

# Enhanced peak growth of global vegetation and its key mechanisms

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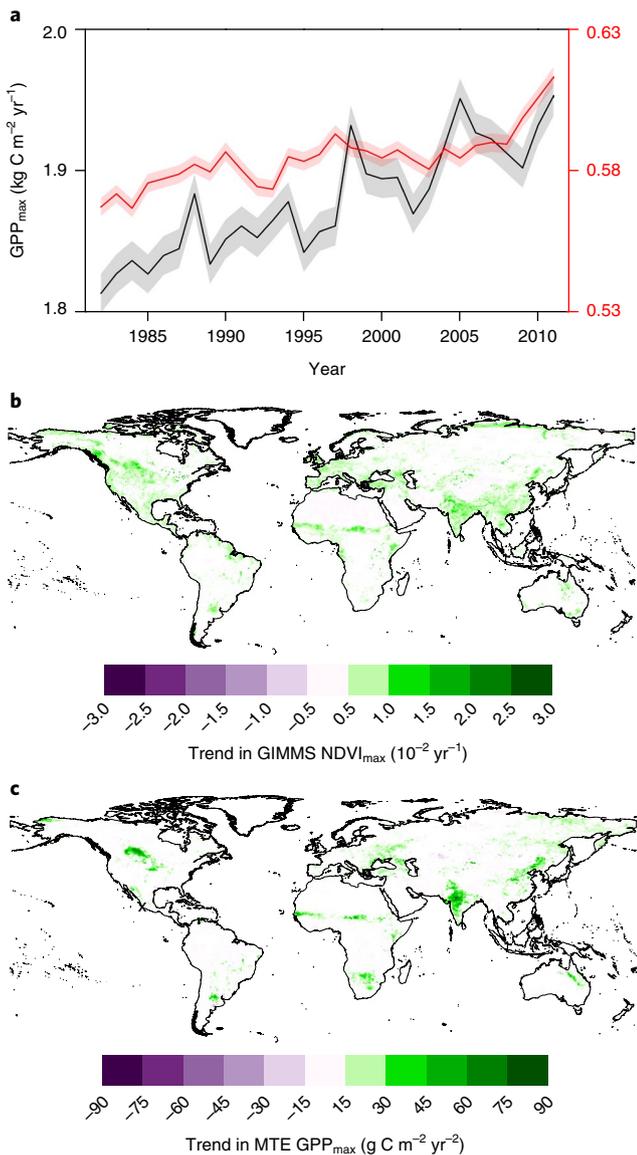
**The annual peak growth of vegetation is critical in characterizing the capacity of terrestrial ecosystem productivity and shaping the seasonality of atmospheric CO<sub>2</sub> concentrations. The recent greening of global lands suggests an increasing trend of terrestrial vegetation growth, but whether or not the peak growth has been globally enhanced still remains unclear. Here, we use two global datasets of gross primary productivity (GPP) and a satellite-derived Normalized Difference Vegetation Index (NDVI) to characterize recent changes in annual peak vegetation growth (that is, GPP<sub>max</sub> and NDVI<sub>max</sub>). We demonstrate that the peak in the growth of global vegetation has been linearly increasing during the past three decades. About 65% of the NDVI<sub>max</sub> variation is evenly explained by expanding croplands (21%), rising CO<sub>2</sub> (22%) and intensifying nitrogen deposition (22%). The contribution of expanding croplands to the peak growth trend is substantiated by measurements from eddy-flux towers, sun-induced chlorophyll fluorescence and a global database of plant traits, all of which demonstrate that croplands have a higher photosynthetic capacity than other vegetation types. The large contribution of CO<sub>2</sub> is also supported by a meta-analysis of 466 manipulative experiments and 15 terrestrial biosphere models. Furthermore, we show that the contribution of GPP<sub>max</sub> to the change in annual GPP is less in the tropics than in other regions. These multiple lines of evidence reveal an increasing trend in the peak growth of global vegetation. The findings highlight the important roles of agricultural intensification and atmospheric changes in reshaping the seasonality of global vegetation growth.**

The temporal dynamics of atmospheric CO<sub>2</sub> concentrations ([CO<sub>2</sub>]) are inversely correlated with that of terrestrial CO<sub>2</sub> uptake<sup>1,2</sup> and vegetation growth<sup>3–7</sup>. Atmospheric monitoring has revealed an increase of 30–60% in the seasonal amplitude of CO<sub>2</sub> concentrations over the Northern Hemisphere since the 1960s<sup>8,9</sup>. The enhanced seasonal CO<sub>2</sub> amplitude is largely driven by the increasing drawdown of the trough of the CO<sub>2</sub> seasonal cycle in the Northern Hemisphere during summer, when CO<sub>2</sub> uptake resulting from vegetation growth also peaks. There is also recent evidence that the interannual variation of terrestrial net carbon uptake correlates more strongly with the peak gross primary productivity (GPP) than any climatic factors<sup>10–12</sup>. In addition, global lands have been greening since the 1980s<sup>13,14</sup>. All of these lines of evidence imply an increasing peak growth of vegetation, but whether such a trend exists globally or mainly in some specific regions remains unknown. A continuing increase of peak vegetation growth is ecologically possible, because measurements of modern-plant traits have found large variations in leaf photosynthetic capacity among and within plant functional types<sup>15</sup>, and palaeoecological studies

have revealed high variability in the maximum individual size of vascular plants under different climatic regimes<sup>16</sup>. Thus, to better predict the temporal trends of land-sink capacity and atmospheric [CO<sub>2</sub>] dynamics, we need to examine whether the peak growth of global vegetation has been enhanced in past years, and understand the global distributions of the change in peak vegetation growth and their driving factors.

Here, we examine the trends of peak vegetation growth using two proxies—the maximum monthly GPP (GPP<sub>max</sub>) and maximum monthly Normalized Difference Vegetation Index (NDVI<sub>max</sub>)—and identify their key driving factors. The global-scale GPP dataset was derived by a machine-learning technique known as the model tree ensemble (MTE) using FLUXNET measurements<sup>17</sup>. The NDVI data were obtained from Global Inventory Modeling and Mapping Studies (GIMMS) corrected for satellite sensor drift<sup>18</sup>. We investigated the difference in photosynthetic capacity among plant functional types using measurements of sun-induced chlorophyll fluorescence (SIF) from Global Ozone Monitoring Experiment 2 (GOME-2)<sup>19</sup>, flux-tower measurements from FLUXNET<sup>10</sup> and plant

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**Fig. 1 | Enhanced monthly vegetation growth peak.** **a**, Annual time series of MTE  $GPP_{max}$  (black line) and GIMMS  $NDVI_{max}$  (red line) over 1982–2011. The shaded areas represent one s.e.m. **b, c**, Spatial patterns of the temporal trend in GIMMS  $NDVI_{max}$  (**b**) and MTE  $GPP_{max}$  (**c**), with white indicating those areas with no significant changes ( $P > 0.05$ ).

functional traits from the TRY database<sup>15</sup> (see Methods). A meta-analysis of 466 experiments was further conducted to compare the contributions of elevated  $CO_2$ , climate warming and nitrogen addition to peak accumulation of plant biomass (see Methods). Finally, using the results of different model scenarios (Supplementary Table 1) from the Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP)<sup>20</sup>, we quantified the contributions of changes in land cover, climate and atmosphere to the simulated trends of global peak GPP.

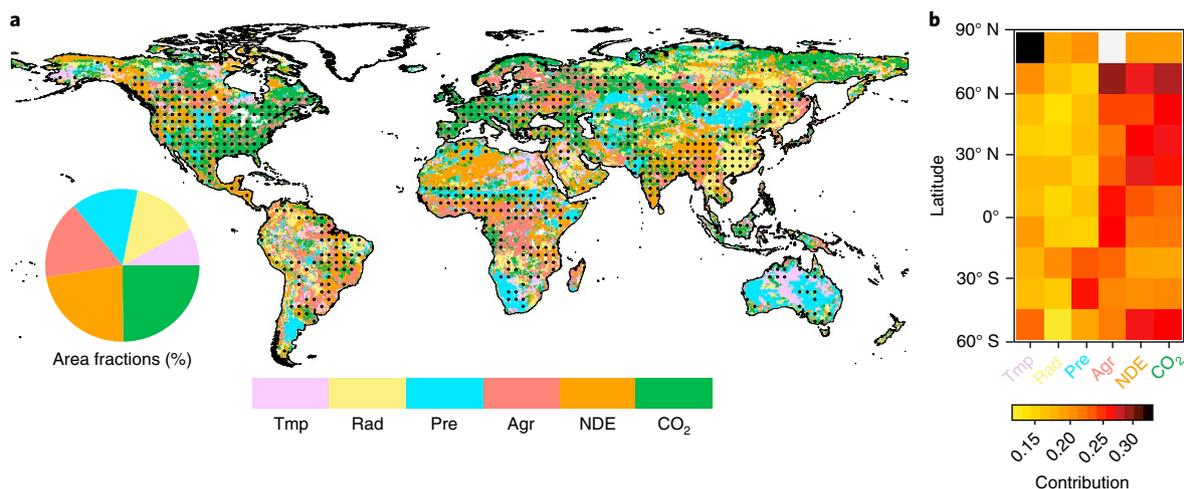
The two indices of peak vegetation growth across the globe (MTE GPP and NDVI) consistently showed linearly increasing trends during the past three decades (1982–2011), with global trends of MTE  $GPP_{max}$  and  $NDVI_{max}$  of  $3.931 \text{ g C m}^{-2} \text{ yr}^{-2}$  ( $P < 0.05$ ) and  $0.0013 \text{ yr}^{-1}$  ( $P < 0.05$ ), respectively (Fig. 1a). The observed increase in global averaged MTE  $GPP_{max}$  was consistent with the observed growth in atmospheric  $CO_2$  amplitude at Point Barrow ( $71.3^\circ \text{N}$ ,  $156.6^\circ \text{W}$ ;  $r^2 = 0.32$ ,  $P < 0.01$ ) (Supplementary Fig. 1). Globally, the

fastest increase in peak vegetation growth occurred in areas of intense agricultural activities, such as northern China, India and North America (Fig. 1b,c and Supplementary Fig. 2). Additionally, the maximum monthly enhanced vegetation index ( $EVI_{max}$ ) also illustrated increasing trends in these agricultural regions over 2000–2011 (Supplementary Fig. 3).

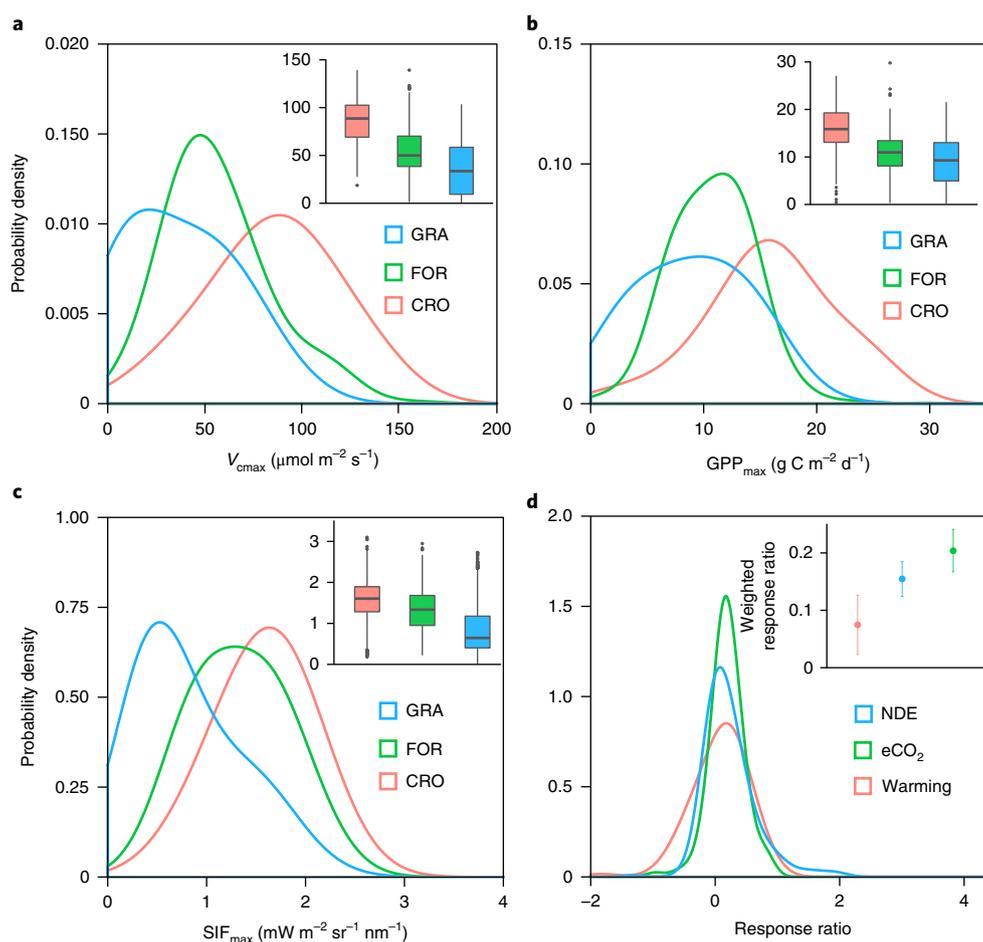
We then applied a relative importance algorithm (see Methods) to attribute the annual change in  $NDVI_{max}$  during 1982–2010 to its drivers (note that we did not attribute MTE  $GPP_{max}$ , because climate and land-use data were used as explanatory variables to train MTE GPP). The driving factors included incoming solar radiation, air temperature, annual precipitation, agricultural activities (for example, fractional change of cropland), rising  $CO_2$  and nitrogen deposition. The contribution of each factor was calculated for each grid cell (Supplementary Fig. 4), and the factor that made the greatest contribution to the  $NDVI_{max}$  variation was identified as the dominant driver (Fig. 2a). At the global scale, around 65% of  $NDVI_{max}$  variation could be explained by the combination of changes in atmospheric  $[CO_2]$  (22%), the rate of nitrogen deposition (22%) and cropland fraction (21%) (Fig. 2a). These factors were also the primary explanatory factors along the global latitudinal gradient (Fig. 2b). Although croplands only accounted for around 13.8% of the land area globally (Supplementary Fig. 5a), they contributed to 31.8% of the global increasing  $GPP_{max}$  trends (Supplementary Fig. 5b). Also, higher intra-biome fractions of significant  $GPP_{max}$  trends were found in croplands compared with other biomes (Supplementary Fig. 5c).

The large contribution of agricultural activities may be related to the higher photosynthetic capacity that crops have over non-crops. Here, we analysed observed multi-level photosynthetic capacity data in three biome groups: cropland, forest and grassland. From 612 observations<sup>21–23</sup> across 81 species, we found that crops had a higher leaf-level maximum carboxylation rate ( $V_{cmax}$ ) ( $85.2 \pm 31.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) compared with trees ( $56.4 \pm 26.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and grasses ( $36.9 \pm 27.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) (Fig. 3a). Ecosystem-level measurements of daily GPP across 125 eddy-flux sites also demonstrated the higher  $GPP_{max}$  in cropland ( $15.9 \pm 5.6 \text{ g C m}^{-2} \text{ d}^{-1}$ ) compared with forest ( $10.8 \pm 3.6 \text{ g C m}^{-2} \text{ d}^{-1}$ ) and grassland ( $9.0 \pm 4.8 \text{ g C m}^{-2} \text{ d}^{-1}$ ) (Fig. 3b). At the biome level, the maximum monthly SIF ( $SIF_{max}$ ), retrieved from the GOME-2 spectral instrument (Fig. 3c), showed that croplands had a higher maximum photosynthetic capacity ( $1.6 \pm 0.4 \text{ mW m}^{-2} \text{ sr}^{-1} \text{ nm}^{-1}$ ) than areas of forest ( $1.3 \pm 0.5 \text{ mW m}^{-2} \text{ sr}^{-1} \text{ nm}^{-1}$ ) and grassland ( $1.2 \pm 0.5 \text{ mW m}^{-2} \text{ sr}^{-1} \text{ nm}^{-1}$ ). These findings were consistent with previous studies that detected a higher maximum photosynthetic capacity in croplands than surrounding dense forests under similar climate conditions<sup>19,24</sup>.

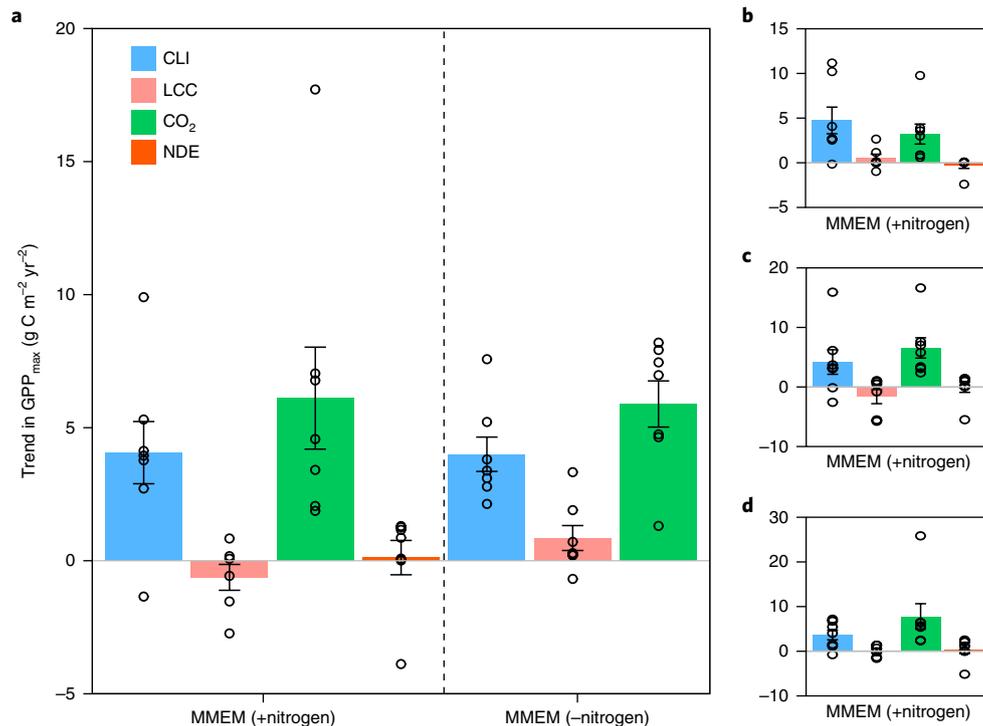
As shown by the meta-analysis of 466 experiments across 719 plant species (Supplementary Fig. 6), peak accumulation of leaf biomass was significantly enhanced by elevated  $CO_2$  (95% confidence interval (CI): 16.7–24.1%) and nitrogen addition (12.4–18.5%), but to a lesser extent by climate warming (2.3–13.6%) (Fig. 3d). There could be multiple reasons for this. First, the results are consistent with the reported strong, worldwide  $CO_2$  fertilization effect<sup>25–27</sup> and nitrogen limitation<sup>28,29</sup> on plant photosynthesis. Second, climate warming benefited plant growth primarily through advancing spring leaf onset<sup>30</sup>, but could suppress plant peak growth by triggering summer water deficiency in dry years or regions<sup>31,32</sup>. Warming could also affect plant growth by increasing soil nitrogen mineralization and availability<sup>33</sup>. In addition, the effects of elevated  $CO_2$  and nitrogen addition on plant biomass were significant in almost all plant functional types, whereas the warming effect was insignificant for herbs (Supplementary Fig. 7). However, it should be noted that croplands are highly managed by humans, so the difference in environmental contributions in cropland regions is uncertain.



**Fig. 2 | Attribution of peak monthly vegetation growth ( $NDVI_{max}$ ).** **a**, The dominant factor influencing variations in  $NDVI_{max}$ , defined as the driving factor that contributes the most to the increase (or decrease) in  $NDVI_{max}$ , is indicated in each grid cell. The statistically significant regions ( $P < 0.05$ ) are labelled with black dots. The six driving factors include incoming shortwave radiation (Rad), annual average air temperature (Tmp), annual precipitation (Pre), annual agriculture cropland fractional changes (Agr), nitrogen deposition (NDE) and rising  $CO_2$  ( $CO_2$ ). Inset, pie chart showing the area fractions of lands dominated by each factor. **b**, Contributions of the six driving factors in  $15^\circ$  latitude bands ( $90^\circ N$ – $60^\circ S$ ).



**Fig. 3 | Higher photosynthetic capacity of croplands.** The probability density functions of three datasets were calculated for cropland (CRO), forest (FOR) and grassland (GRA) ecosystems. **a**, Probability density distributions of photosynthesis capacity by leaf-level  $V_{cmax}$  (from the TRY database) for each biome type. **b**, Ecosystem-level flux-tower-based  $GPP_{max}$  across the FLUXNET2015 sites. **c**, Biome-level  $SIF_{max}$  over 2007–2015 (derived from GOME-2). The inset boxplots in **a–c** show the 25th and 75th percentiles (box edges). Median values are shown by black horizontal bars in each box and the whiskers correspond to  $1.5\times$  inter-quartile range. **d**, Probability density functions of natural log-transformed leaf biomass response ratios to nitrogen deposition, elevated  $CO_2$  ( $eCO_2$ ) and warming treatments. Inset, weighted response ratios  $\pm 95\%$  CIs of leaf biomass response ratios to the treatments using meta-analysis.

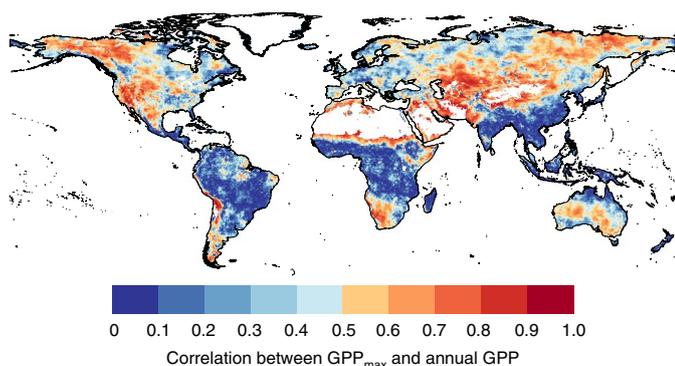


**Fig. 4 | Attribution of peak GPP trends (GPP<sub>max</sub>) using factorial simulations of the ensemble mean of models with (+nitrogen) and without (–nitrogen) a coupled carbon–nitrogen cycle. a–d,** Attributions of modelled GPP<sub>max</sub> trends (g C m<sup>-2</sup> yr<sup>-2</sup>) over the globe (a), northern high latitudes (-60–90° N; b), northern mid-latitudes (-30–60° N; c) and tropics (-0–30° N; d). Modelled trends in GPP<sub>max</sub> were estimated using the multi-model ensemble mean (MMEM) from the MsTMIP by LCC, nitrogen deposition (NDE), climate change (CLI) and rising CO<sub>2</sub> (CO<sub>2</sub>), using a least squares linear regression ( $P < 0.05$ ). The MMEM was calculated in two sub-ensembles: models with nitrogen limitations (+nitrogen) and models without nitrogen limitations (–nitrogen). Error bars show the s.e.m. of GPP<sub>max</sub> trends derived from the model simulations.

We further examined the temporal trend of GPP<sub>max</sub> over 1982–2010 using 15 terrestrial biosphere models from the MsTMIP<sup>34</sup>, and evaluated the ability of these models to project a response of GPP<sub>max</sub> to climate change (varying temperature, precipitation and radiation), land cover change (LCC), rising CO<sub>2</sub> and nitrogen deposition (Supplementary Figs. 8–11). Globally, CO<sub>2</sub> fertilization and climate change were attributed as primary drivers of the modelled GPP<sub>max</sub> trend (Fig. 4), although models disagreed on the relative importance of those two drivers (Supplementary Table 2). We note that the influences of nitrogen deposition might be uncertain because only a few models (8 out of 15) in the ensemble incorporated nitrogen limitation. Here, when using the models to perform factorial simulations that include nitrogen deposition, rising CO<sub>2</sub> accounted for  $63 \pm 20\%$  ( $6.2 \pm 1.91$  g C m<sup>-2</sup> yr<sup>-2</sup>) of the modelled GPP<sub>max</sub> trend globally, followed by climate change ( $42 \pm 12\%$ ,  $4.06 \pm 1.17$  g C m<sup>-2</sup> yr<sup>-2</sup>), nitrogen deposition ( $1 \pm 7\%$ ,  $0.11 \pm 0.64$  g C m<sup>-2</sup> yr<sup>-2</sup>) and LCC ( $-6 \pm 5\%$ ,  $-0.63 \pm 0.49$  g C m<sup>-2</sup> yr<sup>-2</sup>) (Fig. 4a, +nitrogen). Models without carbon–nitrogen couplings demonstrated similar contributions of rising CO<sub>2</sub> and climate change, but positive contributions of LCC to the modelled GPP<sub>max</sub> trend (rising CO<sub>2</sub>:  $55 \pm 8\%$ ,  $5.89 \pm 0.87$  g C m<sup>-2</sup> yr<sup>-2</sup>; climate change:  $37 \pm 6\%$ ,  $4 \pm 0.64$  g C m<sup>-2</sup> yr<sup>-2</sup>; LCC:  $8 \pm 4\%$ ,  $0.85 \pm 0.47$  g C m<sup>-2</sup> yr<sup>-2</sup>). The LCC effect might not be adequately captured by the MsTMIP models since most models do not explicitly represent crops or agricultural management<sup>35</sup>. Similarly, CO<sub>2</sub> fertilization and climate change effects were the main drivers of the modelled GPP<sub>max</sub> trend in the three latitude zones (northern high latitudes, mid-latitudes and tropics), with CO<sub>2</sub> fertilization showing the largest contribution ( $66 \pm 24\%$ ) to the tropical GPP<sub>max</sub> trend (Fig. 4b–d). Examining the correlations of MTE GPP<sub>max</sub> with cropland fractional changes (Supplementary Fig. 12), modelled LCC effects were consistently underestimated in all of the latitude zones

(Fig. 4b–d). The LCC schemes of the models participating in the MsTMIP varied greatly<sup>35</sup>, and differences remained in the model processes relating to the LCCs, including cropland conversion. The underestimated LCC effect could also be due to the fact that agricultural management represented by these models differed significantly by the algorithms specified for the major crop types, such as fertilizer applications, irrigation and tillage practices<sup>36</sup>.

Our study confirms the long-term increase in global vegetation's peak growth during the past three decades. While there is no single driver for the increase in peak vegetation growth, the intensification of agriculture<sup>24,37</sup> and rapid increases in atmospheric [CO<sub>2</sub>]<sup>13,38</sup> and nitrogen deposition<sup>29,39</sup> have served as the most important forcing factors. The expansion of cropland is an important driver, because the enhanced GPP<sub>max</sub> and NDVI<sub>max</sub> (Fig. 1b,c) are largely located in the regions with increasing cropland fractions (Supplementary Fig. 12). In regions with decreasing cropland fractions; for example, the eastern United States and western Europe (Supplementary Fig. 13), no significantly increasing trends in GPP<sub>max</sub> and NDVI<sub>max</sub> were detected (Fig. 1b,c). The cropland expansion also drives the enhanced NDVI<sub>max</sub> in many tropical regions, partially because their peak vegetation growth is not sensitive to the changes in other factors. For example, the peak growth occurs in dry seasons in many tropical forests with high annual precipitation<sup>40</sup>. The higher peak growth of crops compared with non-crop plants results from not only their larger photosynthetic capacity from leaf to community levels (Fig. 3a–c), but also the intense management (irrigation and fertilization)<sup>41,42</sup> in croplands during the growing season<sup>43</sup>, which creates nearly ideal growing conditions that are rare in unmanaged ecosystems. Rising CO<sub>2</sub> largely controls the trends of peak vegetation growth in both satellite-based and modelling analyses.



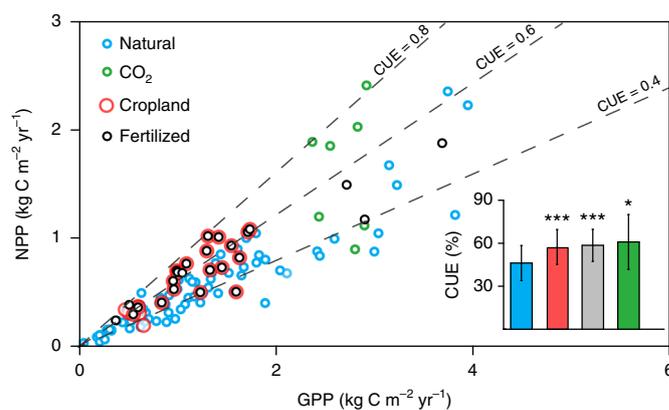
**Fig. 5 | Correlation of MTE  $GPP_{max}$  with annual GPP.** Global distribution of  $r^2$  values between MTE  $GPP_{max}$  and annual GPP over 1982–2011.

It supports the recent finding of a linear relationship between GPP responses and seasonal atmospheric  $CO_2$  amplitude in reaction to rising  $CO_2$ <sup>38</sup>. The dominant role of rising  $CO_2$  rather than other factors in the eastern United States and western Europe has also been reported as part of the analysis of long-term eddy-flux observations<sup>44</sup>. Because nitrogen is a key factor determining plant photosynthetic capacity<sup>28,29</sup>, the large contribution of nitrogen deposition to the enhanced peak growth of vegetation is probably related to plant photosynthetic capacity stimulated by leaf nitrogen concentrations<sup>45</sup>.

Large uncertainty in terrestrial productivity simulated by terrestrial biosphere models has been repeatedly documented over the past few decades<sup>1,46</sup>. This study proposes feasible improvements to ecosystem productivity simulations by emphasizing peak vegetation growth. First, models differ in the design of crop types and the ways in which they deal with crop and agricultural management. MsTMIP models might underestimate the contribution of agricultural activities to the global increase in peak vegetation growth, because most models do not explicitly represent crops and agricultural management<sup>35</sup>. The findings presented here call for an explicit incorporation of agricultural management—such as planting dates and harvesting strategies, cultivar choices, and fertilizer application and irrigation/tillage practices—in global carbon-cycle models<sup>47–50</sup>. Second, further model evaluations and improvements in the control of leaf nitrogen concentrations and environmental variables (for example, temperature, radiation, day length and humidity), when modelling plant photosynthetic capacity (for example,  $V_{cmax}$ ) are needed, as they are conventionally assumed to be constant for each plant functional type or to vary linearly with leaf nitrogen concentrations in current terrestrial biosphere models<sup>45</sup>.

It should be noted that  $GPP_{max}$  contributed less to the temporal changes in annual GPP in the tropics than other regions (Fig. 5). However, whether the enhanced peak growth is associated with an increase of global annual GPP remains uncertain. For example, some recent analyses have shown a minor increasing trend of global annual GPP during the past three decades<sup>14,51</sup>. Also, the efficiency of productivity (for example, the net primary productivity (NPP)-to-GPP ratio) increases with cropland expansion, rising atmospheric  $[CO_2]$  and enhanced nitrogen deposition (Fig. 6). Thus, more research efforts are still needed to explore the long-term trend of global NPP, which has been recognized as a measurable planetary boundary for the biosphere<sup>52</sup>.

The global datasets and attribution methods used here have their own uncertainties. Previous studies have revealed that MTE GPP products depend partly on climate and partly on other parameters (for example, the fraction of absorbed photosynthetically active radiation and light-use efficiency). Thus, the study of



**Fig. 6 | Relationship between measured NPP and GPP.** Points show the CUE (the NPP-to-GPP ratio) across multiple sites comprising forests, grassland and croplands ( $n=24$ ) according to the management status: natural ( $n=83$ ), elevated  $CO_2$  ( $n=7$ ) and fertilized ( $n=25$ ). Inset, graph showing a higher CUE of managed sites than natural sites. Differences between the managed and natural sites were significant using a  $t$ -test. \* $P < 0.05$ ; \*\*\* $P < 0.001$ . Bars and error bars show means  $\pm$  s.d. of the CUE.

peak growth of global vegetation could be improved when independent estimations for global GPP using SIF<sup>53</sup> and/or carbonyl sulfide<sup>54</sup> become available as global GPP tracers in the future. The Lindeman–Merenda–Gold (LMG) method of relative importance calculation allows us to differentiate between the contributions of correlated regressors without considering regressors' order effects in a multiple linear regression<sup>55</sup>, and has been widely used to the attributions of observation-based datasets to global environmental change factors<sup>12,56</sup>, but caution should be taken when evaluating the model factorial experimental results. To address the possible saturation issue of NDVI in the tropics, we found that the  $NDVI_{max}$  values might reach saturation when the maximum leaf area index ( $LAI_{max}$ ) approached a range from 4 to 5 (Supplementary Fig. 14a), and most saturated  $NDVI_{max}$  regions were located in tropical forest (Supplementary Fig. 14b). Although the NDVI data might be saturated and influenced by cloud cover in the tropics, our analyses of  $EVI_{max}$  data that were less influenced by clouds than NDVI showed consistently increasing trends with  $NDVI_{max}$  in many regions (Supplementary Fig. 3).

Overall, this study used multiple data sources and approaches to show an increasing peak growth of global vegetation. The findings of this study have several important implications. First, our results suggest that the recent increase of global peak vegetation growth is not only driven by rising  $CO_2$  and nitrogen deposition, but also by agricultural intensification. Second, soil carbon losses<sup>57</sup> caused by croplands expansion need to be considered in the prediction of future terrestrial carbon sink under the increasing peak plant growth. Lastly, the projections of future atmospheric  $[CO_2]$  seasonality would benefit from a better understanding of the processes regulating peak vegetation growth, such as the seasonal dynamics of leaf photosynthetic capacity ( $V_{cmax}$ )<sup>58–60</sup>, deforestation<sup>24</sup>, natural disturbances such as fires<sup>43</sup> and nutrient limitations<sup>61</sup>.

## Methods

**Flux-tower-based GPP data.** We included 30-year eddy-covariance-flux-based data as large observation-based vegetation productivity datasets. The flux-tower-based GPP products (1982–2011) were provided by the Max Planck Institute for Biogeochemistry (MPI-BGC), with a spatial resolution of  $0.5^\circ \times 0.5^\circ$ , using the machine-learning technique MTE. FLUXNET observations of carbon dioxide, water and energy fluxes were upscaled with the trained MTE to generate global flux fields at a  $0.5^\circ \times 0.5^\circ$  spatial resolution and monthly temporal resolution (<https://www.bgc-jena.mpg.de/geodb/projects/Home.php>).

**Satellite-derived data.** We used the biweekly GIMMS third-generation NDVI (NDVI3g; 1982–2011) dataset (available at <https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v0>), with a spatial resolution of  $1/12^\circ$  ( $\sim 8$  km). The GIMMS-NDVI3g data generated from the calibrated Advanced Very High Resolution Radiometer were carefully corrected for sensor degradation, intersensor differences, cloud cover, solar zenith angle, viewing angle effects due to satellite drift, and volcanic aerosols<sup>62,63</sup>. Here, we investigated the long-term NDVI data, as a proxy of plant photosynthesis, to monitor the vegetation growth. First, we composited the biweekly GIMMS-NDVI3g data to monthly temporal resolution by selecting the higher of the two composites in the same month. These were then aggregated to  $0.5^\circ \times 0.5^\circ$  to match the resolution of GPP data and meteorological data.

Given that NDVI data might suffer from saturation in high-biomass regions, we examined the relationship between NDVI and LAI. The GIMMS-LAI3g was derived from the GIMMS-NDVI3g dataset and Moderate Resolution Imaging Spectroradiometer (MODIS) LAI using the artificial neural network models<sup>64</sup>. The GIMMS-LAI3g dataset provided LAI observations at 15-d temporal resolution and  $1/12^\circ$  spatial resolution. First, we composited the 15-d GIMMS-LAI3g data to monthly LAI. These were then aggregated to the  $0.5^\circ \times 0.5^\circ$  spatial resolution. We also used monthly MODIS EVI data (MOD13C2; collection 6), optimizing the vegetation signal with reductions in atmospheric cloud and aerosol contamination effects<sup>65</sup>, as a complementary proxy to provide more confidence in interpreting peak vegetation growth. The monthly MODIS EVI data at  $0.05^\circ$  spatial resolution (2000–2011) were obtained from the online Data Pool at the National Aeronautics and Space Administration (NASA) Land Processes Distributed Active Archive Centre located at the US Geological Survey Earth Resources Observation and Science Centre (<https://lpdaac.usgs.gov>). The gridded EVI datasets include pixel-level quality assurance flags, as well as statistics of EVI quality and input data. To obtain high-quality EVI composites, we filtered the original data using the following criteria<sup>66</sup> based on the quality assurance layers: (1) corrected product produced at ideal quality for all bands; (2) highest quality for bands 1–7; (3) atmospheric correction; (4) adjacency correction; (5) MOD35 cloud flag indicated 'clear'; (6) no detections of cloud-shadow; and (7) low or average aerosol quantities. Gaps remaining after quality assurance filtering were filled by interpolation in the temporal dimension, computing the values of gaps by fitting linearly between the two adjacent points. The time series with more than two consecutive gaps were excluded from further analyses. The data were then mosaicked and re-projected using the MODIS Reprojection Tool, and mosaicked images were resampled into  $0.5^\circ \times 0.5^\circ$  (latitude  $\times$  longitude) resolution using the nearest-neighbour algorithm.

We analysed the SIF data to investigate vegetation photosynthetic capacity at the biome level. The SIF data were produced using spectra from the GOME-2 instrument onboard the MetOp-A platform<sup>19</sup>. SIF retrievals were performed in the 715–758 nm spectral window with  $\sim 0.5$  nm spectral resolution<sup>67</sup>. The SIF products ([https://avdc.gsfc.nasa.gov/pub/data/satellite/MetOp/GOME\\_F](https://avdc.gsfc.nasa.gov/pub/data/satellite/MetOp/GOME_F)) used in this study were GOME2\_F level 3 monthly retrievals (2007–2015) with a spatial resolution of  $0.5^\circ \times 0.5^\circ$ . The GOME-2 level 3 SIF retrievals were quality filtered, aggregated as monthly averages and gridded globally. Previous studies have reported that SIF could be a robust indicator of GPP, although the uncertainties existed in the GPP-SIF relationship<sup>19,68</sup>.

Gridded GPP<sub>max</sub>, NDVI<sub>max</sub> and SIF<sub>max</sub> datasets were compiled annually by picking out the maximum from the monthly composites of the same year in each grid cell. In particular, the long-term MTE GPP<sub>max</sub> and NDVI<sub>max</sub> products were identified to monitor the linear trends of global peak vegetation growth in the past three decades. The spatial patterns of temporal trends in each dataset were calculated using a least squares linear regression for each grid. All the data calculations were accomplished in R (<http://www.r-project.org/>).

**Forcing datasets.** Forcing datasets were involved to investigate the contribution of multiple factors to annual changes in NDVI<sub>max</sub> over 1982–2010, including radiation, air temperature, precipitation, the fraction of cropland, nitrogen deposition and rising [CO<sub>2</sub>]. Annual climatology (including air temperature and precipitation) data with a spatial resolution of  $0.5^\circ \times 0.5^\circ$  were obtained from meteorological data stored at the Climate Research Unit (CRU) at the University of East Anglia (CRU TS 3.23)<sup>69</sup>. We obtained  $0.5^\circ \times 0.5^\circ$  gridded data of annual downward shortwave radiation at the surface ( $W m^{-2}$ ) from the Terrestrial Hydrology Research Group at Princeton University<sup>70</sup> (<http://hydrology.princeton.edu/data/pgf/v2/0.5deg/monthly/>). The annual global gridded ( $0.5^\circ \times 0.5^\circ$ ) cropland fraction change dataset (1982–2010) was obtained from Hurtt et al.<sup>71</sup> ([http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds\\_id=1248](http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1248)) and used as the agriculture driving factor in analysing the dominators of observed peak plant growth (NDVI<sub>max</sub>). Here, the global gridded ( $0.5^\circ \times 0.5^\circ$ ) atmospheric components were change data for atmospheric nitrogen deposition and atmospheric [CO<sub>2</sub>]. Both of the datasets were obtained from the MsTMIP environmental driver datasets for the historical period<sup>36,72</sup>. The atmospheric [CO<sub>2</sub>] data prepared for the MsTMIP were downloaded from the Oak Ridge National Laboratory Distributed Active Archive Center at a monthly time scale, then averaged to the annual mean to match the NDVI<sub>max</sub> data. Based on Dentener's maps and introduced spatiotemporal variation from nitrogen emissions<sup>73</sup>, time-varying annual nitrogen deposition rate (NH<sub>x</sub>-N and NO<sub>y</sub>-N) data were used in this study.

**Relative importance calculation.** We used a relative importance analysis approach to quantify the relative contributions of each factor (for example, radiation, air temperature, precipitation, the fraction of cropland, nitrogen deposition and rising CO<sub>2</sub>) to the annual changes of NDVI<sub>max</sub> in each grid cell, expressed as the Pearson correlation in a multiple linear regression ( $NDVI_{max} = b_0 + b_1 \times radiation + b_2 \times temperature + b_3 \times precipitation + b_4 \times cropland\ fraction + b_5 \times nitrogen\ deposition + b_6 \times CO_2 + \epsilon$ ).  $\epsilon$  represented other drivers that were not considered but might contribute to NDVI<sub>max</sub> variation. The algorithm was performed with the 'relaimpo' package in R, which was based on variance decomposition for multiple linear regression models<sup>74</sup>. The 'relaimpo' package provides six different methods for analysing the relative importance of each regressor in linear regression. We chose one of the most computer-intensive and commonly used methods named 'LMG', which allows differentiation of the contribution of different correlated regressors in a multiple linear regression. In multiple regression models, the relative importance assessment strongly depended on the order of the regressors. The LMG method estimated the relative importance (RI) of each variable by decomposing the sum of squares into non-negative contributions shared by each variable, and the LMG values were obtained by averaging the sequential sum of squares ( $r^2$ ) for all possible orders. Finally, all RI values were normalized (divided by  $r^2$ ) to sum to 1.

In each grid cell, we calculated the contributions of each factor to interannual NDVI<sub>max</sub> (Supplementary Fig. 4). Then, the global attributions to NDVI<sub>max</sub> were calculated by averaging the values of contributors at the pixel level (statistically significant pixels;  $P < 0.05$ ).

**In situ observation dataset.** To test whether crops have higher photosynthetic capacity than natural plant species, we investigated the measured leaf-level maximum carboxylation rate ( $V_{cmax}$ ) and flux-tower-observed GPP<sub>max</sub> at the ecosystem level, which were analysed using the probability density function. The leaf-level maximum carboxylation rate ( $V_{cmax}$ ,  $\mu mol m^{-2} s^{-1}$ ) data of 612 observations across 81 plant species were compiled from the TRY database<sup>15</sup> (<http://www.try-db.org>)—a coverage of plant trait data representing plant functional diversity at the global scale. Leaf  $V_{cmax}$  data were then divided into crops, trees and grasses to explore the differences in probability density among species<sup>21–23</sup>. Photosynthetic capacity simulations within earth system models were closely associated with  $V_{cmax}$ <sup>45</sup>. The measured multi-species leaf  $V_{cmax}$  in Fig. 3a indicates the overall difference in leaf-level plant photosynthetic capacity differences across crops, trees and grasses.

We also used eddy-covariance-flux-tower data from 125 flux sites (including forest, grassland and cropland) across the globe (see Supplementary Data 1 for a full list). These GPP flux data were obtained from the FLUXNET2015 Tier 1 dataset (November 2016 release; <http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>). Flux-tower GPP values were calculated as the mean of both daytime and night-time partition methods after a data quality check. According to the methods and criteria in Reichstein et al.<sup>75</sup> and Papale et al.<sup>76</sup>, data for each site year in the database were filtered. Due to the inevitable data uncertainties arising from indirect measurement and some negative values in some site years, only site years with more than 300 daily estimates were chosen from the database. There were 960 site years of GPP data in total. Comprehensive fit functions and algorithms were developed to derive the flux-tower GPP<sub>max</sub> of each site in different biomes. Details on the flux GPP<sub>max</sub> calculation methods are described in Xia et al.<sup>10</sup>.

**Meta-analysis of leaf biomass data.** We conducted a systematic meta-analysis to further explain the higher contributions of atmospheric [CO<sub>2</sub>] and nitrogen deposition relative to climate change on NDVI<sub>max</sub>, according to the guidelines listed in the PRISMA (preferred reporting items for systematic reviews and meta-analyses) statement (<http://www.prisma-statement.org/>). We searched peer-reviewed and primary research papers before December 2016 from the Web of Science. Candidate papers were individually examined for data meeting the following criteria: (1) both control and treatment existed; (2) the responses of terrestrial plant growth to changes in environmental factors (CO<sub>2</sub>, nitrogen and temperature) were provided at the species level, and the means ( $X$ ), sample sizes ( $n$ ), and s.d. or s.e.m. values under the control and treatment were also provided; and (3) the examined responsive variables encompassed plant parts; for example, whole, aboveground, belowground, leaf, root, stem, and so on. Since sample sizes and variance of the original studies were included in our data collections, our meta-analysis followed the guidelines set by Vetter et al.<sup>77</sup>. Based on these guidelines, a database of 466 studies (see Supplementary Data 2 for a full list) investigating the response of plant growth under treatment (warming, nitrogen addition and elevated CO<sub>2</sub>) was established for further analysis (Supplementary Fig. 6). Here, we further examined the responses of leaf biomass to warming, nitrogen addition and elevated CO<sub>2</sub> using this database. Moreover, we separated the experimental data into different plant functional types (woody, herb, tree, shrub, grass or forb) and climatic zones (tropical, temperate or boreal). Overall, our meta-analysis considered leaf-growth data from 92 observations for warming, 234 observations for nitrogen addition and 113 observations for elevated CO<sub>2</sub>.

For the studies that provided s.e.m., s.d. was calculated by:

$$s.d. = s.e.m. \cdot \sqrt{n} \quad (1)$$

The meta-analysis followed the techniques described in Hedges et al.<sup>78</sup>. The response of leaf growth to treatments was estimated using the natural log-transformed response ratio (RR):

$$\ln[\text{RR}] = \ln[X_T / X_C] \quad (2)$$

where  $X_C$  is the mean value of leaf biomass under the control treatment and  $X_T$  denotes the mean value of the corresponding treatment (warming, nitrogen addition or elevated  $\text{CO}_2$ ). The variance of the natural log-transformed response ratio was:

$$v = \left( \frac{\text{s.d.}_C^2}{n_C X_C^2} + \frac{\text{s.d.}_T^2}{n_T X_T^2} \right) \quad (3)$$

where  $\text{s.d.}_C$  and  $\text{s.d.}_T$  are the s.d. values of  $X_C$  and  $X_T$ , and  $n_C$  and  $n_T$  are the sample sizes of  $X_C$  and  $X_T$ , respectively.

Then, a mixed-effects model was used to obtain the weighted response ratio of leaf growth to warming, nitrogen addition and elevated  $\text{CO}_2$ , respectively. The weighted response ratio ( $\text{RR}_{++}$ ) was calculated as below ( $m$  and  $k$  are the number of groups and comparison, respectively):

$$\text{RR}_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k W_{ij} \text{RR}_{ij}}{\sum_{i=1}^m \sum_{j=1}^k W_{ij}} \quad (4)$$

where  $W$  is the weight ( $1/v$ ) of each RR, and its s.e.m. was calculated as below:

$$S(\text{RR}_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^k W_{ij}}} \quad (5)$$

The 95% CI was  $\text{RR}_{++} \pm 1.96 \times S(\text{RR}_{++})$ , and was generated by bootstrapping the data using MetaWin 2.1 (Sinauer Associates). The results were back-transformed and are represented as percentage change by  $(\exp(\text{RR}_{++}) - 1) \times 100\%$ . The response was considered significant if the 95% CI did not overlap with zero.

**Processing model outputs from MsTMIP.** To further evaluate the simulated global peak vegetation growth trends and their driving factors, GPP<sub>max</sub> of 15 MsTMIP models were used during 1982–2010. The models were forced with consistent driver datasets. The simulation protocol and details of the forcing data were described by Huntzinger et al.<sup>20</sup> and Wei et al.<sup>36</sup>. We performed a series of experimental simulations to analyse the four main drivers (climate change, LCC,  $\text{CO}_2$  fertilization and nitrogen deposition) of simulated global peak vegetation growth: initial conditions, with all environmental drivers constant (RG1); varying climate (temperature, precipitation and radiation) only (SG1); varying climate and land cover (SG2); varying climate, land cover and  $\text{CO}_2$  (SG3); and varying climate, land cover,  $\text{CO}_2$  and nitrogen deposition (BG1). Simulations SG1-RG1, SG2-SG1, SG3-SG2 and BG1-SG3 were used to evaluate the effects of climate change, LCC,  $\text{CO}_2$  fertilization and nitrogen deposition on peak vegetation growth, respectively. It should be noted that not all 15 models submitted all 4 sensitivity simulations, especially for nitrogen deposition (Supplementary Table 1). Thus, we conducted the factorial experiments in two sub-ensembles: eight models with nitrogen limitation (+nitrogen) and seven models without nitrogen limitation (–nitrogen). An attribution analysis for each individual model in the sub-ensembles was completed, then values were averaged across the models. Additionally, current model intercomparison projects consider the climate change scenario (SG1) as a combination of temperature, precipitation and radiation, making direct comparison with the relative importance calculations less comprehensive. We recommend that future model intercomparison projects request outputs from model simulations under a separated climate factor scenario to allow for more direct comparisons with observation-based attributions. We also request a possible scenario incorporating a combination of varying climate and varying  $\text{CO}_2$  to attribute the LCC effect in future model intercomparison experiments.

**Carbon use efficiency (CUE) dataset.** The CUE was calculated as the ratio of NPP to GPP. Both in situ GPP and NPP data were obtained from the database in DeLucia et al.<sup>79</sup>, Campioli et al.<sup>80</sup> and Chen et al.<sup>81</sup>. Here, we present a CUE dataset of 139 site years (Supplementary Fig. 15) comprising forests, grasslands and croplands. According to the management status and treatments, sites were divided into natural, elevated  $\text{CO}_2$  and fertilized.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Code availability.** The code used to generate the results of this study are available from the corresponding author upon request.

## Data availability

The MTE GPP datasets are available at <https://www.bgc-jena.mpg.de/geodb/projects/Home.php>. The Advanced Very High Resolution Radiometer GIMMS-

NDVI3g datasets are available at <https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v0>. The GOME-2 SIF datasets are available at [https://avdc.gsfc.nasa.gov/pub/data/satellite/MetOp/GOME\\_F](https://avdc.gsfc.nasa.gov/pub/data/satellite/MetOp/GOME_F). The MODIS EVI data are available from the NASA Land Processes Distributed Active Archive Center at <https://lpdaac.usgs.gov>. The in situ GPP observations are available from FLUXNET2015 at <http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>. The  $V_{\text{cmax}}$  data are available from the TRY database<sup>15</sup> at <http://www.try-db.org>. The CRU TS 3.23 climate datasets are available from the CRU (<https://crudata.uea.ac.uk/cru/data/hrg/>). The shortwave radiation datasets are available from the Terrestrial Hydrology Research Group at <http://hydrology.princeton.edu/data/pgf/v2/0.5deg/monthly/>. The MsTMIP modelling results are available at <https://nacp.ornl.gov/mstmpdata/>.

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### Author contributions

J.X. designed the study. K.H. performed the analysis. J.X. and K.H. wrote the first draft. Y.L., Y.Wang, A.A., J.C., E.C., Z.L., J.W., Y.Q., X.X., L.Y. and C.B. contributed to the idea development. C.S., D.N.H., R.B.C., Y.F., J.B.F., A.M.M., K.S. and Y.Wei provided the modelling results. All authors interpreted the results and revised the manuscript.

### Competing interests

The authors declare no competing interests.

### Additional information

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No software was used for data collection.

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We used Metawin 2.1 and the R version 3.3.1.

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Research sample	We used the satellite-derived NDVI data, GPP flux data, SIF data and climate data over the global lands. The spatial resolution of each global data set determines the number of pixels used in the study.
Sampling strategy	We defined the groups based on the existing biome maps and plant species.
Data collection	Global remote sensing data, climate data and in-situ observational data were downloaded from the URLs stated in the article. 466 eligible studies for meta-analysis were found using Web of Science.
Timing and spatial scale	The global GPP, GIMMS NDVI and climate data used in our study were from 1982 to 2011 at a 0.5 degree spatial resolution and a monthly temporal resolution. The MODIS EVI data were provided at a 0.5 degree spatial resolution and a monthly temporal resolution over 2000-2011. The SIF products were GOME2_F level 3 monthly retrievals at a 0.5 degree spatial resolution during 2007-2015. Research papers published before December 2016 from Web of Science were used in the meta-analysis.
Data exclusions	No data were excluded from the data sets in all the analyses.
Reproducibility	Our analyses were mainly based on public satellite products and observational data, and the results could be reproduced.
Randomization	We performed the global trend analysis for each pixel with satellite images and GPP data set, thus randomization is not relevant to our study.
Blinding	The majority of our study were based on existing data, therefore blinding is not relevant to our study.
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