



- 1 Research article
- 2 Title
- Spatially asynchronous changes in strength and stability of terrestrial net ecosystem
 productivity
- 5 Running title
- 6 Spatial variability in terrestrial NEP
- 7 Authors
- 8 Erqian Cui^{1,2} (eqcui@stu.ecnu.edu.cn)
- 9 Chenyu Bian^{1,2} (cybian@stu.ecnu.edu.cn)
- 10 Yiqi Luo³ (yiqi.luo@nau.edu)
- 11 Shuli Niu^{4,5} (sniu@igsnrr.ac.cn)
- 12 Yingping Wang⁶ (Yingping.Wang@csiro.au)
- 13 Jianyang Xia^{1,2,*} (jyxia@des.ecnu.edu.cn)

14 Affiliations

- 15 ¹Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, Shanghai
- 16 Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and
- 17 Environmental Sciences, East China Normal University, Shanghai 200241, China;
- ²Research Center for Global Change and Ecological Forecasting, East China Normal
 University, Shanghai 200241, China;
- ³Center for ecosystem science and society, Northern Arizona University, Arizona, Flagstaff,
- 21 AZ 86011, USA.
- ²² ⁴Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic
- 23 Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China;
- ⁵University of Chinese Academy of Sciences, Beijing, China;
- ²⁵ ⁶CSIRO Oceans and Atmosphere, PMB 1, Aspendale, Victoria 3195, Australia.

26 Correspondence

- 27 Jianyang Xia, School of Ecological and Environmental Sciences, East China Normal
- 28 University, Shanghai 200241, China.
- 29 Email: jyxia@des.ecnu.edu.cn

30 Key words

- 31 Net ecosystem productivity, spatial asynchronous, CO₂ uptake and release, local indicators,
- 32 model





33 Abstract

Multiple lines of evidence have demonstrated the persistence of global land carbon (C) sink 34 during the past several decades. However, both annual net ecosystem productivity (NEP) and its 35 36 inter-annual variation (IAV_{NEP}) keep varying over space. Thus, identifying local indicators for 37 the spatially varying NEP and IAV_{NEP} is critical for locating the major and sustainable C sinks on the land. Here, based on a machine-learning-derived database, we first showed that the 38 variations of NEP and IAV_{NEP} are spatially asynchronous. Then, based on daily NEP 39 observations from eddy covariance sites, we found robust logarithmic correlation between 40 annual NEP and ratio of total CO_2 exchanges during net uptake (U) and release (R) periods 41 (i.e., U/R). The cross-site variation of mean annual NEP can be linearly indicated by $\ln(U/R)$, 42 while the spatial distribution of IAV_{NEP} was well indicated by the slope (i.e., β) of the 43 demonstrated logarithmic correlation. Among biomes, for example, forests and croplands had 44 the largest U/R ratio (1.06 \pm 0.83) and β (473 \pm 112 g C m⁻² yr⁻¹), indicating the highest NEP 45 and IAV_{NEP} in forests and croplands, respectively. We further showed that the spatial variations 46 of NEP and IAV_{NEP} were both underestimated by the machine-learning-based and 47 process-based global models. Overall, this study underscores the asynchronously changes in 48 49 the strength and stability of land C sinks over space, and provides two simple local indicators for their intricate spatial variations. These indicators could be helpful for locating the 50 51 persistent terrestrial C sinks and provides valuable constraints for improving the simulation of 52 land-atmospheric C exchanges. 53





54 1. Introduction

55 Terrestrial ecosystems reabsorb about one-quarter of anthropogenic CO₂ emission (Ciais et al., 2019) and are primarily responsible for the recent temporal fluctuations of the measured 56 57 atmospheric CO₂ growth rate (Randerson, 2013; Le Quéré et al., 2018). However, evidence based on eddy-flux measurements (Baldocchi, Chu, & Reichstein, 2018; Rödenbeck, Zaehle, 58 59 Keeling, & Heimann, 2018), aircraft atmospheric budgets (Peylin et al., 2013), and process-based model simulations (Poulter et al., 2014; Ahlstrom et al., 2015) has shown a large 60 spatial variability in net ecosystem productivity (NEP) on the land. The elusive variation of 61 terrestrial NEP over space refers to both of the dramatic varying mean annual NEP and the 62 divergent inter-annual variability (IAV) in NEP (i.e., IAV_{NEP}; usually quantified as the standard 63 deviation of annual NEP) across space (Baldocchi, Chu, & Reichstein, 2018; Marcolla, 64 Rödenbeck, & Cescatti, 2017). The mean annual NEP is related to the strength of carbon sink 65 of a specific ecosystem (Randerson, Chapin III, Harden, Neff, & Harmon, 2002; Luo, & Weng, 66 2011; Jung et al., 2017), while IAV_{NEP} characterizes the stability of such carbon sink (Musavi 67 et al., 2017). Thus, whether and how NEP and IAV_{NEP} change asynchronously over the space 68 is important for predicting the future locations of carbon sinks on the land (Yu et al., 2014; Niu 69 et al., 2017). 70

The NEP in terrestrial ecosystems is determined by two components, including vegetation 71 72 photosynthesis and ecosystem respiration (Reichstein et al., 2005). Because there is a strong covariance between photosynthesis and respiration over space (Baldocchi, Sturtevant, & 73 74 Contributors, 2015; Biederman et al., 2016), their relative difference could determine the 75 spatial variation of NEP. Many previous analyses have attributed the IAV_{NEP} at the site level to the different sensitivities of ecosystem photosynthesis and respiration to environmental 76 fluctuations among years (Gilmanov et al., 2005; Reichstein et al., 2005; Musavi, 2017). For 77 example, some studies have reported that IAV_{NEP} is more associated with variations in 78 photosynthesis than carbon release (Ahlstrom et al., 2015; Novick, Oishi, Ward, Siqueira, 79 Juang, & Stoy, 2015; Li et al., 2017), whereas others have indicated that respiration is more 80 sensitive to anomalous climate variability (Valentini et al., 2000; von Buttlar et al., 2017). 81 82 Alternatively, the annual NEP of a given ecosystem can be defined numerically as the balance





between the CO₂ uptake and release processes (Gray et al., 2014), which are more direct components for NEP (Fu et al., 2019). It is still unclear whether ecosystem CO₂ uptake and release could be integrated into some simple indicators for the spatially varying NEP and IAV_{NEP} in terrestrial ecosystems.

Conceptually, the total CO_2 uptake flux (U) is determined by the length of CO_2 uptake 87 period (CUP) and the CO_2 uptake rate, while the total CO_2 release flux (R) depends on the 88 89 length of CO₂ release period (*CRP*) and the CO₂ release rate (Fig. 2b). The variations of NEP 90 thus should be innovatively attributed to these decomposed components. A strong spatial 91 correlation between mean annual NEP and length of CO₂ uptake period has been reported in 92 evergreen needle- and broad-leaved forests (Churkina, Schimel, Braswell, & Xiao, 2005; Richardson, Keenan, Migliavacca, Ryu, Sonnentag, & Toomey, 2013; Keenan et al., 2014), 93 whereas atmospheric inversion data and vegetation photosynthesis model indicated a dominant 94 role of the maximal carbon uptake rate (Fu, Dong, Zhou, Stoy, & Niu, 2017; Zhou et al., 2017). 95 However, the relative importance of these phenological and physiological indicators for the 96 spatially varying NEP remains unclear. 97

In this study, we first explored the changes in NEP and IAV_{NEP} at the global scale based 98 on data from a widely-used machine-learning-derived product (i.e., FLUXCOM). To address 99 the local indicators for spatially varying NEP, we decomposed annual NEP into U and R. Then, 100 we examined the relationship of $NEP \propto \frac{U}{R}$ based on the observations at 72 eddy covariance 101 towers which has >5 years measurements in the FLUXNET2015 Dataset (Jung et al., 2017). In 102 addition, we used the observations to evaluate the spatial variations of NEP and IAV_{NEP} in the 103 FLUXCOM database and a process-based model (CLM4.5) (Oleson et al., 2013). The major 104 aim of this study is to explore whether there are useful local indicators for the spatially varying 105 NEP and IAV_{NEP} in terrestrial ecosystems. 106

107 2. Materials and Methods

108 2.1 Datasets

109 Daily NEP observations of eddy covariance sites were obtained from the FLUXNET2015 Tier

110 1 dataset (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/). The FLUXNET2015 dataset





111 provides half-hourly data of carbon, water and energy fluxes at over 210 sites that are standardized and gap-filled (Pastorello et al., 2017). However, time series of most sites are still 112 too short for the analysis of inter-annual variation in NEP. So only the sites that provided the 113 availability of eddy covariance flux measurements for at least 5 years are selected. This leads 114 to a global dataset of 72 sites with different biomes across different climatic regions. Based on 115 the biome classification from the International Geosphere-Biosphere Programme (IGBP) 116 provided for the FLUXNET2015 sites, the selected sites include 35 forests (FOR), 15 117 grasslands (GRA), 11 croplands (CRO), 4 wetlands (WET), 2 shrublands (SHR) and 5 118 savannas (SAV) (Fig. S1 and Table S1). The stand age information of forest sites is the average 119 tree age of the stand, and was obtained from the Biological Ancillary Disturbance and 120 Metadata (BAMD) of the FLUXNET dataset (Musavi, et al., 2017). 121

The FLUXCOM dataset presents an upscaling of carbon flux estimates from 224 flux 122 tower sites based on multiple machine learning algorithms and satellite data (Jung et al., 2017). 123 Meteorological measurements from CRUNCEPv6 and a serious of remotely sensed datasets 124 were used as input. For this study, we downloaded the NEP product from the Data Portal of the 125 Max Planck Institute for Biochemistry (https://www.bgc-jena.mpg.de). Daily outputs from 126 FLUXCOM for the period 1980-2013 were used to map the spatial variation in terrestrial NEP 127 and calculate the local indicators for the spatially varying NEP at the same locations of the flux 128 tower sites. 129

Daily NEP simulations from Community Land Model version 4.5 (CLM4.5) were also used to calculate the local indicators for the spatially varying NEP at the corresponding flux tower sites. We ran the CLM4.5 model from 1990 to 2010 with a spatial resolution of 1° to match the available FLUXCOM dataset. Here, NEP was derived as the difference between GPP and TER, and TER was calculated as the sum of simulated autotrophic and heterotrophic respiration. The daily outputs from CLM4.5 were used to calculate the local indicators for the spatially varying NEP at the same locations of the flux tower sites.

137 2.2 Decomposition of NEP and the calculations for its local indicators



157



- 138 The annual NEP of a given ecosystem can be defined numerically as the difference between
- the CO_2 uptake and release. As illustrated in Figure 2b:

$$NEP = U - R \tag{1}$$

where the total CO_2 uptake flux (U) and the total CO_2 release flux (R) can be further decomposed as:

143
$$U = \overline{U} \times CUP$$
(2)

144
$$R = \overline{R} \times CRP \tag{3}$$

where the \overline{U} (g C m⁻² d⁻¹) is the mean daily CO₂ uptake over *CUP* and \overline{R} (g C m⁻² d⁻¹) represents the mean daily CO₂ release over *CRP*. The calculations of these direct indicators are as follows:

148
$$U = \sum_{i=1}^{m} NEP_i \ (NEP_i > 0; \ CUP = m)$$
(4)

149
$$R = \sum_{i=1}^{n} NEP_i \ (NEP_i < 0; CRP = n)$$
(5)

where NEP_i refers to the daily NEP (g C m⁻² d⁻¹) in the *ith* day. Because many studies have reported that the vegetation CO₂ uptake during the growing season and the non-growing soil respiration are tightly correlated (Luo, & Zhou, 2006; Xia, Chen, Piao, Ciais, Luo, & Wan, 2014; Zhao, Peichl, Öquist, & Nilsson, 2016), we further tested the relationship between annual NEP and the ratio of $\frac{U}{R}$ (i.e., $NEP \propto \frac{U}{R}$). Then we found that annual NEP was closely related with the ratio of $\frac{U}{R}$ (Figure S2). Therefore, NEP in any year of any given ecosystem can be expressed as:

 $NEP = \beta \cdot \ln\left(\frac{U}{R}\right) \tag{6}$

158 where the parameter β represents the slope of the linear relationship of $NEP \propto \ln\left(\frac{U}{R}\right)$. Based 159 on the definitions of U and R, the ratio $\frac{U}{R}$ can be further written as:

160
$$\frac{U}{R} = \frac{\overline{U}}{\overline{R}} \cdot \frac{CUP}{CRP}$$
(7)





161 These components of NEP contain both photosynthesis and respiration flux, which directly indicate the net CO₂ exchange of an ecosystem. Ecologically, the ratio of $\frac{U}{R}$ reflects 162 the relative physiological difference between ecosystem CO₂ uptake and release strength, 163 while the ratio of $\frac{CUP}{CRP}$ is an indicator of net ecosystem CO₂ exchange phenology. 164 Environmental changes may regulate these ecological processes and ultimately affect the 165 166 ecosystem NEP. The slope β indicates the response sensitivity of NEP to the changes in phenology and physiological processes. All of β , $\frac{CUP}{CRP}$ and $\frac{\overline{U}}{\overline{R}}$ were then calculated from the 167 selected eddy covariance sites and the corresponding pixels of these sites in models. These 168 derived indicators from eddy covariance sites were then used to benchmark the results 169 170 extracted from the same locations in models.

171 **2.4 Calculation of the relative contributions**

To further identify the relative contributions of $\frac{U}{\bar{R}}$ and $\frac{CUP}{CRP}$ in driving the spatiotemporal variations in the local indicator $\frac{U}{R}$, we linearized the equation (7) as

174
$$\log\left(\frac{U}{R}\right) = \log\left(\frac{\overline{U}}{\overline{R}}\right) + \log\left(\frac{CUP}{CRP}\right)$$
(8)

Then we used a relative importance analysis method to quantify the relative contributions 175 of each ratio to the spatiotemporal variations in $\frac{U}{R}$. The algorithm was performed with the 176 "ralaimpo" package in R (R Development Core Team, 2011). The "relaimpo" package is based 177 178 on variance decomposition for multiple linear regression models. We chose the most commonly used method named "Lindeman-Merenda-Gold (LMG)" (Grömping, 2007) from 179 the methods provided by the "ralaimpo" package. This method allows us to quantify the 180 181 contributions of explanatory variables in a multiple linear regression model. In each site, we calculated the contributions of $\frac{\overline{U}}{\overline{R}}$ and $\frac{CUP}{CRP}$ in explaining inter-annual variation in $\frac{U}{R}$. Across 182 the 72 FLUXNET sites, we quantified the relative importance of $\frac{\overline{U}}{\overline{R}}$ and $\frac{CUP}{CRP}$ to cross-site 183 changes in $\frac{U}{R}$. 184

185 **3. Results**





186 **3.1 Spatial variability in terrestrial NEP**

Based on the FLUXCOM product, a large spatial variation in terrestrial NEP and IAV_{NEP} 187 existed over 1980-2013. The tropical forests were typically large carbon sinks accompanied by 188 considerable interannual variability. On the contrary, the boreal tundra ecosystems were stable 189 190 carbon sinks and the shrublands in the Southern Hemisphere were variable carbon sources (Fig. 1a). This remarkable spatial difference in terrestrial NEP was particularly obvious from 191 eddy-flux measurements (Fig. S1), and the global average IAV of NEP $(175 \pm 111 \text{ g C m}^{-2} \text{ yr}^{-1})$ 192 was large relative to global annual mean NEP (216 ± 234 g C m⁻² yr⁻¹). These spatial patterns 193 194 were also supported by the model outputs (Jung et al., 2017) and atmospheric inversion product 195 (Marcolla, Rödenbeck, & Cescatti, 2017).

More importantly, we found that the variations of NEP and IAV_{NEP} were spatially asynchronous. Along the latitudinal gradients, terrestrial NEP peaked at equatorial regions, whereas the highest IAV_{NEP} existed in semiarid regions near 37° S (Fig. 1b). The demonstrated spatial asynchrony further revealed the necessary to identify local indicators for the spatially varying NEP and IAV_{NEP} , separately.

201 3.2 Local indicators for spatially varying NEP

To find local indicators for the spatially varying NEP in terrestrial ecosystems, we first tested 202 the relationship between NEP and the $\frac{U}{R}$ ratio across the 72 flux-tower sites. We found robust 203 logarithmic correlation between annual NEP and $\frac{U}{R}$ at all sites (Fig. 2a; Fig. S2), with ~90% 204 of R^2 falling within a range from 0.7 to 1 (Fig. 2c). Across the 72 flux-tower sites, the spatial 205 changes in mean annual NEP were significantly correlated to $\ln\left(\frac{U}{R}\right)$ ($R^2 = 0.65$, P < 0.01) 206 (Fig. 3a). This finding suggests that the mean annual ratio $\ln\left(\frac{U}{p}\right)$ is a good indicator for NEP 207 and its spatial variation. By contrast, the spatial variation of IAV_{NEP} was well explained by the 208 slope (i.e., β) of the temporal correlation between NEP and $\ln\left(\frac{U}{p}\right)$ at each site ($R^2 = 0.39$, P < 0.39, P < 0.3209 0.01; Fig. 3b) rather than $\ln\left(\frac{U}{p}\right)$ (Fig. S3). The wide range of ratio β reveals a large 210 divergence of NEP sensitivity across biomes, ranging from 121 ± 118 g C m⁻² yr⁻¹ in shrubland 211 to 473 ± 112 g C m⁻² yr⁻¹ in cropland. 212





The decomposition of indicator $\frac{U}{R}$ into $\frac{\overline{U}}{\overline{R}}$ and $\frac{CUP}{CRP}$ allowed us to quantify the relative importance of these two ratios in driving $\frac{U}{R}$ variability. The linear regression and relative importance analysis showed a more important role of $\frac{CUP}{CRP}$ (81%) than $\frac{\overline{U}}{\overline{R}}$ (19%) in explaining the cross-site variation of $\frac{U}{R}$ (Fig. 4). Therefore, the spatial distribution of mean annual NEP was mostly driven by the phenological rather than physiological changes.

218 3.3 Simulated spatial variations in NEP by models

We further used these two simple indicators (i.e., $\frac{U}{R}$ and β) to evaluate the simulated spatial 219 variations of NEP by the machine-learning approach (i.e., FLUXCOM) and a widely-used 220 process-based model (i.e., CLM4.5). We found that both of FLUXCOM and CLM4.5 221 underestimated the spatial variation of mean annual NEP and IAV_{NEP} (Fig. 5a). The low spatial 222 variation of mean annual NEP in FLUXCOM and CLM4.5 could be inferred from their more 223 converging $\ln\left(\frac{U}{p}\right)$ than flux-tower measurements (Fig. 5b). The underestimated variation of 224 IAV_{NEP} in these modeling results was also clearly shown by the smaller β values (268.22, 225 126.00 and 145.08 for FLUXNET, FLUXCOM and CLM4.5, respectively) (Fig. 5b). 226

227 4. Discussion

228 4.1 New perspective for locating the major and sustainable land C sinks

Large spatial differences of mean annual NEP and IAV_{NEP} have been well-documented in previous studies (Jung et al., 2017; Marcolla, Rödenbeck, & Cescatti, 2017; Fu et al., 2019). Here we provide a new perspective for quantifying the spatially varying NEP by tracing annual NEP into several local indicators. Therefore, these traceable indicators could provide useful constraints for predicting annual NEP, especially in areas without eddy-covariance towers.

Typically, the C sink capacity and its stability of a specific ecosystem are characterized separately (Keenan et al., 2014; Ahlstrom et al., 2015; Jung et al., 2017). Here we integrated NEP into two simple indicators that could directly locate the major and sustainable land C sink. Among biomes, forests and croplands had the largest $\ln \left(\frac{U}{R}\right)$ and β , indicating the strongest





and the most unstable C sink in forests and croplands, respectively. The highest β in croplands

- implies that the rapid global expansion of cropland may enlarge the IAV_{NEP} on the land. In fact,
- the cropland expansion has been confirmed as one important driver of the recent increasing
- 242 global vegetation growth peak (Huang et al., 2018) and atmospheric CO₂ seasonal amplitude
- 243 (Gary et al., 2014; Zeng et al., 2014).

244 4.2 Phenology-dominant spatial distribution of mean annual NEP

Recent studies have demonstrated that the spatiotemporal variations in terrestrial gross 245 primary productivity are jointly controlled by plant phenology and physiology (Xia et al., 2015; 246 Zhou et al., 2016). Here we demonstrated the dominant role of the phenology indicator $\frac{CUP}{CRP}$ in 247 driving the spatial difference of $\frac{U}{R}$ and therefore the mean annual NEP. The reported low 248 correlation between $\frac{U}{R}$ and the physiological indicator $\frac{\overline{U}}{R}$ could partly be attributed to the 249 convergence of $\frac{\overline{U}}{\overline{R}}$ across FLUXNET sites (Fig. S4). The convergent $\frac{\overline{U}}{\overline{R}}$ across sites was first 250 discovered by Churkina et al. (2005) as 2.73 ± 1.08 across 28 sites, which included DBF, EBF 251 and crop/grass. In this study, we found the $\frac{\overline{U}}{\overline{R}}$ across the 72 sites is 2.71 ± 1.61, which 252 validates the discovery by Churkina *et al.* However, the $\frac{\overline{U}}{\overline{p}}$ varied among biomes (2.86 ± 1.56 253 for forest, 2.16 ± 1.14 for grassland, 3.47 ± 1.98 for cropland, 2.89 ± 1.47 for wetland, $1.89 \pm$ 254 1.10 for shrub, 1.83 ± 0.88 for savanna). This spatial convergence of $\frac{\overline{U}}{\overline{R}}$ at the ecosystem level 255 provides important constraints for global models that simulate various physiological processes 256 (Peng et al., 2015; Xia et al., 2017). These findings imply that the phenology changes will 257 greatly affect the locations of the terrestrial carbon sink by modifying the length of carbon 258 uptake period (Richardson, Keenan, Migliavacca, Ryu, Sonnentag, & Toomey, 2013; Keenan 259 et al., 2014). 260

261 4.3 The underestimated spatial variations of NEP in models

This study showed that the considerable spatial variations in mean annual NEP and IAV_{NEP} were both underestimated by the machine-learning-based and process-based global models, which could also be inferred from their local indicators. The low variations of $\frac{U}{R}$ ratio in the





265 two modeling approaches could be largely due to their simple representations of the diverse terrestrial plant communities into a few plant functional types with parameterized properties 266 (Sakschewski et al., 2015). The ignorance of year-to-year vegetation dynamic could lead to the 267 268 smaller β by allowing for only limited variations of phenological and physiological responses to environmental changes (Reichstein, Bahn, Mahecha, Kattge, & Baldocchi, 2014; Kunstler 269 et al., 2016). Although the magnitude of IAV_{NEP} depends on the spatial resolution (Marcolla, 270 Rödenbeck, & Cescatti, 2017), we recommend future model benchmarking analyses to use not 271 only the machine-learning-based data product (Bonan et al., 2018) but also the site-level 272 measurements or indicators (i.e., $\ln\left(\frac{U}{p}\right)$ and β). 273

274 4.4 Conclusions and further implications

275 In summary, the findings in this study have some important implications for understanding the variation of NEP on the land. First, forest ecosystems have the largest annual NEP due to the 276 largest $\ln\left(\frac{U}{R}\right)$ while croplands show the highest IAV_{NEP} because of the highest β . Second, the 277 spatial convergence of $\frac{\overline{u}}{\overline{p}}$ suggests a tight linkage between plant growth and the non-growing 278 season soil microbial activities (Xia, Chen, Piao, Ciais, Luo, & Wan, 2014; Zhao, Peichl, 279 Öquist, & Nilsson, 2016). However, it remains unclear whether the inter-biome variation in $\frac{U}{R}$ 280 is due to different plant-microbe interactions between biomes. Third, the within-site 281 convergent but spatially varying β needs better understanding. Previous studies have shown 282 that a rising standard deviation of ecosystem functions could indicate an impending ecological 283 state transition (Carpenter, & Brock, 2006; Scheffer et al., 2009). Thus, a sudden shift of the 284 β -value may be an important early-warning signal for the critical transition of IAV_{NEP} of an 285 286 ecosystem.

In addition, considering the limited eddy-covariance sites with long-term observations, these findings need further validation once the longer time-series of measurements from more sites and vegetation types become available. Overall, this study highlights the asynchronous changes in NEP and IAV_{NEP} over space on the land, and provides the $\frac{U}{R}$ ratio and β as two simple local indicators for their spatial variations. These indicators could be helpful for





- locating the persistent terrestrial C sinks in where the $\ln\left(\frac{U}{R}\right)$ ratio is high but the β is low.
- 293 Their estimates based on observations are also valuable for benchmarking and improving the
- simulation of land-atmospheric C exchanges in Earth system models.
- 295 Acknowledgements
- This work was financially supported by the National Key R&D Program of China 296 297 (2017YFA0604600), National Natural Science Foundation of China (31722009, 41630528) and National 1000 Young Talents Program of China. This work used eddy covariance dataset 298 acquired and shared by the FLUXNET community, including these networks: AmeriFlux, 299 AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, 300 301 Fluxnet-Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia, and USCCC. The ERA-Interim reanalysis data are provided by ECMWF and processed by 302 LSCE. The FLUXNET eddy covariance data processing and harmonization was carried out by 303 the European Fluxes Database Cluster, AmeriFlux Management Project, and Fluxdata project 304 of FLUXNET, with the support of CDIAC and ICOS Ecosystem Thematic Center, and the 305 OzFlux, ChinaFlux and AsiaFlux offices. 306
- 307 *Data availability statement.* Eddy flux data are available at 308 http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/; the data supporting the findings of this 309 study are available within the article and the Supplementary Information.
- *Author contribution.* E. Cui and J. Xia devised and conducted the analysis. Y. Luo, S. Niu, Y.
 Wang and C. Bian provided critical feedback on the method and results. All authors
 contributed to discussion of results and writing the paper.
- 313 *Competing interests.* The authors declare that there is no conflict of interest.





314 FIGURES

- 315 Figure 1 Locations of carbon sinks (mean annual NEP) and their stability (IAV_{NEP}) on the land.
- a, Spatial patterns of mean annual NEP and IAV_{NEP} . b, Latitudinal patterns of mean annual
- 317 NEP and IAV_{NEP} .

Figure 2 Relationship between annual NEP and $\frac{U}{R}$ for 72 FLUXNET sites (of the form NEP = $\beta \cdot \ln(\frac{U}{R})$). a, Dependence of annual NEP on the ratio between total CO₂ exchanges during net uptake (U) and release (R) periods (i.e., $\frac{U}{R}$). Each line represents one flux site with at least 5 years of observations. b, Conceptual figure for the decomposition framework introduced in this study. Annual NEP can be quantitatively decomposed into the following indicators: NEP = U - R. c, Distribution of the explanation of $\frac{U}{R}$ on temporal variability of NEP (R^2) for FLUXNET sites.

Figure 3 Contributions of the two indicators in explaining the spatial patterns of mean annual NEP and IAV_{NEP}. a, The relationship between annual mean NEP and $\ln\left(\frac{U}{R}\right)$ across FLUXNET sites ($R^2 = 0.65$, P < 0.01). The insets show the variation of $\ln\left(\frac{U}{R}\right)$ for different terrestrial biomes. b, The explanation of β on IAV_{NEP} ($R^2 = 0.39$, P < 0.01). The insets show the distribution of parameter β for different terrestrial biomes. The number of site-years at each site is indicated with the size of the point.

Figure 4 The linear regression between $\frac{U}{R}$ with $\frac{CUP}{CRP}$ ($R^2 = 0.71$, P < 0.01) and $\frac{\overline{U}}{R}$ ($R^2 = 0.09$, P < 0.01) across sites. The insets show the relative contributions of each indicator to the spatial variation of $\frac{U}{R}$. The number of site-years at each site is indicated with the size of the point.

Figure 5 Representations of the spatially varying NEP and its local indicators in FLUXCOM product and the Community Land Model (CLM4.5). a, The variation of mean annual NEP and IAV_{NEP} derives from FLUXNET, FLUXCOM and CLM4.5. Variation in mean annual NEP: the standard deviation of mean annual NEP across sites; Variation in IAV_{NEP}: the standard deviation of IAV_{NEP} across sites. b, Representations of the local indicators for NEP in FLUXNET, FLUXCOM and CLM4.5. The corresponding distributions of $\ln\left(\frac{U}{R}\right)$ and β are

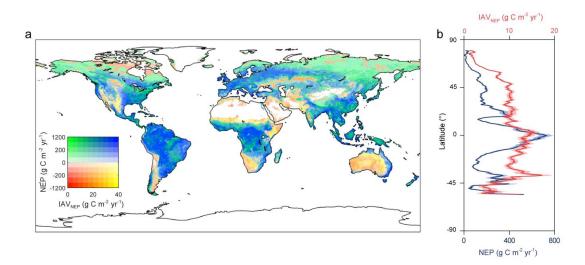




- 341 shown at the top and right. Significance of the relationship between annual NEP and $\ln\left(\frac{U}{R}\right)$
- for each site is indicated by the circle: closed circles: P < 0.05; open circles: P > 0.05. Note that
- 343 the modeled results are from the pixels extracted from the same locations of the flux tower
- 344 sites.
- 345







346

- **Figure 1** Locations of carbon sinks (mean annual NEP) and their stability (IAV_{NEP}) on the land.
- 348 a, Spatial patterns of mean annual NEP and IAV_{NEP}. b, Latitudinal patterns of mean annual
- 349 NEP and IAV_{NEP} .





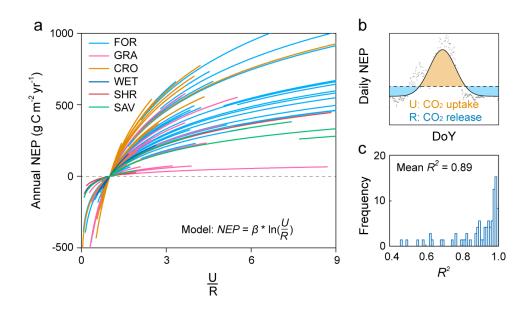
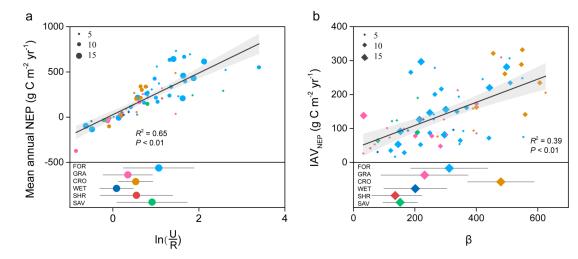


Figure 2 Relationship between annual NEP and $\frac{U}{R}$ for 72 FLUXNET sites (of the form NEP = $\beta \cdot \ln(\frac{U}{R})$). **a**, Dependence of annual NEP on the ratio between total CO₂ exchanges during net uptake (U) and release (R) periods (i.e., $\frac{U}{R}$). Each line represents one flux site with at least 5 years of data. **b**, Conceptual figure for the decomposition framework introduced in this study. Annual NEP can be quantitatively decomposed into the following indicators: NEP = U - R. **c**, Distribution of the explanation of $\frac{U}{R}$ on temporal variability of FLUXNET NEP (R^2) for FLUXNET sites.

359





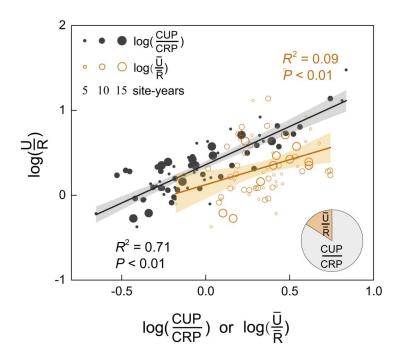


360

Figure 3 Contributions of the two indicators in explaining the spatial patterns of mean annual NEP and IAV_{NEP}. **a**, The relationship between annual mean NEP and $\ln\left(\frac{U}{R}\right)$ across FLUXNET sites ($R^2 = 0.65$, P < 0.01). The insets show the variation of $\ln\left(\frac{U}{R}\right)$ for different terrestrial biomes. **b**, The explanation of β on IAV_{NEP} ($R^2 = 0.39$, P < 0.01). The insets show the distribution of parameter β for different terrestrial biomes. The number of site-years at each site is indicated with the size of the point.







368

Figure 4 The linear regression between $\frac{U}{R}$ with $\frac{CUP}{CRP}$ ($R^2 = 0.71$, P < 0.01) and $\frac{\overline{U}}{\overline{R}}$ ($R^2 = 0.09$, P < 0.01) across sites. The insets show the relative contributions of each indicator to the spatial variation of $\frac{U}{R}$. The number of site-years at each site is indicated with the size of the point.





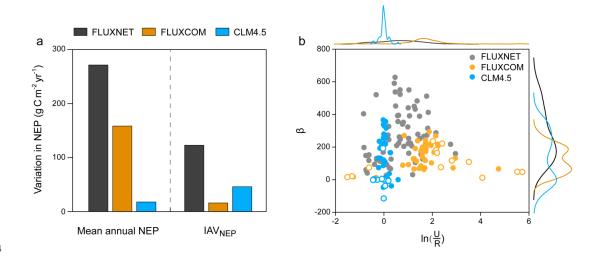




Figure 5 Representations of the spatially varying NEP and its local indicators in FLUXCOM 375 product and the Community Land Model (CLM4.5). a, The variation of mean annual NEP and 376 IAV_{NEP} derives from FLUXNET, FLUXCOM and CLM4.5. Variation in mean annual NEP: 377 the standard deviation of mean annual NEP across sites; Variation in IAV_{NEP}: the standard 378 deviation of IAV_{NEP} across sites. b, Representations of the local indicators for NEP in 379 FLUXNET, FLUXCOM and CLM4.5. The corresponding distributions of $\ln\left(\frac{U}{R}\right)$ and β are 380 shown at the top and right. Significance of the relationship between annual NEP and 381 $\ln\left(\frac{U}{R}\right)$ for each site is indicated by the circle: closed circles: P < 0.05; open circles: P > 0.05. 382 383 Note that the modeled results are from the pixels extracted from the same locations of the flux 384 tower sites.

385





387 **References**

- Ahlström, A., Raupach, M. R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M.,
 Canadell, J. G., Friedlingstein, P., Jain, A. K., Kato, E., Poulter, B., Sitch, S., Stocker, B.
 D., Viovy, N., Wang, Y., Wiltshire, A., Zaehle, S., and Zeng, N.: The dominant role of
 semi-arid ecosystems in the trend and variability of the land CO₂ sink. Science, 348,
 895-899, 2015.
- Baldocchi, D., Chu, H., and Reichstein, M.: Inter-annual variability of net and gross ecosystem
 carbon fluxes: A review. Agric. For. Meteorol., 249, 520-533, 2018.
- Baldocchi, D., Sturtevant, C., and Contributors, F.: Does day and night sampling reduce
 spurious correlation between canopy photosynthesis and ecosystem respiration? Agric.
 For. Meteorol., 207, 117-126, 2015.
- Biederman, J. A., Scott, R. L., Goulden, M. L., Vargas, R., Litvak, M. E., Kolb, T. E., Yepez, E.
 A., Oechel, W. C., Blanken, P. D., Bell, T. W., Garatuza-Payan, J., Maurer, . E., Dore, S.,
 and Burns, S. P.: Terrestrial carbon balance in a drier world: the effects of water
 availability in southwestern North America. Glob. Change Biol., 22, 1867-1879, 2016.
- Bonan, G. B., Patton, E. G., Harman, I. N., Oleson, K. W., Finnigan, J. J., Lu, Y., and
 Burakowski, E. A.: Modeling canopy-induced turbulence in the Earth system: a unified
 parameterization of turbulent exchange within plant canopies and the roughness sublayer
 (CLM-ml v0). Geosci. Model Dev., 11, 1467-1496, 2018.
- Carpenter, S. R., and Brock, W. A.: Rising variance: a leading indicator of ecological transition.
 Ecol. Lett., 9, 311-318, 2006.
- Churkina, G., Schimel, D., Braswell, B. H., and Xiao, X.: Spatial analysis of growing season
 length control over net ecosystem exchange. Glob. Change Biol., 11, 1777-1787, 2005.
- Ciais, P., Tan, J., Wang, X., Roedenbeck, C., Chevallier, F., Piao, S. L., Moriarty, R., Broquet,
 G., Le Quéré, C., Canadell, J. G., Peng, S., Poulter, B., Liu Z., and Tans, P.: Five decades
 of northern land carbon uptake revealed by the interhemispheric CO₂ gradient. Nature,
 568, 221-225, 2019.
- Fu, Z., Dong, J., Zhou, Y., Stoy, P. C., and Niu, S.: Long term trend and interannual variability
 of land carbon uptake-the attribution and processes. Environ. Res. Lett., 12, 014018,
 2017.
- Fu, Z., Stoy, P. C., Poulter, B., Gerken, T., Zhang, Z., Wakbulcho, G., and Niu, S.: Maximum
 carbon uptake rate dominates the interannual variability of global net ecosystem
 exchange. Glob. Change Biol., 25, 3381-3394, 2019.
- Gilmanov, T. G., Tieszen, L. L., Wylie, B. K., Flanagan, L. B., Frank, A. B., Haferkamp, M. R.,
 Meyers, T. P., and Morgan, J. A.: Integration of CO₂ flux and remotely-sensed data for
 primary production and ecosystem respiration analyses in the Northern Great Plains:
- 423 Potential for quantitative spatial extrapolation. Global Ecol. Biogeogr., 14, 271-292,424 2005.





Gray, J. M., Frolking, S., Kort, E. A., Ray, D. K., Kucharik, C. J., Ramankutty, N., and Friedl, 425 M. A.: Direct human influence on atmospheric CO₂ seasonality from increased cropland 426 productivity. Nature, 515, 398-401, 2014. 427 428 Grömping, U.: Estimators of relative importance in linear regression based on variance decomposition. Am. Stat., 61, 139-147, 2007. 429 Huang, K., Xia, J., Wang, Y., Ahlström, A., Chen, J., Cook, R. B., Cui, E., Fang, Y., Fisher, J. 430 B., Huntzinger, D. N., Li, Z., Michalak, A. M., Qiao, Y., Schaefer, K., Schwalm, C., Wang, 431 J., Wei, Y., Xu, X., Yan, L., Bian C., and Luo, Y.: Enhanced peak growth of global 432 vegetation and its key mechanisms. Nat. Ecol. Evol., 2, 1897-1905, 2018. 433 434 Jung, M., Reichstein, M., Schwalm, C. R., Huntingford, C., Sitch, S., Ahlström, A., Arneth, A., Camps-Valls, G., Ciais, P., Friedlingstein, P., Gans, F., Ichii, K., Jain, A. K., Kato, E., 435 Papale, D., Poulter, B., Raduly, B., Rödenbeck, C., Tramontana, G., Viovy, N., Wang, Y., 436 Weber, U., Zaehle S., and Zeng, N.: Compensatory water effects link yearly global land 437 438 CO₂ sink changes to temperature. Nature, 541, 516-520, 2017. Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., 439 O'Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., and Richardson, A. D.: Net carbon 440 uptake has increased through warming-induced changes in temperate forest phenology. 441 Nat. Clim. Change, 4, 598-604, 2014. 442 Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., 443 Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., 444 445 Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., 446 Ruiz-Benito, P., Sun, I., Ståhl, G., Swenson, N. G., Thompson, J., Westerlund, B., Wirth, 447 C., Zavala, M. A., Zeng, H., Zimmerman, J. K., Zimmermann N. E., and Westoby, M.: 448 Plant functional traits have globally consistent effects on competition. Nature, 529, 449 204-207, 2016. 450 451 Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., Pickers, P. A., Korsbakken, J. I., Peters, G. P., Canadell, J. G., Arneth, A., Arora, V. K., Barbero, L., 452 Bastos, A., Bopp, L., Chevallier, F., Chini, L. P., Ciais, P., Doney, S. C., Gkritzalis, T., 453 Goll, D. S., Harris, I., Haverd, V., Hoffman, F. M., Hoppema, M., Houghton, R. A., Hurtt, 454 G., Ilyina, T., Jain, A. K., Johannessen, T., Jones, C. D., Kato, E., Keeling, R. F., 455 Goldewijk, K. K., Landschützer, P., Lefèvre, N., Lienert, S., Liu, Z., Lombardozzi, D., 456 Metzl, N., Munro, D. R., Nabel, J. E. M. S., Nakaoka, S., Neill, C., Olsen, A., Ono, T., 457 Patra, P., Peregon, A., Peters, W., Peylin, P., Pfeil, B., Pierrot, D., Poulter, B., Rehder, G., 458 Resplandy, L., Robertson, E., Rocher, M., Rödenbeck, C., Schuster, U., Schwinger, J., 459 460 Séférian, R., Skjelvan, I., Steinhoff, T., Sutton, A., Tans, P. P., Tian, H., Tilbrook, B., Tubiello, F. N., van der Laan-Luijkx, I. T., van der Werf, G. R., Viovy, N., Walker, A. P., 461 Wiltshire, A. J., Wright, R., Zaehle, S., and Zheng, B.: Global carbon budget 2018. Earth 462 Syst. Sci. Data, 10, 405, 2018. 463





Li, G., Han, H., Du, Y., Hui, D., Xia, J., Niu, S., Li, X., and Wan, S.: Effects of warming and 464 increased precipitation on net ecosystem productivity: a long-term manipulative 465 experiment in a semiarid grassland. Agric. For. Meteorol., 232, 359-366, 2017. 466 Luo, Y., and Weng, E.: Dynamic disequilibrium of the terrestrial carbon cycle under global 467 change. Trends Ecol. Evol., 26, 96-104, 2011. 468 Luo, Y., and Zhou, X.: Soil respiration and the environment. Elsevier, 2006. 469 Marcolla, B., Rödenbeck, C., and Cescatti, A.: Patterns and controls of inter-annual variability 470 in the terrestrial carbon budget. Biogeosciences, 14, 3815-3829, 2017. 471 Musavi, T., Migliavacca, M., Reichstein, M., Kattge, J., Wirth, C., Black, T. A., Janssens, I., 472 473 Knohl, A., Loustau, D., Roupsard, O., Varlagin, A., Rambal, S., Cescatti, A., Gianelle, D., Kondo, H., Tamrakar, R., and Mahecha, M. D.: Stand age and species richness dampen 474 interannual variation of ecosystem-level photosynthetic capacity. Nat. Ecol. Evol., 1, 475 0048, 2017. 476 477 Niu, S., Fu, Z., Luo, Y., Stoy, P. C., Keenan, T. F., Poulter, B., Zhang, L., Piao, S., Zhou, X., Zheng, H., Han, J., Wang, Q., and Yu, G.: Interannual variability of ecosystem carbon 478 exchange: From observation to prediction. Global Ecol. Biogeogr., 26, 1225-1237, 2017. 479 Novick, K. A., Oishi, A. C., Ward, E. J., Siqueira, M. B., Juang, J. Y., and Stoy, P. C.: On the 480 difference in the net ecosystem exchange of CO2 between deciduous and evergreen 481 forests in the southeastern United States. Glob. Change Biol., 21, 827-842, 2015. 482 Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, 483 484 S., Li, F., Riley, W. J., Subin, Z. M., Swenson, S. C., Thornton, P. E., Bozbiyik, A., Fisher, R., Heald, C. L., Kluzek, E., Lamarque, J.-F., Lawrence, P. J., Leung, L. R., Lipscomb, W., 485 Muszala, S., Ricciuto, D. M., Sacks, W., Sun, Y., Tang, J., and Yang, Z.-L.: Technical 486 description of version 4.5 of the Community Land Model (CLM), NCAR Earth System 487 Laboratory-Climate and Global Dynamics Division, Boulder, Colorado, USA, Tech. Rep. 488 http://www.cesm.ucar.edu/models/cesm1.2/clm/CLM45 Tech Note.pdf 489 TN-503+STR, 490 (last access: 27 September 2017), 2013. Pastorello, G., Papale, D., Chu, H., Trotta, C., Agarwal, D., Canfora, E., Baldocchi, D., and 491 492 Torn, M.: A new data set to keep a sharper eye on land-air exchanges. Eos, 98, 2017. Peng, S., Ciais, P., Chevallier, F., Peylin, P., Cadule, P., Sitch, S., Piao, S., Ahlström, A., 493 Huntingford, C., Levy, P., Li, X., Liu, Y., Lomas, M., Poulter, B., Viovy, N., Wang, T., 494 Wang, X., Zaehle, S., Zeng, N., Zhao, F., and Zhao, H.: Benchmarking the seasonal cycle 495 of CO₂ fluxes simulated by terrestrial ecosystem models. Global Biogeochem. Cy., 29, 496 46-64, 2015. 497 Peylin, P., Law, R. M., Gurney, K. R., Chevallier, F., Jacobson, A. R., Maki, T., Niwa, Y., Patra, 498 499 P. K., Peters, W., Rayner, P. J., Rödenbeck, C., van der Laan-Luijkx, I. T., and Zhang, X.: Global atmospheric carbon budget: results from an ensemble of atmospheric CO2 500 501 inversions. Biogeosciences, 10, 6699-6720, 2013. Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., 502





- 503 Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S., and van der Werf, G. R.: Contribution
 504 of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature, 509,
 505 600-603, 2014.
- Randerson, J. T.: Climate science: Global warming and tropical carbon. Nature, 494, 319-320,
 2013.
- Randerson, J. T., Chapin III, F. S., Harden, J. W., Neff, J. C., and Harmon, M. E.: Net
 ecosystem production: a comprehensive measure of net carbon accumulation by
 ecosystems. Ecol. Appl., 12, 937-947, 2002.
- R Development Core Team.: R: A Language and Environment for Statistical Computing
 3-900051-07-0, R Foundation for Statistical Computing, Vienna, Austria, 2011.
- Reichstein, M., Bahn, M., Mahecha, M. D., Kattge, J., and Baldocchi, D. D.: Linking plant and
 ecosystem functional biogeography. Proc. Natl Acad. Sci. USA, 111, 13697-13702, 2014.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C.,
 Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H.,
- 510 Buchmann, N., Ohmanov, I., Oranici, A., Orunwald, T., Havrankova, K., Hveshenn, H.,
- Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T.,
 Miglietta, F., Ourcival, J., Pumpanen J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen,
- J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net
- second algorithm. Glob. Change Biol., 11, 1424-1439, 2005.
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., and Toomey, M.:
 Climate change, phenology, and phenological control of vegetation feedbacks to the
 climate system. Agric. For. Meteorol., 169, 156-173, 2013.
- Rödenbeck, C., Zaehle, S., Keeling, R., and Heimann, M.: How does the terrestrial carbon
 exchange respond to inter-annual climatic variations? Biogeosciences, 15, 2481-2498,
 2018.
- Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñuelas, J., and
 Thonicke, K.: Leaf and stem economics spectra drive diversity of functional plant traits in
 a dynamic global vegetation model. Glob. Change Biol., 21, 2711-2725, 2015.
- Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H.,
 van Nes, E. H., Rietkerk, M., and Sugihara, G.: Early-warning signals for critical
 transitions. Nature, 461, 53-59, 2009.
- Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C. J. M. E. A. G., Moors,
 E. J., Granier, A., Gross, P., Jensen, N. O., Pilegaard, K., Lindroth, A., Grelle, A.,
- Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A. S., Vesala, T.,
- 537 Rannik, Ü., Berbigier, P., Loustau, D., Guðmundsson, J., Thorgeirsson, H., Ibrom, A.,
- Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi S., and Jarvis, P. G.:
- Respiration as the main determinant of carbon balance in European forests. Nature, 404,
- 540 861-865, 2000.
- 541 Von Buttlar, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M.,





542	Menzer, O., Arain, M., Buchmann, N., Cescatti, A., Geinelle, D., Kiely, G., Law, B.,
543	Magliudo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., Montagnani,
544	L., Oechel, W., Pavelka, M., Pelchl, M., Rambal, S., Raschi, A., Scott, R.L., Vaccari, F.,
545	Van Gorsel, E., Varlagin, A., Wohlfahrt, G., and Mahecha, M.: Impacts of droughts and
546	extreme temperature events on gross primary production and ecosystem respiration: a
547	systematic assessment across ecosystems and climate zones. Biogeosciences, 15,
548	1293-1318, 2017.
549	Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., and Wan, S.: Terrestrial carbon cycle affected by
550	non-uniform climate warming. Nat. Geosci., 7, 173-180, 2014.
551	Xia, J., McGuire, A. D., Lawrence, D., Burke, E., Chen, G., Chen, X., Delire, C., Koven, C.,
552	MacDougall, A., Peng, S., Rinke, A., Saito, K., Zhang, W., Alkama, R., Bohn, T. J., Ciais,
553	P., Decharme, B., Gouttevin, I., Hajima, T., Hayes, D. J., Huang, K., Ji, D., Krinner, G.,
554	Lettenmaier, D. P., Miller, P. A., Moore, J. C., Smith, B., Sueyoshi, T., Shi, Z., Yan, L.,
555	Liang, J., Jiang, L., Zhang, Q., and Luo, Y.: Terrestrial ecosystem model performance in
556	simulating productivity and its vulnerability to climate change in the northern permafrost
557	region. J. Geophys. Res-Biogeo., 122, 430-446, 2017.
558	Xia, J., Niu, S., Ciais, P., Janssens, I. A., Chen, J., Ammann, C., Arain, A., Blanken, P. D.,
559	Cescatti, A., Bonal, D., Buchmann, N., Curtis, P. S., Chen, S., Dong, J., Flanagan, L. B.,
560	Frankenberg, C., Georgiadis, T., Gough, C. M., Hui, D., Kiely, G., Li, J., Lund, M.,
561	Magliulo, V., Marcolla, B., Merbold, L., Montagnani, L., Moors, E. J., Olesen, J. E., Piao,
562	S., Raschi, A., Roupsard, O., Suyker, A. E., Urbaniak, M., Vaccari, F. P., Varlagin, A.,
563	Vesala, T., Wilkinson, M., Weng, E., Wohlfahrt, G., Yan, L., and Luo, Y.: Joint control of
564	terrestrial gross primary productivity by plant phenology and physiology. Proc. Natl Acad.
565	Sci. USA, 112, 2788-2793, 2015.
566	Yu, G., Chen, Z., Piao, S., Peng, C., Ciais, P., Wang, Q., Li, X., and Zhu, X.: High carbon
567	dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. Proc.
568	Natl Acad. Sci. USA, 111, 4910-4915, 2014.
569	Zeng, N., Zhao, F., Collatz, G. J., Kalnay, E., Salawitch, R. J., West, T. O., and Guanter, L.:
570	Agricultural Green Revolution as a driver of increasing atmospheric CO ₂ seasonal
571	amplitude. Nature, 515, 394-397, 2014.
572	Zhao, J., Peichl, M., Öquist, M., and Nilsson, M. B.: Gross primary production controls the
573	subsequent winter CO ₂ exchange in a boreal peatland. Glob. Change Biol., 22, 4028-4037,
574	2016. Zhan S. Zhang V. Cisis D. Xing V. Lug V. Carden K. K. Harres V. and Wang C.
575	Zhou, S., Zhang, Y., Ciais, P., Xiao, X., Luo, Y., Caylor, K. K., Huang, Y., and Wang, G.:
576 577	Dominant role of plant physiology in trend and variability of gross primary productivity in North America. Sci. Rep., 7, 41366, 2017.
577 579	m norm America. Sci. Kep., /, 41500, 201/.
578	