiles and the whiskers indicate

579 the 5th and 95th percentiles of the data. The acronyms of PFTs in (c) stand for croplands (CRO),  
580 deciduous broadleaf forests (DBF), evergreen broadleaf forests (EBF), evergreen needleleaf  
581 forests (ENF), mixed forests (MF) and grasslands (GRA). ‘\*’ indicates that  $\gamma_A$  of CRO is  
582 statistically different than  $\gamma_A$  of other PFTs (*t*-test,  $p < 0.05$ ); (d) The impact of VPD on  $\gamma_A$ . The  
583 significance level of light acclimation and the sign of  $\gamma_A$  change with VPD. For each box, the  
584 point indicates the mean, the box indicates the upper and lower quartiles and the whiskers  
585 indicate the 5th and 95th percentiles of the data. Red indicates bins with  $\gamma_A > 0$  and blue box  
586 indicates bins with  $\gamma_A < 0$ .

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588

589 **Fig. 3 | Incorporating photosynthetic light acclimation into terrestrial biosphere models.** (a)

590 The distribution of  $\gamma_A$  derived from eddy-covariance measurements (black) and from the GPP  
591 estimates of 9 terrestrial biosphere models (TBMs; other colors) participating in the North  
592 American Carbon Program. (b) Incorporating the optimality model into a TBM (the boreal  
593 ecosystem productivity simulator (BEPS)) to improve the estimation of photosynthetic light  
594 acclimation. The distribution of eddy covariance-based  $\gamma_A$  is in black, the distribution of  $\gamma_A$   
595 derived from BEPS estimates is in blue and the distribution of  $\gamma_A$  derived from BEPS improved  
596 by the optimality model (BEPS-opt) is in red. (c) The intra-annual variation and (d) inter-annual  
597 variation of estimated and “measured” gross primary productivity (GPP). BEPS and BEPS-opt  
598 stand for the GPP estimated by the two models; GPP-DT stands for “measured” GPP derived  
599 from net carbon fluxes using the day-time partition method. For each box, the cross indicates the  
600 mean, the center line indicates the median, the box indicates the lower and upper quartiles and

601 the whiskers indicate the 5th and 95th percentiles of the data. '\*' indicates that BEPS-opt is  
602 significantly improved ( $t$ -test,  $p < 0.05$ ) compared to BEPS.





