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# Joint control of terrestrial gross primary productivity by plant phenology and physiology

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**Terrestrial gross primary productivity (GPP) varies greatly over time and space. A better understanding of this variability is necessary for more accurate predictions of the future climate-carbon cycle feedback. Recent studies have suggested that variability in GPP is driven by a broad range of biotic and abiotic factors operating mainly through changes in vegetation phenology and physiological processes. However, it is still unclear how plant phenology and physiology can be integrated to explain the spatiotemporal variability of terrestrial GPP. Based on analyses of eddy-covariance and satellite-derived data, we decomposed annual terrestrial GPP into the length of the CO<sub>2</sub> uptake period (CUP) and the seasonal maximal capacity of CO<sub>2</sub> uptake (GPP<sub>max</sub>). The product of CUP and GPP<sub>max</sub> explained >90% of the temporal GPP variability in most areas of North America during 2000–2010 and the spatial GPP variation among globally distributed eddy flux tower sites. It also explained GPP response to the European heatwave in 2003 ( $r^2 = 0.90$ ) and GPP recovery after a fire disturbance in South Dakota ( $r^2 = 0.88$ ). Additional analysis of the eddy-covariance flux data shows that the interbiome variation in annual GPP is better explained by that in GPP<sub>max</sub> than CUP. These findings indicate that terrestrial GPP is jointly controlled by ecosystem-level plant phenology and photosynthetic capacity, and greater understanding of GPP<sub>max</sub> and CUP responses to environmental and biological variations will, thus, improve predictions of GPP over time and space.**

ecosystem carbon uptake | growing season length | photosynthetic capacity | spatiotemporal variability | climate extreme

Large variability exists among estimates of terrestrial carbon sequestration, resulting in substantial uncertainty in modeled dynamics of atmospheric CO<sub>2</sub> concentration and predicted future

climate change (1). The variability in carbon sequestration is partially caused by variation in terrestrial gross primary productivity (GPP) (2), which is the cumulative rate over time of gross plant

## Significance

**Terrestrial gross primary productivity (GPP), the total photosynthetic CO<sub>2</sub> fixation at ecosystem level, fuels all life on land. However, its spatiotemporal variability is poorly understood, because GPP is determined by many processes related to plant phenology and physiological activities. In this study, we find that plant phenological and physiological properties can be integrated in a robust index—the product of the length of CO<sub>2</sub> uptake period and the seasonal maximal photosynthesis—to explain the GPP variability over space and time in response to climate extremes and during recovery after disturbance.**

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photosynthesis at the ecosystem level. Plant photosynthesis has been successfully modeled at the biochemical level (3, 4). When leaf-level biochemical models of photosynthesis are scaled up to estimate annual GPP over a region and the globe, however, great uncertainty arises from both vegetation properties, such as biome-dependent leaf parameters (5, 6), and environmental factors, such as climate variability (7–9) and episodic disturbances (10–12). As a consequence, estimated present day global GPP varies from 105 to 177 Pg C  $y^{-1}$  in the fifth phase of the Coupled Model Intercomparison Project (13). Additionally, spatiotemporal patterns of GPP (2, 14), their responses to extreme climate events (12) and disturbances (10), and the underlying mechanisms are still not well-understood. Previous studies have indicated that vegetation properties and environmental factors shape annual GPP of an ecosystem directly or indirectly through affecting plant physiological activities (15) and/or phenology (16–21). Thus, integrating plant physiological and phenological properties may provide a unified approach to explain the variability of GPP over time and space and in response to disturbance.

In this study, we show that annual GPP in grams C meter $^{-2}$  year $^{-1}$ , the rate at which terrestrial ecosystems take up CO $_2$  from the atmosphere in a given year, can be quantitatively decomposed into

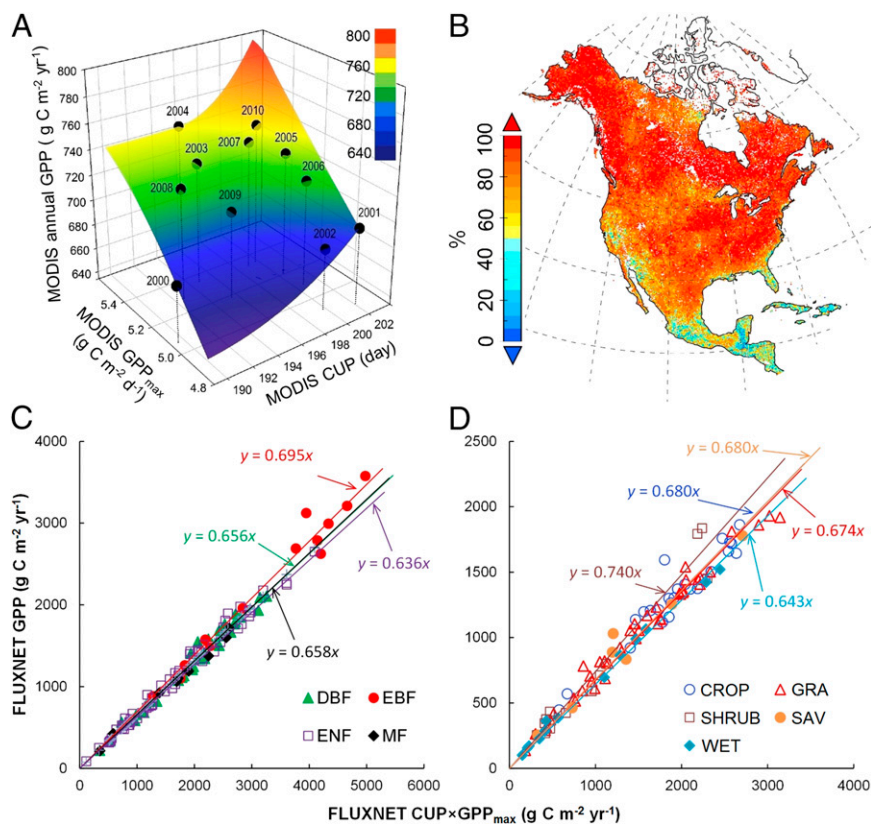
$$\text{GPP} = \alpha \cdot \text{CUP} \cdot \text{GPP}_{\text{max}}, \quad [1]$$

where the carbon dioxide uptake period (CUP; number of days per year) is a phenological indicator of the duration of ecosystem CO $_2$  assimilation within a given year. GPP $_{\text{max}}$  (grams C meter $^{-2}$  day $^{-1}$ ) is

the maximal daily rate of gross photosynthesis during the CUP and represents a property of plant canopy physiology. The ratio between annual GPP and the product of CUP and GPP $_{\text{max}}$  is represented by  $\alpha$ . We estimated  $\alpha$ , CUP, and GPP $_{\text{max}}$  for 213 globally distributed terrestrial sites with daily GPP from the global network of micrometeorological tower sites (FLUXNET; La Thuile Database) (22) (*SI Appendix, section S1.1.1 and Table S1*) and all  $0.1^\circ \times 0.1^\circ$  land grid cells in North America during 2000–2010 with an 8-d GPP product from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the National Aeronautics and Space Administration Terra satellite (23) (*Materials and Methods*). Here, we show how CUP and GPP $_{\text{max}}$  jointly control the spatiotemporal variability of GPP and its response to and recovery from disturbances in different terrestrial ecosystems.

## Results and Discussion

Using regression analysis, we first evaluated to what extent the product of CUP and GPP $_{\text{max}}$  (CUP  $\times$  GPP $_{\text{max}}$ ) explained the variability of satellite-derived GPP over broad temporal and spatial scales. CUP  $\times$  GPP $_{\text{max}}$  explained 94.9% of the interannual variability of the averaged MODIS GPP across North America from 2000 to 2010, with the minimum annual GPP (678 g C m $^{-2}$  y $^{-1}$ ) in 2000 and the maximum (748 g C m $^{-2}$  y $^{-1}$ ) in 2010 (Fig. 14). The joint control of CUP and GPP $_{\text{max}}$  on the interannual variability of GPP was robust in most MODIS grid cells across North America but weak in tropical and Mediterranean climates, such as the



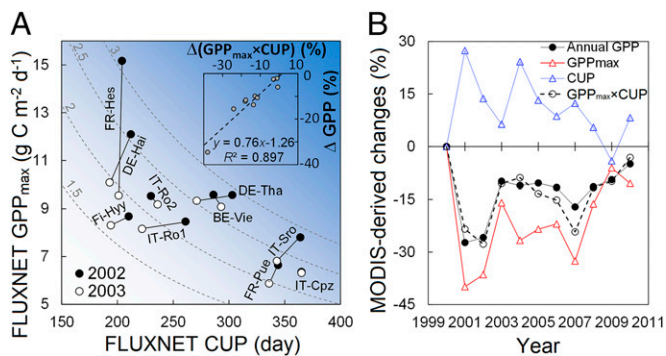
**Fig. 1.** Joint control of the temporal variability of satellite-derived annual GPP and the spatial variability of FLUXNET annual GPP by CUP and GPP $_{\text{max}}$ . (A) The temporal variability of GPP in North America from 2000 to 2010 can be better understood by splitting annual GPP into GPP $_{\text{max}}$  and CUP. The flat color interpolated surface reflects a good relationship between annual GPP and GPP $_{\text{max}}$   $\times$  CUP ( $R^2 = 0.95$ ,  $P < 0.001$ ). Vertical lines were added to improve readability. (B) Contribution of GPP $_{\text{max}}$   $\times$  CUP to GPP temporal variability over 2000–2010. The contribution in each grid cell was derived from the  $R^2$  in the linear regression analysis between GPP and GPP $_{\text{max}}$   $\times$  CUP. C and D show relationships between GPP and GPP $_{\text{max}}$   $\times$  CUP across FLUXNET sites in forest and nonforest biomes, respectively. Each data point in C and D represents one flux site with average data over different years. CROP, cropland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; MF, mixed forest; SAV, savanna; SHRUB, shrubland; WET, wetland.



Caribbean region and California (Fig. 1B). Spatially, across all FLUXNET sites, although there was no relationship between CUP and  $GPP_{max}$  (SI Appendix, Fig. S1),  $CUP \times GPP_{max}$  explained >95% of the spatial variation of annual observed GPP in all biomes (all  $P < 0.001$ ) (Fig. 1C and D).

The product of CUP and  $GPP_{max}$  also explains the impact of a climate extreme on ecosystem  $CO_2$  uptake. Linear regression analysis showed that the GPP reduction caused by the European heatwave in 2003 (12) across FLUXNET sites was well-explained by  $CUP \times GPP_{max}$  ( $R^2 = 0.90$ ,  $P < 0.001$ ) (Fig. 2A, Inset). However, CUP and  $GPP_{max}$  played different roles in heatwave-induced GPP reduction among sites. For example, the reduction in annual GPP mainly resulted from a decrease of  $GPP_{max}$  (−37%) for a beech forest in Sarrebourg, France but a shortening of CUP (−11%) for a spruce site in Tharandt, Germany (Fig. 2A).

We also analyzed the dynamics of satellite-derived annual GPP, CUP, and  $GPP_{max}$  during recovery from a wildfire that occurred on August 24, 2000 in the Black Hills National Forest in South Dakota (24) (SI Appendix, Fig. S2). Although  $GPP_{max}$  and CUP followed contrasting postfire trajectories, the recovery trajectory of annual GPP was well-captured by the product of CUP and  $GPP_{max}$  ( $R^2 = 0.88$ ,  $P < 0.001$ ) (Fig. 2B). Immediately after the fire, GPP was sharply reduced by 27% in 2001 ( $624 \text{ g C m}^{-2} \text{ y}^{-1}$ ) and 26% in 2002 ( $636 \text{ g C m}^{-2} \text{ y}^{-1}$ ) relative to GPP before the disturbance in 2000 ( $858 \text{ g C m}^{-2} \text{ y}^{-1}$ ). Thereafter, annual GPP gradually recovered to  $816 \text{ g C m}^{-2} \text{ y}^{-1}$  in 2010 (Fig. 2B). The dynamics of  $GPP_{max}$  after the fire paralleled those of annual GPP, with 40% and 36% reduction in 2001 and 2002, respectively, and then gradual recovery to 89% of prefire levels in 2010. In contrast, the CUP was extended by 30 to 60 days from 2000 (219 d) and then gradually shortened and returned to predisturbance values (Fig. 2B). The rapid extension of the CUP may have resulted from the return of grass in spring after fire disturbance (25).



**Fig. 2.** Applications of the convergence of  $\alpha$  (the ratio between annual GPP and  $GPP_{max} \times CUP$ ) to explain GPP response to and recovery from disturbances. (A) Determination of the annual GPP reduction during the European heatwave in 2003 (12) by  $GPP_{max}$  and CUP. The dashed hyperbolic curves represent constant values (shown near the curves) of  $GPP_{max} \times CUP$  (kilograms C meter<sup>-2</sup> year<sup>-1</sup>), and the darker background blue color means a larger  $GPP_{max} \times CUP$ . Inset shows the dependences of the relative changes in annual GPP ( $\Delta GPP$ ; percentage) in 2003 from those in 2002 on the relative changes in  $GPP_{max} \times CUP$  [ $\Delta(GPP_{max} \times CUP)$ ; percentage; black circles]. The ten sites are: BE-Vie (Vielsalm, Belgium), DE-Hai (Hainich, Germany), DE-Tha (Tharandt, Germany), Fi-Hyy (Hyytiälä, Finland), FR-Hes (Hesse Forest- Sarrebourg, France), FR-Pue (Puechabon, France), IT-Cpz (Castelporziano, Italy), IT-Ro1 and IT-Ro2 (Roccarespanpani, Italy), IT-Sro (San Rossore, Italy). Detailed information about each FLUXNET site can be found in SI Appendix, Fig. S9 and Table S1. (B) Contrasting dynamics of  $GPP_{max}$  and CUP after an extensive wildfire in the Black Hills National Forest in South Dakota. The data were extracted from a burned  $0.1^\circ \times 0.1^\circ$  grid cell ( $43.85^\circ \text{ N}$ ,  $103.95^\circ \text{ W}$ ) (original data are plotted in SI Appendix, Fig. S2). The ratio  $\alpha$  was close to 0.62 during the 11-y span (SI Appendix, Fig. S10).

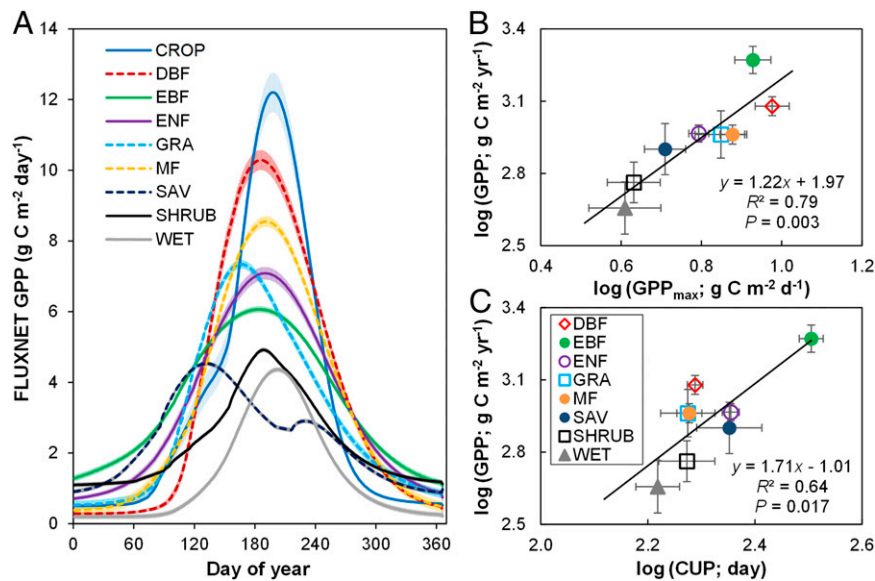
Not only did the product of CUP and  $GPP_{max}$  capture the variability in annual GPP over space and time and after disturbances, but the ratio  $\alpha$  between annual GPP and  $CUP \times GPP_{max}$  also converged across a broad range of vegetation types and environmental conditions (Fig. 3). The most frequent value of  $\alpha$  was 0.62, with 90% of  $\alpha$ -values falling within a range from 0.61 to 0.76 (Fig. 3A) based on an analysis of 213 FLUXNET sites. Those sites with  $\alpha > 0.76$  were mainly located in tropical and subtropical climate zones (Fig. 3A and SI Appendix, Fig. S3). The analysis of the MODIS product showed a similar convergence of  $\alpha$  over North America (Fig. 3B), with the most frequent value of 0.62 and a 90% range from 0.61 to 0.83. To explore the spatial distribution of  $\alpha$ , we mapped the mean annual GPP, CUP,  $GPP_{max}$ , and  $\alpha$  over 2000–2010. Although annual GPP, CUP, and  $GPP_{max}$  showed great spatial variability (SI Appendix, Fig. S4),  $\alpha$  was relatively constant around 0.62 in most areas at a latitude of  $37^\circ \text{ N}$  northward and gradually approached 1.0 toward the tropical regions of North America (Fig. 3C). Across North America, the temporal linear correlation between  $CUP \times GPP_{max}$  and annual GPP was the highest in regions with  $\alpha$  around 0.62 and gradually reduced with the ratio  $\alpha$  approaching 1.0 (Fig. 3D).

High  $\alpha$ -values were mainly distributed in tropical evergreen forest and regions with multiple growing seasons, where  $GPP_{max}$  and CUP exert weak controls over GPP variability (Fig. 3A, Inset). Values of  $\alpha$  were high in tropical evergreen ecosystems, because GPP seasonality and amplitude were minimal, with plants assimilating  $CO_2$  all year round. For example, daily GPP varied minimally across seasons in a tropical rain forest in Brazil (SI Appendix, Fig. S1.3.1), with  $\alpha$  ranging between 0.77 and 0.80 from 2001 to 2003. The nontropical regions with high  $\alpha$ -values usually have two or more peaks of daily GPP within a single year. For example, the Le Bray site in France, which is comprised of a maritime pine forest, had two separate GPP peaks in late May and September of 2005 (SI Appendix, Fig. S5). This phenomenon may also occur in Mediterranean regions with hot and dry summers (26) or double/triple cropping systems, where two or more crops are grown within a single year, such as winter wheat during winter and maize during summer in the North China Plain (27). Seasonally water-limited regions where two growing season peaks are present are widely distributed in the southern part of North America, leading to an abrupt increase in  $\alpha$  at latitudes lower than about  $30^\circ \text{ N}$  (Fig. 3C).

The decomposition of annual GPP into  $GPP_{max}$  and CUP allowed us to investigate the relative importance of  $GPP_{max}$  and CUP individually in regulating annual GPP variability among/within biomes (Fig. 4A). The linear correlation analysis across eight noncrop biomes showed that the biome-level GPP variability was significantly correlated to the variations in both  $GPP_{max}$  ( $r^2 = 0.79$ ,  $P = 0.003$ ) (Fig. 4B) and CUP ( $r^2 = 0.64$ ,  $P = 0.017$ ) (Fig. 4C). The partial correlation analysis across noncrop biomes revealed a larger contribution of  $GPP_{max}$  (partial  $r^2 = 0.78$ ,  $P = 0.004$ ) than CUP (partial  $r^2 = 0.21$ ,  $P < 0.001$ ) to GPP variability. A more important role of  $GPP_{max}$  than CUP in explaining the spatial variability of FLUXNET GPP was found within most biome types, including grassland (partial  $r^2 = 0.70$ ,  $P = 0.005$ ), shrubland (partial  $r^2 = 0.52$ ,  $P = 0.005$ ), savanna (partial  $r^2 = 0.89$ ,  $P = 0.001$ ), wetland (partial  $r^2 = 0.91$ ,  $P < 0.001$ ), and all forest types (partial  $r^2 = 0.79$ – $0.87$ , all  $P < 0.01$ ) (SI Appendix, Fig. S6 and Table S2). A recent analysis has found that temperature and precipitation changes impact the net primary productivity of woody plant ecosystems mainly through their effects on growing season length, standing biomass, and stand age (28). Thus, standing biomass and stand age might be very important determinants of  $GPP_{max}$  in forest ecosystems.

The joint control of  $GPP_{max}$  and CUP on GPP variability indicates that environmental changes influence annual GPP by simultaneously affecting vegetation phenology and photosynthetic capacity. For example, climate warming leads to greater ecosystem  $CO_2$  uptake by extending CUP in most cold regions (7, 17, 29) but could reduce ecosystem  $CO_2$  uptake when





**Fig. 4.** (A) Dynamic of daily GPP in different biomes based on the FLUXNET dataset. The curves are obtained by averaging daily GPP over all site-years of each biome type, with the shaded areas representing SEs on GPP. *B* and *C* show dependence of annual FLUXNET GPP variability on  $GPP_{max}$  and CUP, respectively, among biomes. Note that there were, in total, 12 EBF sites in this analysis, and 7 of them were distributed in the temperate zone according to the MODIS IGBP (International Geosphere-Biosphere Programme) land cover classification ([glcf.umd.edu/data/lc/](http://glcf.umd.edu/data/lc/)) (*SI Appendix, Table S1*). CROP, cropland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; MF, mixed forest; SAV, savanna; SHRUB, shrubland; WET, wetland.

The representation of interannual and spatial variations in GPP by the product of CUP and  $GPP_{max}$  was strong in those ecosystems with  $\alpha$ -values close to 0.62 but weaker toward the tropics or in seasonally water-limited regions, where  $\alpha$ -values approached 1.0. The strong correlation of annual GPP with the product of CUP and  $GPP_{max}$  in several different ecosystem types may be useful in detecting shifts in vegetation state and for monitoring short- and long-term response of GPP to extreme climate conditions and disturbances. Given that  $GPP_{max}$  better explains GPP variability than CUP, future studies need to emphasize the regulatory mechanisms for the dynamics of ecosystem photosynthetic capacity in terrestrial ecosystems.

## Materials and Methods

GPP estimates (positive GPP means  $CO_2$  uptake) from 213 FLUXNET sites from the La Thuile Database ([www.fluxdata.org/default.aspx](http://www.fluxdata.org/default.aspx)) (*SI Appendix, Table S1*) and the MODIS aboard National Aeronautics and Space Administration Terra satellites (MOD17A2 GPP) (23) were used in the analyses (*SI Appendix, section S1.1*). For FLUXNET sites, only those site-years with >300 daily estimates were chosen from the database. Because the MODIS GPP product was well-evaluated in North America (52), we only performed our analysis on MODIS GPP in this region from 2000 to 2010.

The determinations of CUP and  $GPP_{max}$  were from the method introduced by Gu et al. (53, 54) (*SI Appendix, section S1.2*). The CUP,  $GPP_{max}$ , and the ratio between annual GPP and  $CUP \times GPP_{max}$  (i.e.,  $\alpha$ ) were estimated for each selected FLUXNET site and each  $0.1^\circ \times 0.1^\circ$  land grid cell of the MODIS product by the following steps (*SI Appendix, section S1.3*). (i) We judged if the site-year or grid cell is evergreen or not by counting the number of days with larger daily GPP than a given value (a site or land grid cell was defined as evergreen if there were more than 360 d with daily GPP >  $1 \text{ g C m}^{-2} \text{ d}^{-1}$  within 1 y). (ii) The number of seasons in the non-evergreen site-years or land grid cells was determined by a model function (*SI Appendix, section S1.3 and Eq. S6*) suggested by the TIMESAT software (55). For those site-years and grid cells with one season, we fitted a five-parameter Weibull function to the data from that year. For those site-years or land grid cells with more than one season, we fitted the Weibull function to each season.

The nonlinear data fitting was performed with the function nls in R ([www.r-project.org/](http://www.r-project.org/)) (*SI Appendix, section S1.4*). The robustness of the method was carefully validated by various approaches, including an evaluation with the data from all long-term FLUXNET sites (*SI Appendix, section S1.5*), a parameter sensitivity analysis of the Weibull function (*SI Appendix, section S1.6*), and a

random resampling test of the Weibull function (*SI Appendix, section S1.7*). Linear regression analysis was used to examine the contribution of  $CUP \times GPP_{max}$  to the temporal and spatial variations of annual GPP. The global daily record of landscape freeze/thaw data from January 1, 2000 to December 31, 2010 was analyzed for an additional indicator of CUP (*SI Appendix, section S1.8*).

To further identify the relative contribution of  $GPP_{max}$  and CUP to GPP variability, we first linearized Eq. 1 by replacing all variables with their logarithms (base 10) as

$$\log(\text{GPP}) = \log(\alpha) + \log(\text{CUP}) + \log(\text{GPP}_{max}). \quad [2]$$

Then, we applied the partial correlation analysis to examine the relative contributions of CUP and  $GPP_{max}$  to FLUXNET GPP variability among and within biomes.

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