AGU ADVANCING EARTH AND SPACE SCIENCE

Geophysical Research Letters

RESEARCH LETTER
10.1029/2021GL094870

Key Points:

- CO_2 fertilization effect and climate warming have led to greening of Europe, but it has not promoted an increase in ecosystem carbon uptake
- The increase in gross primary productivity related to greening is offset by the increase in ecosystem respiration
- Frequent European heatwaves also caused significant losses in the regional ecosystem carbon uptake

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

B. He,
hebin@bnu.edu.cn

Citation:

Liu, X., He, B., Guo, L., Huang, L., Yuan, W., Chen, X., et al. (2021). European carbon uptake has not benefited from vegetation greening. *Geophysical Research Letters*, *48*, e2021GL094870. https://doi.org/10.1029/2021GL094870

Received 15 JUN 2021
Accepted 26 SEP 2021

European Carbon Uptake has Not Benefited From Vegetation Greening

Xuebang Liu[1], Bin He[1], Lanlan Guo[2], Ling Huang[3], Wenping Yuan[4], Xiuzhi Chen[4], Xingming Hao[5], Xiaoming Xie[1], Yafeng Zhang[1], Ziqian Zhong[1], Tiewei Li[2], and Aifang Chen[6]

[1]State Key Laboratory of Earth Surface Processes and Resource Ecology, College of Global Change and Earth System Science, Beijing Normal University, Beijing, China, [2]State Key Laboratory of Earth Surface Processes and Resource Ecology, School of Geography, Beijing Normal University, Beijing, China, [3]College of Urban and Environmental Sciences, Peking University, Beijing, China, [4]School of Atmospheric Sciences, Guangdong Province Key Laboratory for Climate Change and Natural Disaster Studies, Zhuhai Key Laboratory of Dynamics Urban Climate and Ecology, Sun Yat-sen University, Zhuhai, China, [5]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China, [6]School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, China

Abstract Substantial evidences indicate a widespread increase in European vegetation greenness since the 1980s due to CO_2 fertilization effects (eCO_2) and climate warming, but the impact of this process on the regional terrestrial carbon cycle has not been systematically evaluated. Using empirical models based on eddy covariance and process-based models, we found that the widespread greening did not contribute to an increase in European carbon uptake (decrease in net ecosystem exchange) with a non-significant trend from 2000 to 2018. The greening-associated increase in gross primary productivity (GPP) is offset by the simultaneous increase in ecosystem respiration (TER). Moreover, frequent heatwaves cause stronger reductions in GPP than TER, preventing the increase of carbon uptake. These results reveal the double-edged sword effect of warming on European ecosystems and will help constrain regional models.

Plain Language Summary In the past decades, elevating CO_2 concentration and rising temperature have promoted the photosynthesis of European vegetation, thus increasing the greenness of vegetation. However, whether these processes could promote the ability of terrestrial ecosystems to absorb CO_2 still lacks systematic evaluation. By using a variety of advanced vegetation dynamic models, we found that enhanced vegetation growth which absorbed more CO_2, but also an enhancement of ecosystem respiration which released more CO_2 in Europe during 2000–2018. The offsetting effect of these two processes has resulted in non-significant trend in the European net CO_2 uptake. In addition, the extremely high temperature events (heatwaves) frequently occurred in Europe in recent years, which have caused vegetation damage or even death, triggered forest fires, etc., thereby severely inhibited the carbon sink capacity of the terrestrial ecosystem.

1. Introduction

Climate warming has been suggested to contribute to high-latitude greening by lengthening the growing season and simulating plant photosynthesis, and thus, enhanced terrestrial ecosystem productivity (Chen et al., 2019; Ciais et al., 2019; Zhu et al., 2016). In addition, elevating atmospheric CO_2 concentration also enhanced vegetation productivity by the fertilization effects, although it appears to decline across most regions worldwide in recent years (Wang et al., 2020). However, mounting evidences indicate that respiration has an explicit dependency on productivity, and increasing productivity has simultaneously stimulated the increase of ecosystem respiration (Bahn et al., 2008; Hogberg et al., 2001; Moyano et al., 2007). Continued warming also contributes to the decomposition of large amounts of organic matter stored in permafrost soils and enhances the respiration of vegetation, increasing the terrestrial carbon losses to the atmosphere (Commane et al., 2017; Su-Jong et al., 2018). Thus, the balance between gross primary productivity (GPP) and ecosystem respiration (TER) has the potential to alter ecosystem carbon dynamics and the magnitude and seasonality of atmospheric CO_2 concentrations (Anderegg et al., 2015; Graven et al., 2013).

10.1029/2021GL094870

Great concerns have been focused on the change of European ecosystem productivity. A study based on satellite observations derived a large European sink of 1.02 ± 0.30 PgC in 2010, which greatly absorbs the anthropogenic CO_2 emissions (Reuter et al., 2014). At biomes scale, due to eCO_2, climate change (CLI), nitrogen deposition and forest management, the mean net primary productivity (NPP) of European forests was 520 ± 75 gC m^{-2} yr^{-1} during 1990–2005 (Luyssaert et al., 2010), and European forests have accumulated 3.1 PgC since 1750 (Naudts et al., 2016). Model and yield statistics based NPP estimation of European cropland ranged between 490 and 846 gC m^{-2} yr^{-1} over the period of 1990–2000s (Ciais et al., 2010). The net biome productivity (NBP) of European grassland was estimated to be a net uptake of 15 gC m^{-2} yr^{-1} over the period 1961–2010 (Chang et al., 2015). The widespread greening contributes to an increase in ecosystem productivity, it inevitably leads to an increase in ecosystem respiration. However, the balance between them across ecosystems of the European continent has not been carefully evaluated.

In recent years, Europe has been affected by several summer mega-heatwaves and droughts, for example, in western Europe (2003) (Ciais et al., 2005), western Russia (2010) (Barriopedro et al., 2011), and central and northern Europe (2018) (Liu et al., 2020; Peters et al., 2020). The 2003 heatwave has caused a large carbon loss (−500 TgC), equivalent to 4 years of net carbon uptake by the European ecosystems (Ciais et al., 2005). A remarkably high NPP anomaly of about −100 TgC was observed in Europe during the 2010 heatwave (Barriopedro et al., 2011). In summer 2018, central Europe and southern Sweden experienced the record-low carbon sinks, with CO_2 uptake dropping locally by more than 50% (−30 gC m^{-2} $month^{-1}$) (Bastos et al., 2020). While several studies have analyzed the impact of a single heatwave on terrestrial ecosystem carbon in a particular year, less attention has been devoted to the influence of heatwaves on the long-term carbon cycle trend in Europe.

Here, we focus our analysis on geographic Europe (including western Russia) and address three questions: (a) How does the European carbon uptake respond to the widespread vegetation greening trend? (b) What are the factors influencing the changes in European carbon fluxes? (c) How do the frequent European heatwaves affect the long-term carbon cycle?

2. Materials and Methods

2.1. Carbon Fluxes Data

To evaluate the trend of European carbon uptake, we used simulations for the period 2000–2018 of eight dynamic global vegetation models (DGVMs) from the TRENDY: CABLE, CLASS, DLEM, JSBACH, JULES, ORCHIDEE, SDGVM, and VISIT. The TRENDY intercomparing project integrates simulations from state-of-the-art DGVMs (Sitch et al., 2015). The DGVMs provide autotrophic respiration (RA) and heterotrophic respiration (RH), and the TER was calculated as the sum of RA and RH. The net ecosystem exchange (NEE) was derived as the difference between TER and GPP. For the NEE, a positive (negative) value indicates carbon release (uptake). The TRENDY provides several simulations, including: S1, varying CO_2; S2, varying CO_2 and climate; S3, varying CO_2 and climate and landcover. Therefore, the differences of simulations represent the eCO_2, CLI and landcover change, respectively. Similar to previous studies (Fu et al., 2020; Jung et al., 2017), we used the S2 simulations to examine the trend of carbon fluxes change.

We also used the carbon fluxes from independent FLUXCOM data set to compare with the TRENDY. The FLUXCOM has the same drive setting as the S2 simulations of TRENDY. The FLUXCOM provides carbon and energy fluxes based on three machine learning methods (Random Forests, Artificial Neural Networks, Multivariate Adaptive Regression Splines), which were trained on daily carbon flux estimates from 224 flux tower sites with meteorological measurements and satellite data as inputs (Jung et al., 2020). Here, we used the aggregated estimate of carbon fluxes driven by different remote sensing (RS) and meteorological datasets (Meteo) for the period of 2000–2018.

The monthly net ecosystem productivity (NEP) from CMIP6 historical simulations for the period of 2000–2014 were also used as a validation. Because CMIP6 simulations do not provide NEE, we use NEP (-NEE) instead. We selected the following 11 models: ACCESS-ESM, BCC-CSM-MR, CanESM, CESM-WACCM, CMCC-CM-SR, CMCC-ESM, EC-Earth-Veg, EC-Earth-Veg-LR, IPSL-CM6A-LR, MPI-ESM-LR, and TaiESM.

The eddy covariance (EC) measurements of carbon fluxes from tower sites were obtained from the Integrated Carbon Observation System (ICOS) 2018 and the FLUXNET Network 2015. When evaluating the long-term trend of European carbon uptake, we used sites that cover all ecosystem types and has been updated until 2018 with complete records of at least 9 years. This led to a final list of 40 sites (Table S1 in Supporting Information S1). When evaluating the impact of heatwave on seasonal carbon uptake, we chose the sites located in the center of heatwaves and has been updated until the heatwave years. Finally, 42 sites were selected.

2.2. Vegetation Index Data

Two satellite-based vegetation indices were used to evaluate vegetation greenness. Monthly gridded Enhanced Vegetation Index (EVI) with a spatial resolution of 0.05° for 2000–2018 were retrieved from the Moderate resolution Imaging Spectroradiometer (MODIS). Compared with commonly used Normalized Difference Vegetation Index (NDVI), EVI is less prone to suffer from saturation problems, so it can well capture the change of vegetation greenness (Huete et al., 2006; Vicca et al., 2016). Monthly gridded leaf area indices (LAI) were provided from the Global Land Surface Satellite (GLASS) with a spatial resolution of 0.05° for the period of 2000–2017. The GLASS LAI algorithm is based on time-series reflectance data using general regression neural networks, and is trained by the combined LAI from MODIS and CYCLOPES LAI products (Xiao et al., 2013).

2.3. Climate Data

Several climatic factors were selected to explore the drivers of the European carbon fluxes, including air temperature (TMP), shortwave radiation (SWR), soil moisture (SM) and vapor pressure deficit (VPD). Monthly gridded TMP with a 0.5° spatial resolution from 2000 to 2018 were obtained from the Climatic Research Unit (CRU TS v4.03) at the University of East Anglia (Harris et al., 2014). Monthly gridded SWR at 0.25° spatial resolution from ERA5 data set was provided by the European Centre for Medium Range Weather Forecasts (Hersbach & Dee, 2016). Monthly gridded SM at 0.25° spatial resolution for the period of 2000–2018 was retrieved from the Global Landsurface Evaporation: the Amsterdam Methodology (Brecht et al., 2016). Monthly VPD was calculated based on above TMP and the following equations (Buck, 1981):

$$\mathrm{AVP} = 0.5 \times \left(0.611 \times e^{\frac{17.3 \times T_{\min}}{T_{\min} + 237.3}} + 0.611 \times e^{\frac{17.3 \times T_{\max}}{T_{\max} + 237.3}} \right) \tag{1}$$

$$\mathrm{VPD} = \mathrm{SVP} - \mathrm{AVP} \tag{2}$$

where $T_{\min}$ and $T_{\max}$ are maximum and minimum temperature (°C), respectively. SVP and AVP are saturated vapor pressure and actual vapor pressure (kPa), respectively.

2.4. Statistical Analysis

The nonparametric Mann–Kendall (MK) test was used to analyze the trend of carbon fluxes, vegetation indices, and the meteorological factors at each pixel. The MK test has the advantage that no assumptions are made about the distributions of the samples, and it is rarely susceptible to abnormal values (Alexander et al., 2006; Kendall, 1948). Partial correlation analysis between carbon fluxes and climate factors was performed to determine the main drivers. The partial least squares regression (PLSR) was used to identify the sensitivity of carbon fluxes to climate factors. These two methods can effectively overcome the multicollinearity problem existing among explanatory variables (Cohen, 1992; Mehmood et al., 2012). The significances of the trend and correlation were assessed at a p-value less than 0.05.

We calculated the contribution of landcover classes to the mean European carbon fluxes (mean carbon fluxes of landcover class as a proportion of mean European carbon fluxes), European carbon fluxes trend (landcover class carbon fluxes trend as a proportion of European carbon fluxes trend), and the interannual variation of European carbon fluxes using the following equation (Ahlstrom et al., 2015).

$$f_j = \frac{\sum_t \frac{|X_t| x_{jt}}{X_t}}{\sum_t | X_t |} \tag{3}$$

where x_{jt} is the carbon fluxes anomaly (departure from a long-term trend) for region j at time t (in years), and X_t is the European carbon fluxes anomaly.

To evaluate the effects of heatwaves on terrestrial carbon cycle in Europe, a heatwave was defined as a period when at least five consecutive days during which the daily maximum temperature exceeded the climatological mean over the reference period 1961–1990 by at least 5 K (Liu et al., 2020). A heatwave year was defined as a year in which a mega-heatwave occurred. The occurrence of heatwave is often accompanied by a decrease in precipitation and a decrease in air humidity (Boeck et al., 2010), which are also the primary characteristics of drought, this study calls these compound events as heatwave.

3. Results

3.1. Trend of European Carbon Fluxes

3.1.1. Spatial Variation Trend of European Carbon Fluxes

This study used the carbon fluxes (GPP, TER, and NEE) from process-based models (TRENDY), machine learning algorithms models (FLUXCOM) and EC measurements, to analyze the carbon cycle over the European land. And two vegetation indices, EVI and LAI from MODIS and GLASS respectively, were used to study the change trend of vegetation. Over the period 2000–2018, we observed a widespread greening over Europe (Figures 1a and 1c, Table S2 in Supporting Information S1). The regions where EVI significantly increased (decreased) accounted for 33.82% (17.35%) of the total land area. LAI had similar spatial patterns to EVI that significantly increased in 19.08% of the total land area, and significantly decreased in 5.41%.

Increased vegetation greenness leads to an increase in GPP, and both independent carbon datasets indicate a widespread increase in southern, central, and northern Europe (Figures 1d and 1g, Table S2 in Supporting Information S1). TRENDY shows that GPP significantly increased in 21.73% of the total land area, while FLUXCOM shows 5.87%. The spatial patterns of TER variation are highly consistent with those of GPP (Figures 1e and 1h, Table S2 in Supporting Information S1). TRENDY shows a significant increase in 31.05% of the total land area, while FLUXCOM shows a significant increase in 10.64%. The increased GPP was largely offset by the simultaneous increase of TER, resulting in almost no significant change in the European NEE (Figures 1f and 1i, Table S2 in Supporting Information S1). For most EC sites, the sign of trend in carbon fluxes agrees well with that of TRENDY and FLUXCOM, but there are disagreements in significance level (Figures 1d–1f, Figure S1 and Table S1 in Supporting Information S1).

3.1.2. Temporal Trend of European Carbon Fluxes

On the continental scale, both EVI and LAI increased significantly (Figure 2b), with a trend of $8.90 \pm 1.26 \times 10^{-4}$ yr^{-1} and $2.43 \pm 1.1 \times 10^{-3}$ yr^{-1}, respectively. Accompanying with this strong greening, all eight TRENDY models present an increasing trend of European GPP (Figure 2d), five with significant increases; the ensemble mean of the TRENDY models and FLUXCOM both have a significant increase, with a trend of 0.036 ± 0.01 TgC yr^{-1} and 0.007 ± 0.004 PgC yr^{-1}, respectively. Simultaneously, seven of the eight TRENDY models show a significant increase in European TER (Figure 2c), and the ensemble mean shows a significant increase of 0.037 ± 0.007 PgC yr^{-1}. Although, FLUXCOM shows a smaller increasing trend of 0.007 ± 0.003 TgC yr^{-1}, it is highly consistent with TRENDY in the fluctuation of the trend line. Due to the compensation between GPP and TER, all the TRENDY models show a non-significant trend of the European NEE (Figure 2e), with an ensemble mean of $4.79 \pm 4.9 \times 10^{-5}$ PgC yr^{-1}, and the FLUXCOM shows a non-significant increase of $2.43 \pm 2.8 \times 10^{-6}$ PgC yr^{-1}. During the period of 2000–2014, CMIP6, TRENDY and FLUXCOM all show a slight change of European carbon uptake, but CMIP6 shows a significant trend (Figure S2 in Supporting Information S1). In conclusion, carbon uptake across Europe did probably not change over the period 2000–2018, partly due to the simultaneous increase of GPP and TER.

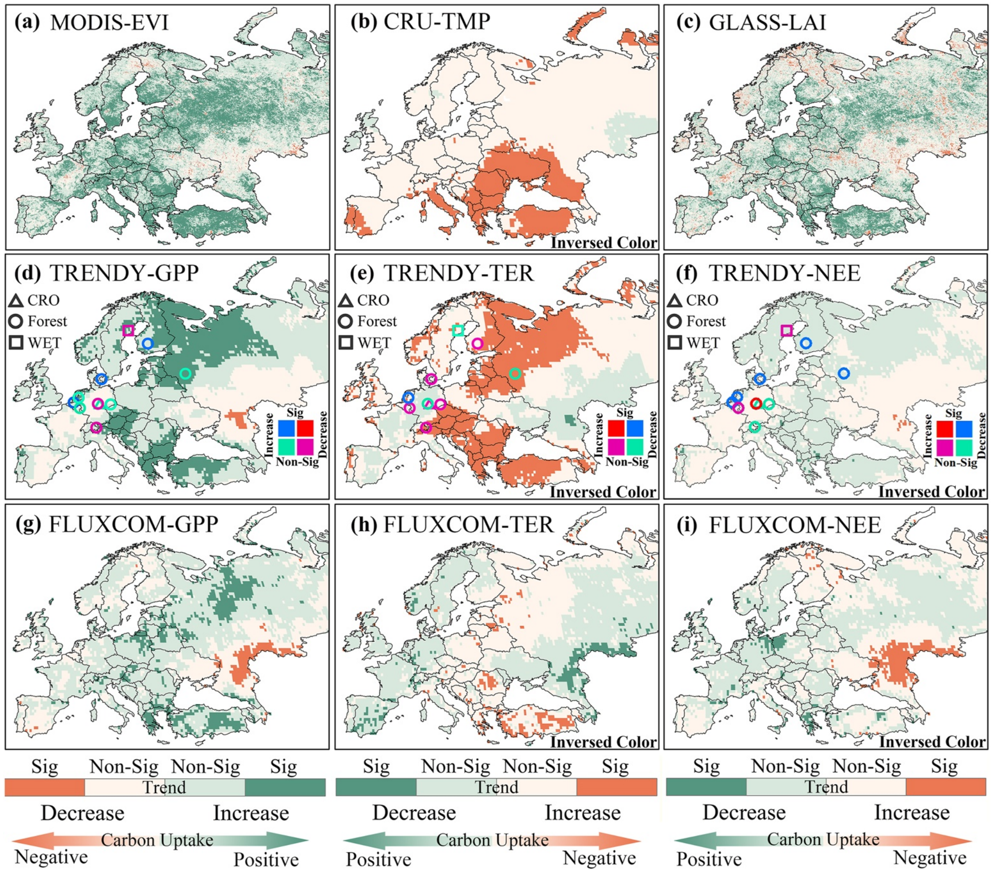

Figure 1. Spatial patterns of Manner–Kendall (MK) trend in vegetation indices, temperature, and carbon fluxes over Europe during 2000–2018. The first (a–c) row shows Enhanced Vegetation Index, temperature, and leaf area indices, respectively. The second (d–f) and third (g–i) rows show carbon fluxes of gross primary productivity, ecosystem respiration, and net ecosystem exchange from the TRENDY and FLUXCOM, respectively. Symbols in the second row indicate the trend of carbon fluxes from eddy covariance sites (names in Table S1 in Supporting Information S1), whose monitoring time spans 2000–2018. To highlight the impact on European carbon uptake, the second and third columns (except c) reverse the color scale used in the first column, so that green indicates a positive effect, orange indicates a negative effect. Sig is short for significant, and Non-Sig is short for non-significant. CRO and WET indicate cropland and wetland, respectively. The significance level is $p < 0.05$.

3.1.3. Trends in Seasonal and Landcover Class Variation of European Carbon Fluxes

On the seasonal time-scale, European NEE from TRENDY in spring has a significant decreasing trend of 0.018 PgC yr^{-1} (Figure 2f), which may be related to the advance of the start of the growing season (Fu et al., 2014; Vico et al., 2021). This advanced spring phenology makes the trend of GPP (0.060 PgC yr^{-1}) greater than that of TER (0.042 PgC yr^{-1}), resulting in a net carbon increase. Similarly, the trend of GPP (0.070 PgC yr^{-1}) in summer is greater than that of TER (0.062 PgC yr^{-1}), but the slight difference does not lead to a significant decrease in NEE (0.008 PgC yr^{-1}). Relatively high temperature and evaporation in summer can easily lead to water stress on vegetation growth, which in turn leads to reduced productivity (Reich et al., 2018). In the autumn, we observed a significant increase in NEE (−0.013 PgC yr^{-1}), mainly because TER increases more quickly than GPP. This conclusion is consistent with the advanced autumn zero-crossing date in the Northern Hemisphere, which is the time when the detrended seasonal CO_2 variations cross the zero line from below (Piao et al., 2008). In general, the positive trend of NEE in spring and summer in Europe is offset by the negative trend in autumn, resulting in no significant trend of interannual NEE (-4.78×10^{-5} PgC yr^{-1}), and the trends in carbon fluxes in spring and summer dominate the trend throughout the year.

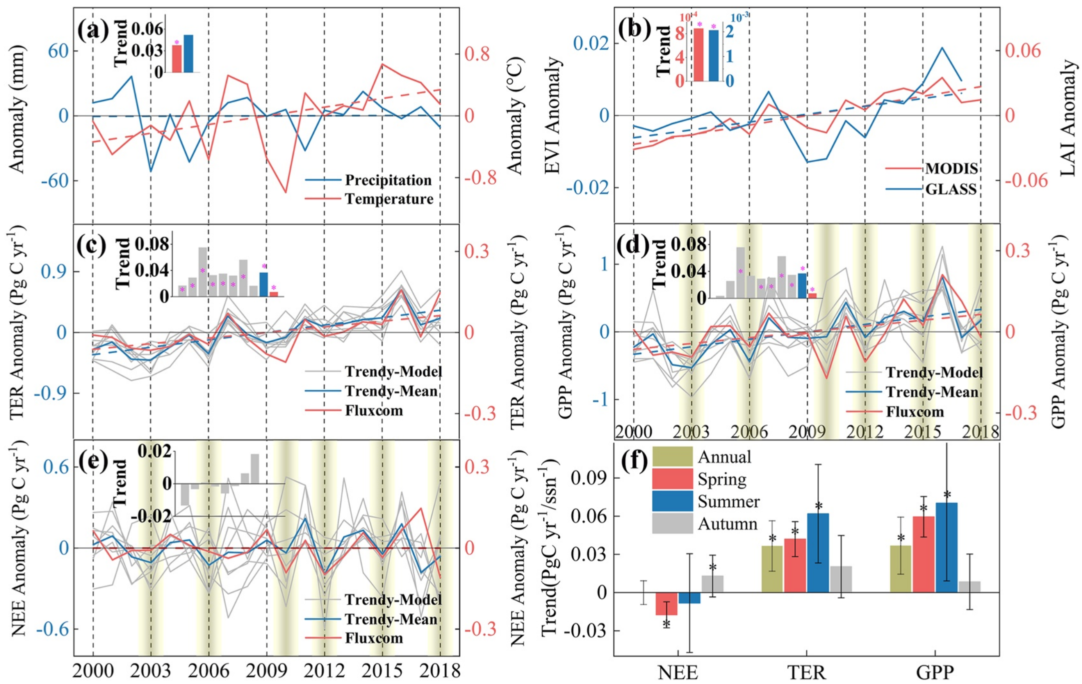

Figure 2. Changes in European climate data, vegetation indices, and carbon fluxes during 2000–2018. (a) Soil moisture and temperature, (b) Enhanced Vegetation Index and leaf area indices, (c) ecosystem respiration (TER), (d) gross primary productivity (GPP), (e) net ecosystem exchange (NEE), and (f) Interannual and seasonal trends in European carbon fluxes (NEE, TER, and GPP). The inset histograms indicate the values of the trends in each case. The gray lines in (c–e) represent the TRENDY models: CABLE, CLASS, DLEM, JSBACH, JULES, ORCHIDEE, SDGVM, and VISIT. The shaded areas in (d and e) represent heatwave years in Europe. The dashed line in (a–e) represents the trend, the asterisks in (f) represent the significance level: $p < 0.05$.

When the European mean NEE and its trend (2000–2018) are partitioned among the land cover classes, we find that forest accounts for the largest fraction (37.43%, 0.21 PgC $year^{-1}$) of the average sink over this period (0.56 PgC $year^{-1}$) (Figure S3 in Supporting Information S1). However, we found that cropland dominates the positive European NEE trend (62.76%, 1.70 TgC $year^{-2}$; Europe, 2.71 TgC $year^{-2}$). One possible reason is that cropland is more affected by human disturbance than forest, and anthropogenic activities such as irrigation, weeding, and pest control can promote carbon absorption (Ciais et al., 2010). Another possible reason is related to the large uncertainty in the forest TER trend (Figure S3 in Supporting Information S1). Forest and cropland dominate the change of mean and trend for TER and GPP, and forest has a larger effect than cropland. Moreover, the forest is found to account for the largest fraction (41.14%) of European NEE interannual variation (IAV), exceeding cropland (39.89%), and grassland (3.07%); it also makes a dominant contribution to European TER and GPP IAV.

3.2. Factors Affecting Changes in European Carbon Fluxes

3.2.1. Influence of CO_2 and Climate Change on European Carbon Fluxes

To investigate the drivers of ecosystem carbon fluxes, we calculated the trend of carbon fluxes in different simulation experiments based on TRENDY models. Our analyses show that the eCO_2 dominates the trend of GPP and TER. Spatially, the increasing trend of GPP due to eCO_2 in most regions of Europe is slightly greater than that of TER, thus leading to a non-significant increase in NEE in most regions except northwest Russia (Figure S4 in Supporting Information S1). On the continental scale, rising CO_2 greatly promoted the increase of GPP and TER (Figure S5 in Supporting Information S1), but due to the offsetting effect between these two fluxes, it only had an insignificantly negative effect on NEE (−6 TgC $year^{-1}$). The climatic effects on GPP and TER (NEE) are positive (negative) in southern and northern Europe, but negative (positive) in western Europe and southeastern Russia. Due to the spatial compensation, CLI ultimately led to an increase

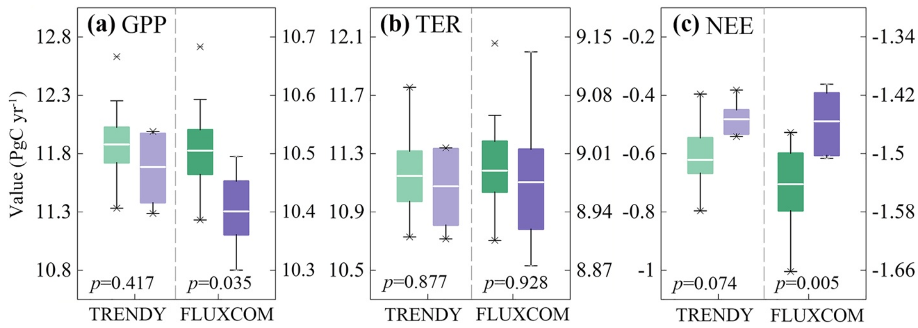

Figure 3. Differences in European carbon fluxes between normal and heatwave years by TRENDY (light color boxes) and FLUXCOM (dark color boxes). (a) Gross primary productivity. (b) Ecosystem respiration. (c) Net ecosystem exchange. The green boxes represent normal years, and the purple boxes represent heatwave years. The *p* indicates the significance of the differences in carbon fluxes between normal and heatwave years based on the method of one-way ANOVA.

in NEE (6 TgC year^{-1}). Compared to the eCO_2 and CLI, the individual effect of the landcover change is apparently limited in carbon fluxes.

To further explore the climatic drivers of carbon fluxes, we examined the partial correlations between carbon fluxes and climate variables (Figure S6 and Table S3 in in Supporting Information S1). There is a strong positive correlation between GPP, TER and TMP over almost the whole of Europe, the significant areas are 40.31% and 62.16% of the continental land, respectively. SM also exerted a significantly positive influence over southern Europe on GPP and TER for 25.44% and 31.03% of continental land, respectively. VPD and SWR have a weak correlation with GPP and TER. In terms of NEE, we found that all climate variables exerted limited influence. In addition, we used the PLSR method to determine which climate variables had the strongest effects on the trend of GPP and TER. We observed that a rising TMP has led to an increase in GPP and TER over western Europe, but a decreased in northern Europe (Figures 1d–1i and Figure S7 in Supporting Information S1). The increase in SM and the decrease in VPD, that is, the increase in water availability, have contributed to the increase of GPP and TER in central Europe. We also calculated the sensitivities of regional mean GPP and TER to climate variables based on the PLSR method (Figure S8 in Supporting Information S1). GPP and TER are mainly sensitive to TMP and SM, and their sensitivity to TMP is greater than that of SM. In addition, the sensitivity of TER to climate variables is usually greater than that of GPP.

3.2.2. Influence of Heatwaves on European Carbon Fluxes

Compared with other regions in mid- and high-latitudes, Europe has experienced frequent heatwaves in recent years, which have caused crop yield reduction, fire outbreak and tree deaths, and led to a reduction of the net CO_2 uptake in the ecosystem (Bastos et al., 2020; Beillouin et al., 2020; Liu et al., 2020). There are apparent differences in European carbon fluxes between heatwave and normal years, we estimated non-significant decrease in the GPP and TER with 196 and 71 TgC, and a non-significant increase in the NEE with 129 TgC based on TRENDY (Figure 3). Based on FLUXCOM, we estimated a significant ($p = 0.035$) 105 TgC decrease in GPP, a non-significant 15 TgC decrease in TER, and a significant ($p = 0.005$) 86 TgC increase in NEE. The decrease of GPP was greater than that of TER in heatwave years, leading to the increase of NEE.

To further investigate the effect of European heatwaves on the seasonal variation of net carbon uptake, three representative heatwaves (2003, 2010, and 2018) were selected for analysis. The heatwaves of 2003, 2010, and 2018 occurred in western Europe, western Russia, central and northern Europe, respectively (Figures S9–S11 in Supporting Information S1). There were obvious seasonal differences of NEE in the central region of the heatwaves, which were consistent among data sets at varying spatial scales, all three heatwaves were preceded by increased carbon uptake in springs, followed by great carbon release in summer (Figure S12 and Table S4 in Supporting Information S1). The reason is that the increase of GPP in spring of heatwave years is larger than that of TER, while the decrease of GPP in summer is also larger than that of TER (Figures S13 and S14 in Supporting Information S1).

4. Discussion

Our results revealed that persistent and widespread greening of European vegetation led to the increase of GPP, and eCO_2 is the dominant driver (Figures S4 and S5 in Supporting Information S1) (Keenan et al., 2016; Wang et al., 2020). Elevating CO_2 also has pronouncedly increased TER due to carbon supplied through increased GPP (Janssens et al., 2001; Migliavacca et al., 2011). The eCO_2 tends to benefit photosynthesis more than respiration and therefore contributes to a slight increase in European carbon uptake. The effect of CLI on European carbon uptake was smaller than that of CO_2. There is strong positive correlation between GPP, TER, and TMP in Europe, that is, warming is the primary climate driver of the regional carbon uptake. These findings have been proved on a larger spatial scale of Northern Hemisphere (Ciais et al., 2019; Keenan & Riley, 2018; Zhu et al., 2016). However, due to the reduced water availability in western Europe (Figure S7 in in Supporting Information S1), warming has led to a decline in GPP and TER in these areas. Finally, CLI has slightly reduced European net carbon uptake. In general, the eCO_2 and CLI are the dominant factors of European carbon uptake, but their effects are opposite, the positive effect of the former partially alleviate the negative effect of the latter.

The frequent heatwaves are another important factor affecting the carbon cycle in Europe (Figure 3). Although, the GPP and TER in Europe have gradually increased, they have greatly decreased in heatwave years (Figures 2c and 2d). The trend of NEE is non-significant, partly due to the NEE increased in the heatwave years (Figure 2e). These results are consistent with those studies based on the atmospheric CO_2 measurements and atmospheric inversion models on the 2018 heatwave (Rodenbeck et al., 2020; Thompson et al., 2020). Under normal circumstances, an increase in temperature could promote an increase in respiration, but the severe deficit of SM and extreme TMP during the heatwaves could stress plants and hence reduce photosynthesis and autotrophic respiration (Doughty et al., 2015; Shi et al., 2014). Meanwhile, due to the reduced supply of plant carbon substrates and the decline of microbial decomposition, soil heterotrophic respiration also showed a decreased trend (Thakur et al., 2018; Zeglin et al., 2013).

Our results indicate that the heatwaves were preceded by decreased NEE in spring, followed by increased NEE in summer (Figure S12 and Table S4 in Supporting Information S1). This seasonal compensation weakened the carbon loss, but it is still difficult to make up for the annual loss. These findings are supported by the research that only focused on the 2018 European heatwave, which showed that the carbon uptake in northern Europe enhanced in spring and reduced in summer during the 2018 heatwave (Smith et al., 2020). In the heatwave years, the sunny spring advanced vegetation activities so that increased net carbon uptake, but these processes would also exacerbate the consumption of soil moisture through evapotranspiration, and this water deficit would persist into the following summer (Fischer et al., 2007; Lian et al., 2020). However, the lack of soil moisture has been widely proved as an important reason for the devastating heatwave in Europe (Liu et al., 2020; Miralles et al., 2014). While these heatwaves were exceptional at the time, their probability of occurrence increases in the coming century due to anthropogenic global warming (Barriopedro et al., 2011). In other words, heatwaves may become a regular factor that will affect the European carbon cycle in the future in addition to temperature, rather than an occasional factor.

Due to differences in the data at spatial scales and temporal resolutions, there are uncertainty in estimating European carbon uptake. TRENDY and FLUXCOM show a high spatial consistency for carbon fluxes on the sign of the trend, but FLUXCOM shows smaller area and magnitude of significant trend in carbon fluxes (Figures 1 and 2), which may be because it is known to underestimate the magnitude of interannual variability (Jung et al., 2020). Despite the good agreement in trend between TRENDY/FLUXCOM and EC sites, there is still a few disagreements in sign and significance (Figures 2d–2f), which may be related to the fact that the ecosystem type in which EC sites are located is monotonous, while the type of TRENDY and FLUXCOM at corresponding pixels are mixed due to the coarse spatial resolution. In addition, CMIP6 indicated a significant trend of European NEE compared to that of TRENDY/FLUXCOM, the discrepancy may be due to an over-sensitivity of CMIP6 to CO_2 fertilization effect (Smith et al., 2016). Therefore, more work is needed to enhance observations and improve the accuracy and resolution of models. Our study indicated the spatial heterogeneity of carbon fluxes changes in Europe, future studies can further attribution from the aspects of biome type and human activities. In addition, the legacy of extreme weather, such as heatwaves, on the European carbon cycle deserves further investigation.

Conflict of Interest

The authors declare have no competing interests.

Data Availability Statement

The dynamic global vegetation models (DGVMs) from the TRENDY-v8 ensemble (https://sites.exeter.ac.uk/trendy/protocol/). Another carbon fluxes data set was provided by the FLUXCOM (https://www.bgc-jena.mpg.de/geodb/projects/FileDetails.php). The in-situ eddy covariance flux measurements were obtained from the ISCOS (https://www.icos-cp.eu/data-products/YVR0-4898) and FLUXNET Network (https://fluxnet.org/data/fluxnet2015-dataset/). The Enhanced Vegetation Index (EVI) was retrieved from the Moderate resolution Imaging Spectroradiometer (MODIS) (https://modis.gsfc.nasa.gov/data/dataprod/mod13.php). The leaf area indices (LAI) data set is taken from the Global Land Surface Satellite product (GLASS) (http://www.glass.umd.edu/Download.html). The air temperature data was obtained from the Climatic Research Unit (CRU) (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.05/). The shortwave radiation data set was provided by ERA5 (https://cds.climate.copernicus.eu/cdsapp#!/search?type=dataset). The soil moisture data was obtained from the Global Landsurface Evaporation: the Amsterdam Methodology (GLEAM) (https://www.gleam.eu/#downloads).

Acknowledgments
This work was supported by the National Key Scientific Research and Development Program of China (Grant no. 2017YFA0603601 and 2018YFC1508901) and the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDA20060402).

References

Ahlstrom, A., Raupach, M. R., Schurgers, G., Smith, B., Arneth, A., Jung, M., et al. (2015). The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. *Science*, *348*(6237), 895–899. https://doi.org/10.1126/science.aaa1668

Alexander, L. V., Zhang, X. B., Peterson, T. C., Caesar, J., Vazquez-Aguirre, J. L., Klein Tank, A. M. G., et al. (2006). Global observed changes in daily climate extremes of temperature and precipitation. *Journal of Geophysical Research*, *111*(D5). https://doi.org/10.1029/2005JD006290

Anderegg, W. R. L., Ballantyne, A. P., Smith, W. K., Majkut, J., Rabin, S., Beaulieu, C., et al. (2015). Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink. *Proceedings of the National Academy of Sciences*, *112*(51), 15591–15596. https://doi.org/10.1073/pnas.1521479112

Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drosler, M., et al. (2008). Soil respiration in European grasslands in relation to climate and assimilate supply. *Ecosystems*, *11*(8), 1352–1367. https://doi.org/10.1007/s10021-008-9198-0

Barriopedro, D., Fischer, E. M., Luterbacher, J., Trigo, R. M., & Garcia-Herrera, R. (2011). The hot summer of 2010: Redrawing the temperature record map of Europe. *Science*, *332*(6026), 220–224. https://doi.org/10.1126/science.1201224

Bastos, A., Ciais, P., Friedlingstein, P., Sitch, S., Zaehle, S., Fan, L., et al. (2020). Direct and seasonal legacy effects of the 2018 heat wave and drought on European ecosystem productivity. *Science Advances*, *6*(24), eaba2724. https://doi.org/10.1126/sciadv.aba2724

Beillouin, D., Schauberger, B., Bastos, A., Ciais, P., & Makowski, D. (2020). Impact of extreme weather conditions on European crop production in 2018. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *375*(1810). https://doi.org/10.1098/rstb.2019.0510

Boeck, H., Dreesen, F. E., Janssens, I. A., & Nijs, I. (2010). Climatic characteristics of heat waves and their simulation in plant experiments. *Global Change Biology*, *16*(7), 1992–2000. https://doi.org/10.1111/j.1365-2486.2009.02049.x

Brecht, M., Miralles, D. G., Hans, L., Robin, V., De, J., Diego, F. P., et al. (2016). GLEAM v3: Satellite-based land evaporation and root-zone soil moisture. *Geoscientific Model Development Discussions*, *10*(5), 1903–1925. https://doi.org/10.5194/gmd-10-1903-2017

Buck, A. L. (1981). New equations for computing vapor pressure and enhancement factor. *Journal of Applied Meteorology*, *20*(12), 1527–1532. https://doi.org/10.1175/1520-0450(1981)020<1527:NEFCVP>2.0.CO;2

Chang, J. F., Ciais, P., Viovy, N., Vuichard, N., Sultan, B., & Soussana, J. F. (2015). The greenhouse gas balance of European grasslands. *Global Change Biology*, *21*(10), 3748–3761. https://doi.org/10.1111/gcb.12998

Chen, J. M., Ju, W., Ciais, P., Viovy, N., Lu, X., Liu, Y., & Lu, X. (2019). Vegetation structural change since 1981 significantly enhanced the terrestrial carbon sink. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-12257-8

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., et al. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, *437*(7058), 529–533. https://doi.org/10.1038/nature03972

Ciais, P., Tan, J., Wang, X., Roedenbeck, C., Chevallier, F., Piao, S. L., et al. (2019). Five decades of northern land carbon uptake revealed by the interhemispheric CO_2 gradient. *Nature*, *568*(7751), 221–225. https://doi.org/10.1038/s41586-019-1078-6

Ciais, P., Wattenbach, M., Vuichard, N., Smith, P., Piao, S. L., Don, A., et al. (2010). The European carbon balance. Part 2: Croplands. *Global Change Biology*, *16*(5), 1409–1428. https://doi.org/10.1111/j.1365-2486.2009.02055.x

Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*(1), 155–159. https://doi.org/10.1037/0033-2909.112.1.155

Commane, R., Lindaas, J., Benmergui, J., Luus, K. A., Chang, R. Y.-W., Daube, B. C., et al. (2017). Carbon dioxide sources from Alaska driven by increasing early winter respiration from Arctic tundra. *Proceedings of the National Academy of Sciences*, *114*(21), 5361–5366. https://doi.org/10.1073/pnas.1618567114

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amezquita, F. F., Cabrera, D. G., Huasco, W. H., et al. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, *519*(7541), 78–82. https://doi.org/10.1038/nature14213

Fischer, E. M., Seneviratne, S. I., Vidale, P. L., Luthi, D., & Schar, C. (2007). Soil moisture—Atmosphere interactions during the 2003 European summer heat wave. *Journal of Climate*, *20*(20), 5081–5099. https://doi.org/10.1175/JCLI4288.1

Fu, Y. S. H., Piao, S. L., Op de Beeck, M., Cong, N., Zhao, H. F., Zhang, Y., et al. (2014). Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology and Biogeography*, *23*(11), 1255–1263. https://doi.org/10.1111/geb.12210

Fu, Z., Ciais, P., Bastos, A., Stoy, P. C., Yang, H., Green, J. K., et al. (2020). Sensitivity of gross primary productivity to climatic drivers during the summer drought of 2018 in Europe. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *375*(1810). https://doi.org/10.1098/rstb.2019.0747

Graven, H. D., Keeling, R. F., Piper, S. C., Patra, P. K., Stephens, B. B., Wofsy, S. C., et al. (2013). Enhanced seasonal exchange of CO_2 by northern ecosystems since 1960. *Science*, *341*(6150), 1085–1089. https://doi.org/10.1126/science.1239207

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations—The CRU TS3.10 Dataset. *International Journal of Climatology*, *34*(13), 623–642. https://doi.org/10.1002/joc.3711

Hersbach, H., & Dee, D. (2016). ERA5 reanalysis is in production. *ECMWF newsletter*, *147*(7), 5–6.

Hogberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Hogberg, M. N., et al. (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, *411*(6839), 789–792. https://doi.org/10.1038/35081058

Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyra, L. R., et al. (2006). Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters*, *33*(6). https://doi.org/10.1029/2005gl025583

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., et al. (2001). Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, *7*(3), 269–278. https://doi.org/10.1046/j.1365-2486.2001.00412.x

Jung, M., Reichstein, M., Schwalm, C. R., Huntingford, C., Sitch, S., Ahlstrom, A., et al. (2017). Compensatory water effects link yearly global land CO_2 sink changes to temperature. *Nature*, *541*(7638), 516–520. https://doi.org/10.1038/nature20780

Jung, M., Schwalm, C., Migliavacca, M., Walther, S., Camps-Valls, G., Koirala, S., et al. (2020). Scaling carbon fluxes from eddy covariance sites to globe: Synthesis and evaluation of the FLUXCOM approach. *Biogeosciences*, *17*(5), 1343–1365. https://doi.org/10.5194/bg-17-1343-2020

Keenan, T. F., Prentice, I. C., Canadell, J. G., Williams, C. A., Wang, H., Raupach, M., & Collatz, G. J. (2016). Recent pause in the growth rate of atmospheric CO_2 due to enhanced terrestrial carbon uptake. *Nature Communications*, *7*. https://doi.org/10.1038/ncomms13428

Keenan, T. F., & Riley, W. J. (2018). Greening of the land surface in the world's cold regions consistent with recent warming. *Nature Climate Change*, *8*(9), 825–828. https://doi.org/10.1038/s41558-018-0258-y

Kendall, M. G. (1948). *Rank correlation methods*. Oxford, England: Griffin.

Lian, X., Piao, S., Li, L. Z. X., Li, Y., Huntingford, C., Ciais, P., et al. (2020). Summer soil drying exacerbated by earlier spring greening of northern vegetation. *Science Advances*, *6*(1), eaax0255. https://doi.org/10.1126/sciadv.aax0255

Liu, X., He, B., Guo, L., Huang, L., & Chen, D. (2020). Similarities and differences in the mechanisms causing the European summer heatwaves in 2003, 2010, and 2018. *Earth's Future*, *8*(4). https://doi.org/10.1029/2019ef001386

Luyssaert, S., Ciais, P., Piao, S. L., Schulze, E. D., Jung, M., Zaehle, S., et al. (2010). The European carbon balance. Part 3: Forests. *Global Change Biology*, *16*(5), 1429–1450. https://doi.org/10.1111/j.1365-2486.2009.02056.x

Mehmood, T., Liland, K. H., Snipen, L., & Sb, S. (2012). A review of variable selection methods in partial least squares regression. *Chemometrics & Intelligent Laboratory Systems*, *118*, 62–69. https://doi.org/10.1016/j.chemolab.2012.07.010

Migliavacca, M., Reichstein, M., Richardson, A. D., Colombo, R., Sutton, M. A., Lasslop, G., et al. (2011). Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites. *Global Change Biology*, *17*(1), 390–409. https://doi.org/10.1111/j.1365-2486.2010.02243.x

Miralles, D. G., Teuling, A. J., Van Heerwaarden, C. C., & Jordi, V. G. D. A. (2014). Mega-heatwave temperatures due to combined soil desiccation and atmospheric heat accumulation. *Nature Geoscience*, *7*(5), 345–349. https://doi.org/10.1038/ngeo2141

Moyano, F. E., Kutsch, W. L., & Schulze, E. D. (2007). Response of mycorrhizal, rhizosphere and soil basal respiration to temperature and photosynthesis in a barley field. *Soil Biology & Biochemistry*, *39*(4), 843–853. https://doi.org/10.1016/j.soilbio.2006.10.001

Naudts, K., Chen, Y., McGrath, M. J., Ryder, J., Valade, A., Otto, J., & Luyssaert, S. (2016). Europe's forest management did not mitigate climate warming. *Science*, *351*(6273), 597–600. https://doi.org/10.1126/science.aad7270

Peters, W., Bastos, A., Ciais, P., & Vermeulen, A. (2020). A historical, geographical and ecological perspective on the 2018 European summer drought. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *375*(1810). https://doi.org/10.1098/rstb.2019.0505

Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., et al. (2008). Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, *451*(7174), 49–52. https://doi.org/10.1038/nature06444

Reich, P. B., Sendall, K. M., Stefanski, A., Rich, R. L., Hobbie, S. E., & Montgomery, R. A. (2018). Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature*, *562*(7726), 263–267. https://doi.org/10.1038/s41586-018-0582-4

Reuter, M., Buchwitz, M., Hilker, M., Heymann, J., Schneising, O., Pillai, D., et al. (2014). Satellite-inferred European carbon sink larger than expected. *Atmospheric Chemistry and Physics*, *14*(24), 13739–13753. https://doi.org/10.5194/acp-14-13739-2014

Rodenbeck, C., Zaehle, S., Keeling, R., & Heimann, M. (2020). The European carbon cycle response to heat and drought as seen from atmospheric CO_2 data for 1999–2018. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *375*(1810). https://doi.org/10.1098/rstb.2019.0506

Shi, Z., Thomey, M. L., Mowll, W., Litvak, M., Brunsell, N. A., Collins, S. L., et al. (2014). Differential effects of extreme drought on production and respiration: Synthesis and modeling analysis. *Biogeosciences*, *11*(3), 621–633. https://doi.org/10.5194/bg-11-621-2014

Sitch, S., Friedlingstein, P., Gruber, N., Jones, S. D., Murray-Tortarolo, G., Ahlstrom, A., et al. (2015). Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences*, *12*(3), 653–679. https://doi.org/10.5194/bg-12-653-2015

Smith, N. E., Kooijmans, L. M. J., Koren, G., van Schaik, E., van der Woude, A. M., Wanders, N., et al. (2020). Spring enhancement and summer reduction in carbon uptake during the 2018 drought in northwestern Europe. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *375*(1810). https://doi.org/10.1098/rstb.2019.0509

Smith, W. K., Reed, S. C., Cleveland, C. C., Ballantyne, A. P., Anderegg, W. R. L., Wieder, W. R., et al. (2016). Large divergence of satellite and Earth system model estimates of global terrestrial CO_2 fertilization. *Nature Climate Change*, *6*(3), 306–310. https://doi.org/10.1038/Nclimate2879

Su-Jong, J., Anthony, B. A., David, S., Colm, S., Parazoo, N. C., David, M., et al. (2018). Accelerating rates of Arctic carbon cycling revealed by long-term atmospheric CO_2 measurements. *Science Advances*, *4*(7), eaao1167. https://doi.org/10.1126/sciadv.aao1167

Thakur, M. P., Reich, P. B., Hobbie, S. E., Stefanski, A., Rich, R., Rice, K. E., et al. (2018). Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nature Climate Change*, *8*(1), 75–78. https://doi.org/10.1038/s41558-017-0032-6

Thompson, R. L., Broquet, G., Gerbig, C., Koch, T., Lang, M., Monteil, G., et al. (2020). Changes in net ecosystem exchange over Europe during the 2018 drought based on atmospheric observations. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *375*(1810). https://doi.org/10.1098/rstb.2019.0512

Vicca, S., Balzarolo, M., Filella, I., Granier, A., Herbst, M., Knohl, A., et al. (2016). Remotely-sensed detection of effects of extreme droughts on gross primary production. *Scientific Reports*, *6*. https://doi.org/10.1038/srep28269

Vico, G., Karacic, A., Adler, A., Richards, T., & Weih, M. (2021). Consistent Poplar clone ranking based on leaf phenology and temperature along a latitudinal and climatic gradient in northern Europe. *Bioenergy Research*, *14*(2), 445–459. https://doi.org/10.1007/s12155-021-10249-5

Wang, S. H., Zhang, Y. G., Ju, W. M., Chen, J. M., Ciais, P., Cescatti, A., et al. (2020). Recent global decline of CO_2 fertilization effects on vegetation photosynthesis. *Science*, *370*(6522), 1295–1300. https://doi.org/10.1126/science.abb7772

Xiao, Z., Liang, S., Wang, J., Chen, P., Yin, X., Zhang, L., & Song, J. (2013). Use of general regression neural networks for generating the GLASS leaf area index product from time-series MODIS surface reflectance. *IEEE Transactions on Geoscience & Remote Sensing*, *52*(1), 209–223. https://doi.org/10.1109/tgrs.2013.2237780

Zeglin, L. H., Bottomley, P. J., Jumpponen, A., Rice, C. W., Arango, M., Lindsley, A., et al. (2013). Altered precipitation regime affects the function and composition of soil microbial communities on multiple time scales. *Ecology*, *94*(10), 2334–2345. https://doi.org/10.1890/12-2018.1

Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., et al. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, *6*(8), 791–795. https://doi.org/10.1038/NCLIMATE3004