# Eco-evolutionary Modelling of Global Vegetation Dynamics and the Impact of $CO_2$ during the late Quaternary: Insights from Contrasting Periods

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***Ms for: Earth System Dynamics***

## Abstract

Changes in climate have had major impacts on global vegetation during the Quaternary. However, variations in $CO_2$ levels also play a role in shaping vegetation dynamics by influencing plant productivity and water-use efficiency, and consequently the relative competitive success of the $C_3$ and $C_4$ photosynthetic pathways. We use an eco-evolutionary optimality (EEO) based modelling approach to examine the impacts of climate fluctuations and $CO_2$-induced alterations on gross primary production (GPP). We considered two contrasting periods, the Last Glacial Maximum (LGM, 21,000 years before present) and the mid-Holocene (MH, 6,000 years before present) and compared both to pre-industrial conditions (PI). The LGM, characterised by generally colder and drier climate, had a $CO_2$ level close to the minimum for effective $C_3$ plant operation. In contrast, the MH had warmer summers and increased monsoonal rainfall in the northern hemisphere, although with a $CO_2$ level still below PI. We simulated vegetation primary production at the LGM and the MH compared to the PI baseline using a light-use efficiency model that simulates GPP coupled to an EEO model that simulates leaf area index (LAI) and $C_3$/$C_4$ competition. We found that low $CO_2$ at the LGM was nearly as important as climate in reducing tree cover, increasing the abundance of $C_4$ plants and lowering GPP. Global GPP in the MH was similar to the PI (although greater than the LGM), also reflecting $CO_2$ constraints on plant growth despite the positive impacts of warmer and/or wetter climates experienced in the northern hemisphere and tropical regions. These results emphasise the importance of taking account of impacts of changing $CO_2$ levels on plant growth to model ecosystem changes.

## 1 Introduction

Vegetation regulates the exchanges of energy, water, and carbon dioxide between the land and the atmosphere (Williams and Torn, 2015; Forzieri et al., 2020; Hoek van Dijke et al., 2020). Gross primary production (GPP), defined as the carbon uptake by vegetation through photosynthesis at the ecosystem scale, determines the extent to which the terrestrial biosphere can mitigate $CO_2$ emissions (Bonan, 2008; Zeng et al., 2017; Chen et al., 2019). There is a tight coupling between $CO_2$ uptake and water loss via stomata, such that when ambient $CO_2$ is high water-use efficiency (the amount of water required for transpiration to achieve a unit of $CO_2$ assimilation) is also high (Medlyn et al., 2017). Recent global greening trends are thought to reflect both changes in climate, particularly warming at high latitudes, and the effect of increasing $CO_2$ on water-use efficiency (Cai and Prentice, 2020; Piao et al., 2020). However, there is still uncertainty about the relative importance of these two effects on recent changes in global GPP, in part because recent climate changes have been largely driven by the increase in $CO_2$.

Past climate states provide opportunities to examine the role of climate and $CO_2$ in modulating GPP when there is a greater de-coupling between changes in $CO_2$ and climate. The contrast between glacial and interglacial states during the Late Quaternary offers an ideal opportunity to separate the impact of these two factors on vegetation. Glacial-interglacial shifts in climate are largely driven by changes in orbital configuration which resulted in changes in the seasonal and latitudinal patterns of incoming solar radiation (Berger, 1978; Berger and Loutre, 1991). The Last Glacial Maximum (LGM), ca 21,000 years ago, had an orbital configuration similar to the present but was characterised by the presence of large continental ice sheets and generally colder and drier climates (Kageyama et al., 2021). The $CO_2$ level was ca 190 ppm, which is close to the minimum for effective $C_3$ plant operation (Gerhart and Ward, 2010). The mid-Holocene (MH), ca 6000 years ago, was characterised by a significantly different seasonal and latitudinal distribution of incoming solar radiation (a result of changes in obliquity and precession) which affected light availability for photosynthesis and produced warmer summers in the northern hemisphere and wetter conditions in the sub-tropics (Brierley et al., 2020). However, ambient $CO_2$ was only ca 264 ppm (Otto-Bleisner et al., 2017), somewhat lower than the pre-industrial (PI) period (285 ppm) and considerably lower than today.

Three sets of factors could potentially impact vegetation productivity changes between the LGM, MH and pre-industrial periods: changes in climate, atmospheric $CO2$ and solar radiation. Several published studies have simulated LGM climate impacts on vegetation (and/or fire, interacting with vegetation), with – or without – consideration of the additional physiological effects of low $CO2$ on plants (Levis et al. 1999, Harrison and Prentice 2003, Martin Calvo et al. 2014). Other studies have performed factorial experiments to more formally separate the effects of climate and $CO2$ (Woillez et al. 2011, O'ishi & Abe-Ouchi 2013, Claussen et al. 2013, Martin Calvo & Prentice 2015, Chen et al. 2019, Haas et al. 2023).

Comparison among these studies of LGM-to-recent primary production shifts is approximate at best because they have used different climate models and experimental protocols. Some have used pre-industrial conditions as a reference; others, modern (higher-$CO2$) conditions. However, they all have used land ecosystem models based on the plant functional type (PFT) concept. Uncertainty in the delimitation of PFTs and the parameter values assigned to them is endemic to this type of model, as variation of quantitative traits within PFTs in the real world is generally much larger than variation between them (Kattge et al., 2011). In some cases, the model PFT representation has resulted in an unrealistic simulation of LGM vegetation patterns (e.g. Woillez et al. 2011). Here we use the P model (Stocker et al. 2020), which accounts for acclimation and adaptation to environment independently of PFTs on the basis of universal eco-evolutionary optimality (EEO) hypotheses. The P model has been subject to extensive evaluation against worldwide data from eddy covariance flux towers across all biomes. We include an extension of the P model which simulates foliage cover and its seasonal cycle – also independently of PFTs. This extended model has been shown to reproduce foliage amounts and seasonal dynamics more accurately than any state-of-the-art vegetation model (Zhou et al., 2025). We use a simple process-based scheme to represent the relative competitive success of $C_3$ versus C4 plants, which has been validated against worldwide soil carbon stable isotope data (Lavergne et al., 2024). This combination of three independently tested, PFT-independent modelling components enables us, for the first time, to apply an EEO-based approach to simulate LGM and recent vegetation function in a globally uniform way

There has been some work on the implications of MH climate for biome distributions (e.g. Kaplan et al., 2003; Wohlfahrt et al., 2008) but little consideration of the impacts of climate and CO2 on global productivity changes since the MH (Foley, 1994; François et al. 1999). Here, we use the same consistent methodology that we apply to the LGM to estimate MH-to-pre-industrial changes in global GPP. Our analysis includes the effect of changes in the light regime, which are a necessary consequence of changes in the seasonal and latitudinal distribution of insolation due to orbital forcing, as well as changes in cloud cover linked to monsoon shifts.

EEO-based modelling approaches provide parameter-sparse representations of plant and vegetation processes, thus considerably reducing uncertainties due to model parameterisation (Harrison et al, 2021). They have been shown to perform as well or better than more complex models under recent conditions (Cai et al., 2025; Zhou et al., 2025) and thus can provide a robust way of modelling vegetation changes under different climate regimes. We use a series of counter-factual experiments to examine the magnitude of changes due to individual drivers (climate parameters, solar radiation and $CO_2$) on the simulated GPP and to determine the regions where specific factors are most influential.

## 2 Methods

### 2.1 Modelling Scheme

We simulated vegetation changes at the LGM and the MH compared to the pre-industrial (PI) state using a sequence of linked models that predict GPP, leaf area index (LAI) and $C_3$/$C_4$ competition based on EEO theory (Fig. 1).

The P model (Wang et al., 2017, Stocker et al., 2020) is a light-use efficiency model that simulates GPP. It uses the Farquhar-von Caemmerer-Berry photosynthesis model (Farquhar et al., 1980) for instantaneous biochemical processes combined with two EEO hypotheses describing photosynthetic acclimation, the ‘coordination’ and ‘least- cost’ hypotheses (Prentice et al., 2014, Wang et al., 2017), to account for the spatial and temporal acclimation of carboxylation and stomatal conductance to environmental variations at weekly to monthly time scales. Although the P model simulates both $C_3$ and $C_4$ photosynthesis, it does not need to make any other distinctions between plant functional types. The required inputs to the model (Fig. 1) are air temperature (°C), vapour pressure deficit (VPD, Pa) derived from relative humidity, air pressure (Pa) (to account for the effect of elevation on photosynthesis, incident photosynthetic photon flux density (PPFD, $\mu$mol $m^{-2}$ $s^{-1}$) estimated from short wave solar radiation, and ambient $CO_2$ concentration. The P model has been extensively validated and shown to predict the geographic patterns of GPP under modern conditions successfully (Wang et al., 2017; Stocker et al., 2020). Furthermore, it correctly predicts related physiological characteristics, including the global pattern of the maximum carboxylation ($V_{cmax}$) rate in relation to gradients in PPFD, temperature and VPD (Smith et al., 2019), the seasonal variation of $V_{cmax}$ in different biomes (Jiang et al., 2020), its response to atmospheric $CO_2$ (Smith and Keenan, 2020), and the variation of photosynthetic traits along elevational gradients (Peng et al., 2020). The responses of photosynthetic properties to enhanced $CO_2$ as simulated by the P model have been validated against both Free Air Carbon dioxide Enrichment (FACE) experiments (Wang et al., 2017) and controlled-environment experiments (Smith and Keenan, 2020). Moreover, the model's implied response of photosynthetic capacity to $CO_2$ has been validated by measurements on plants experimentally grown at low (160 ppm) $CO_2$ (Harrison et al., 2021).

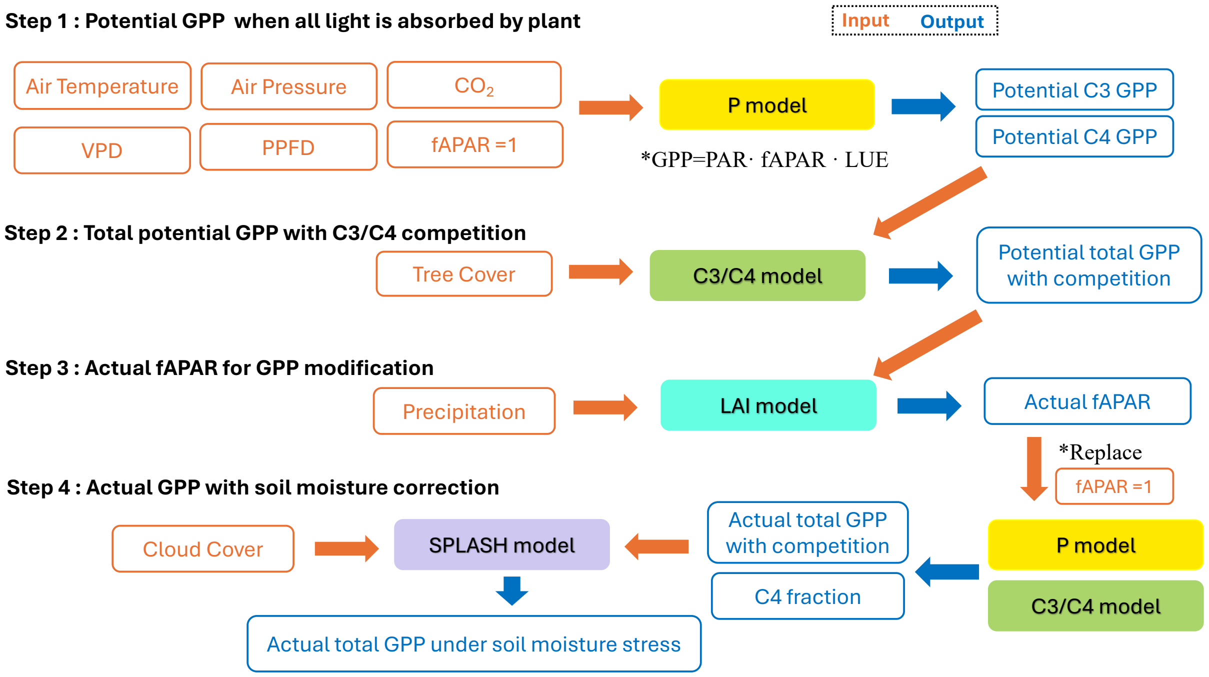

**Figure 1**: *Flowchart showing the steps in the modelling procedure.*

The P model simulates potential GPP for $C_3$ and $C_4$ plants separately (Figure 1). These estimates were fed into a simple model of $C_3/C_4$ competition based on the P model (Lavergne et al., 2024). The relative advantage of $C_4$ plants is estimated as the difference between the monthly potential GPP for $C_3$ and $C_4$ plants, summed over the year. The $C_4$ share of total GPP was then estimated by fitting a logistic curve between the model estimated $C_4$ relative advantage and observed $C_4$ abundance. These calculations assume that neither water nor nutrients are limiting growth. However, under these conditions, $C_3$ trees out-compete $C_4$ grasses through shading, even where the $C_4$ pathway would yield higher rates of photosynthesis. The model accounts for this using an additional function relating the proportion of GPP from trees to total potential GPP based on a power function for the relationship between prescribed annual mean percentage tree cover and the simulated annual GPP of $C_3$ plants. Thus, tree cover is an additional required input to the competition model (Figure 1). The competition model also uses a minimum temperature threshold to define conditions under which $C_4$ plants cannot grow, where this limit is set to a minimum temperature of the coldest month of –24°

based on experimental data. The competition model has been shown to reproduce global patterns in the relative abundance of $C_3$/$C_4$ plants as well as the observed rate of $\Delta^{13}C$ in recent decades, as shown by independent atmospheric estimates (Lavergne et al., 2020).

To convert potential GPP to actual GPP, we used an LAI model (Figure 1) that predicts the seasonal cycle of LAI based on environmental conditions and an estimate of the potential GPP, i.e. the GPP predicted when the fraction of absorbed photosynthetically active radiation, fAPAR, is set to 1 (Zhou et al., 2025). The seasonal LAI is calculated using a moving average to represent the time lag between allocation to leaves and modelled steady-state LAI. A seasonal maximum fAPAR model was embedded in this model to limit seasonal LAI predictions (Zhu et al., 2022; Cai et al., 2025). The calculation of seasonal maximum fAPAR incorporates a water-carbon trade-off: it is defined as the lesser of an energy-limited (maximising GPP) and a water-limited (maximising the use of available precipitation) estimate (Zhu et al., 2022; Cai et al., 2025). The seasonal LAI is calculated using a moving average to represent the time lag between allocation to leaves and modelled steady-state LAI. The model has been shown to capture observed LAI dynamics across all biomes at different temporal scales (weekly, seasonal, annual and interannual variability) both at individual eddy-covariance flux measurement sites and when compared to satellite-derived LAI (Zhou et al., 2025). Furthermore, it predicts both the multi-year average LAI and the annual trends in LAI better than the biosphere models used in the Trends and Drivers of Terrestrial Sources and Sinks of Carbon Dioxide (TRENDY) project (Zhou et al., 2025). The seasonal cycle of fAPAR is calculated from the seasonal cycle of LAI using Beer's law (Swinehart, 1962) and this is then used to calculate seasonal changes in actual GPP. Finally, we apply an empirical soil moisture correction ($\beta(\theta)$: Stocker et al., 2020) to account for the impact of soil moisture stress on GPP, using the Simple Process-Led Algorithms for Simulating Habitats (SPLASH) model (Davis et al., 2017).

### 2.2. Derivation of LGM, MH and PI climate inputs

We use LGM, MH and pre-industrial (PI) climate simulations (Supplementary Table 1) run using the low-resolution version of the Max Planck Institute Earth System Model (MPI-ESM1.2-LR; Mauritsen et al., 2019; doi:10.22033/ESGF/CMIP6.6642) made as part of the fourth phase of the Palaeoclimate Modelling Intercomparison Project (PMIP4; Kageyama et al., 2017; Otto-Bleisner et al., 2019). This model is amongst the best performing of the PMIP models when evaluated using reconstructions of land and ocean climates (Brierley et al., 2020; Kageyama et al., 2021) and uniquely has archived all the necessary outputs needed to run the EEO-based models (Fig. 1). The experiments were run following the PMIP4 protocols for each time period (Kageyama et al., 2017; Otto-Bleisner et al., 2019). The PI experiment was run for 1000 years using modern ice sheet and land-sea configurations and a $CO_2$ level of 284.3 ppm (SI Table 1). The MH experiment uses the same ice sheet and land-sea configurations as the PI but uses appropriate changes in orbital parameters and a $CO_2$ level of 264.4 ppm (SI Table 1). The MPI-ESM1.2-LR LGM experiment uses the ICE6G_C ice sheet and corresponding modification in land-sea geography, appropriate orbital parameters and a $CO_2$ level of 190 ppm (SI Table 1). The LGM simulation was re-started from a previous LGM simulation and then spun-up for 3850 years.

The MPI-ESM1.2-LR model has a spectral resolution of T63 (192 x 96 longitude/latitude). The outputs necessary to run the EEO-based models were down-scaled to a resolution of 0.5° using spline interpolation. The daily data necessary to run the EEO-based models was obtained from monthly data, also using nearest neighbour and bilinear interpolation. Although many previous vegetation modelling studies have used climate anomalies from a baseline experiment (e.g. LGM minus PI), here we used model outputs directly – because although the anomaly approach is well-suited to adjust climate variables, it cannot be used to adjust simulated tree cover.

### 2.3. Stein-Alpert decomposition

Climate, light availability and atmospheric $CO_2$ concentration have independent effects on plant growth. To evaluate the unique effects of these different factors, and potential synergies between them, on the changes in GPP between the PI and the LGM and MH experiments, we used the Stein-Alpert decomposition method (Stein and Alpert, 1993), an approach that has been previously shown to be useful in evaluating the impacts of different factors on past vegetation changes (e.g. Martin-Calvo and Prentice, 2015; Sato et al., 2021). We used the pre-industrial simulation as the reference case (f0) and ran a series of factorial experiments in which specific factors were changed to their LGM or MH conditions as follows:

Experiment f1: LGM (or MH) climate, PI $CO_2$ and PPFD
Experiment f2: LGM (or MH) $CO_2$, PI climate and PPFD
Experiment f3: LGM (or MH) PPFD, PI climate and $CO_2$
Experiment f12: LGM (or MH) climate and $CO_2$, PI PPFD
Experiment f13: LGM (or MH) climate and PPFD, PI $CO_2$
Experiment f23: LGM (or MH) $CO_2$ and PPFD, PI climate
Experiment f123: LGM (or MH) climate, $CO_2$ and PPFD

The impact of each factor or combination of factors was then calculated as:

$$\langle f1\rangle = f1 - f0$$
$$\langle f2\rangle = f2 - f0$$
$$\langle f3\rangle = f3 - f0$$
$$\langle f12\rangle = f12 - (f1 + f2) + f0$$
$$\langle f13\rangle = f13 - (f1 + f3) + f0$$
$$\langle f23\rangle = f23 - (f2 + f3) + f0$$
$$\langle f123\rangle = f123 - (f12 + f13 + f23) + (f1 + f2 + f3) - f0$$

where the first three experiments represent the influence of the single changed factor, the second three experiments represent synergies between pairs of factors, and the final experiment represents the three-way synergy between all three factors.

The comparisons can only be made for the common land area between the PI and each palaeoclimate experiment. The LGM factorial experiments therefore have a baseline GPP value for the f0 experiment that does not include the areas exposed by lowered sea level, although these are considered in the full LGM experiment. The full LGM and MH experiments include changes to both air pressure and tree cover; these are not considered in the factorial experiments because preliminary analyses indicated that the impact of these changes on simulated global GPP was less than 0.2PgC $yr^{-1}$ and therefore negligible.

## 3. Results

Simulated global GPP at the LGM was 83.9 PgC $yr^{-1}$ (Table 1), considerably lower than the simulated global value during the pre-industrial period (109.6 PgC $yr^{-1}$). The largest reductions in GPP compared to the pre-industrial baseline were in the northern hemisphere extra-tropics

(Figure 2, Table 2), which experienced a more than 50% reduction in GPP. There was a more modest decrease (13%) in the southern extra-tropics and only a small decrease in the tropics (3%). Part of the reduction (10.5 PgC yr$^{-1}$) in global GPP reflects the loss of vegetation from areas that were covered by ice at the LGM; this was only partially compensated by vegetation growth on the continental shelves exposed by the reduced sea level (8.3 PgC yr$^{-1}$). Although there was a reduction overall and across most of the world, some regions experienced a small increase in productivity at the LGM compared to the PI (Figure 3). These are all in now-arid regions and the increase therefore presumably reflects the fact that moisture constraints on vegetation growth were reduced in the colder climate of the LGM.

**Table 1**: *Contribution to global changes in gross primary production (GPP) in the Last Glacial Maximum (LGM), the mid-Holocene (MH), and the pre-industrial (PI) experiments. The table gives the global total in each experiment, the GPP of land exposed by lowered sea level at the LGM, the GPP of land that was covered by ice sheets at the LGM and was exposed in the MH and PI experiments, and GPP for the land area in common between all three experiments.*

| | Total non-glaciated land area | Land area covered by ice at LGM | Land area exposed by lowered sea level at LGM | Common land area between the experiments |
|---|---|---|---|---|
| GPP LGM | 83.9 PgC yr$^{-1}$ | n/a | 8.3 PgC yr$^{-1}$ | 75.5 PgC yr$^{-1}$ |
| GPP MH | 110.3 PgC yr$^{-1}$ | 10.6 PgC yr$^{-1}$ | n/a | 99.6 PgC yr$^{-1}$ |
| GPP PI | 109.6 PgC yr$^{-1}$ | 10.5 PgC yr$^{-1}$ | n/a | 99.1 PgC yr$^{-1}$ |

**Table 2**: *Regional contributions to total annual gross primary production (GPP) in the tropics, the northern extra-tropics (NET) and the southern extra-tropics (SET) in the Last Glacial Maximum (LGM), the mid-Holocene (MH), and the pre-industrial (PI) experiments.*

| | LGM | MH | PI |
|---|---|---|---|
| Tropics (25°N-25S) | 56.4 PgC yr$^{-1}$ | 57.7 PgC yr$^{-1}$ | 58.3 PgC yr$^{-1}$ |
| NET (>25°N) | 21.4 PgC yr$^{-1}$ | 46.2 PgC yr$^{-1}$ | 44.3 PgC yr$^{-1}$ |
| SET (>25°S) | 6.0 Pg C yr$^{-1}$ | 6.4 PgC yr$^{-1}$ | 6.9 PgC yr$^{-1}$ |

Simulated GPP increased to 110.3 PgC yr$^{-1}$ in the MH compared to 83.9 PgC yr$^{-1}$ at the LGM. Part of this increase (10.6 PgC yr$^{-1}$) was a result of vegetation growth in areas that were covered by ice sheets during the LGM. However, there were notable increases in the non-glaciated high latitudes (northern Siberia and Beringia), in tropical regions, and in areas influenced by MH monsoon expansion (Sahel, south-east Asia, southern African savannas and the South American cerrado) (Figure 2). GPP increased in the common area between the LGM and MH experiments by ca 32% (Table 1), with the largest increase in the NET (Table 2). The transition from the MH to the PI resulted in a very small decrease in global GPP (Figure 3. Simulated GPP in the MH was slightly higher (4%) than in the PI experiment in the northern extra-topics, although still lower than in the PI in other regions (Table 2).

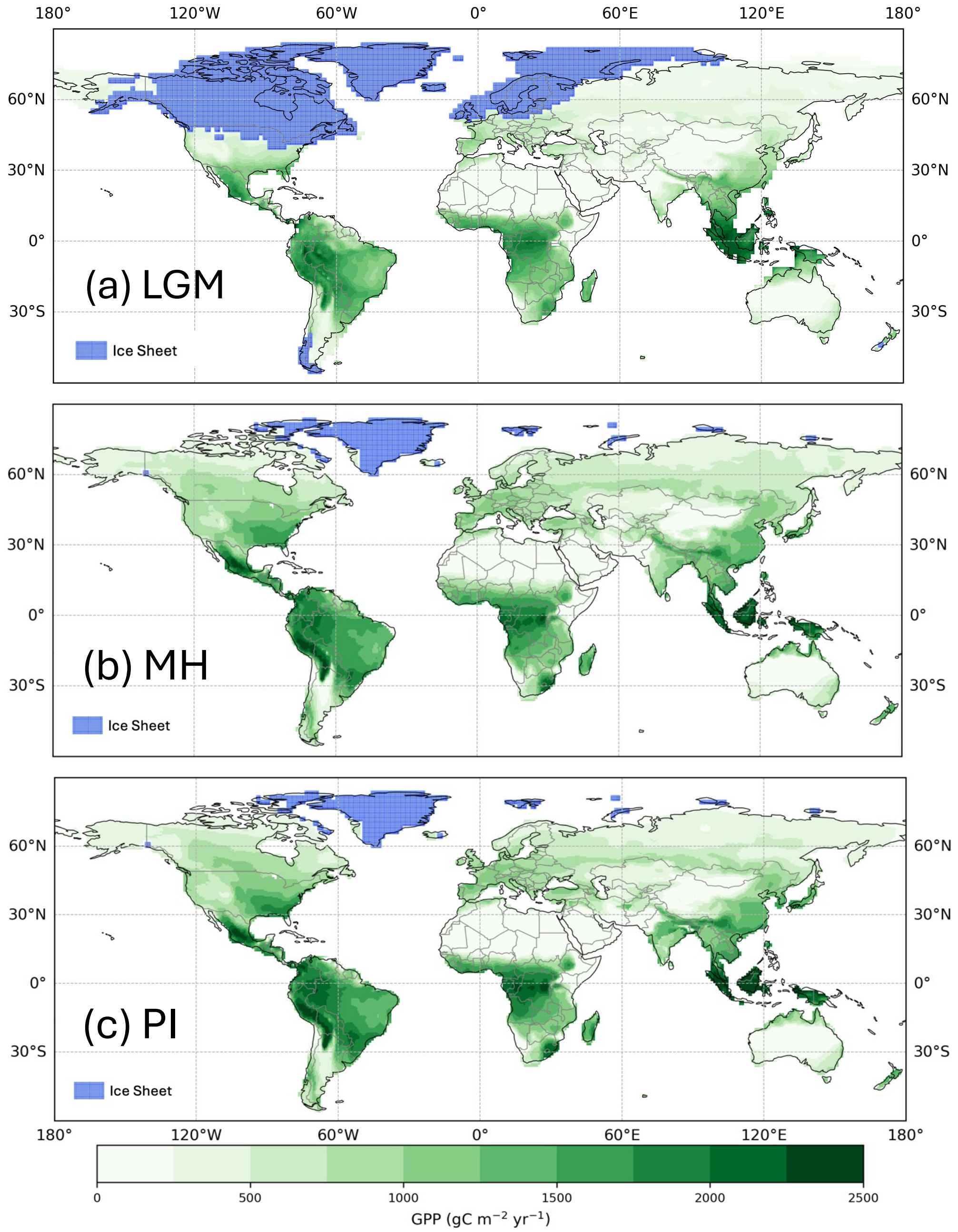

**Figure 2**: *Simulated total annual gross primary production (GPP). The plots show simulated GPP for (a) the Last Glacial Maximum (LGM), (b) the mid-Holocene (MH), and (c) the pre-industrial (PI).*

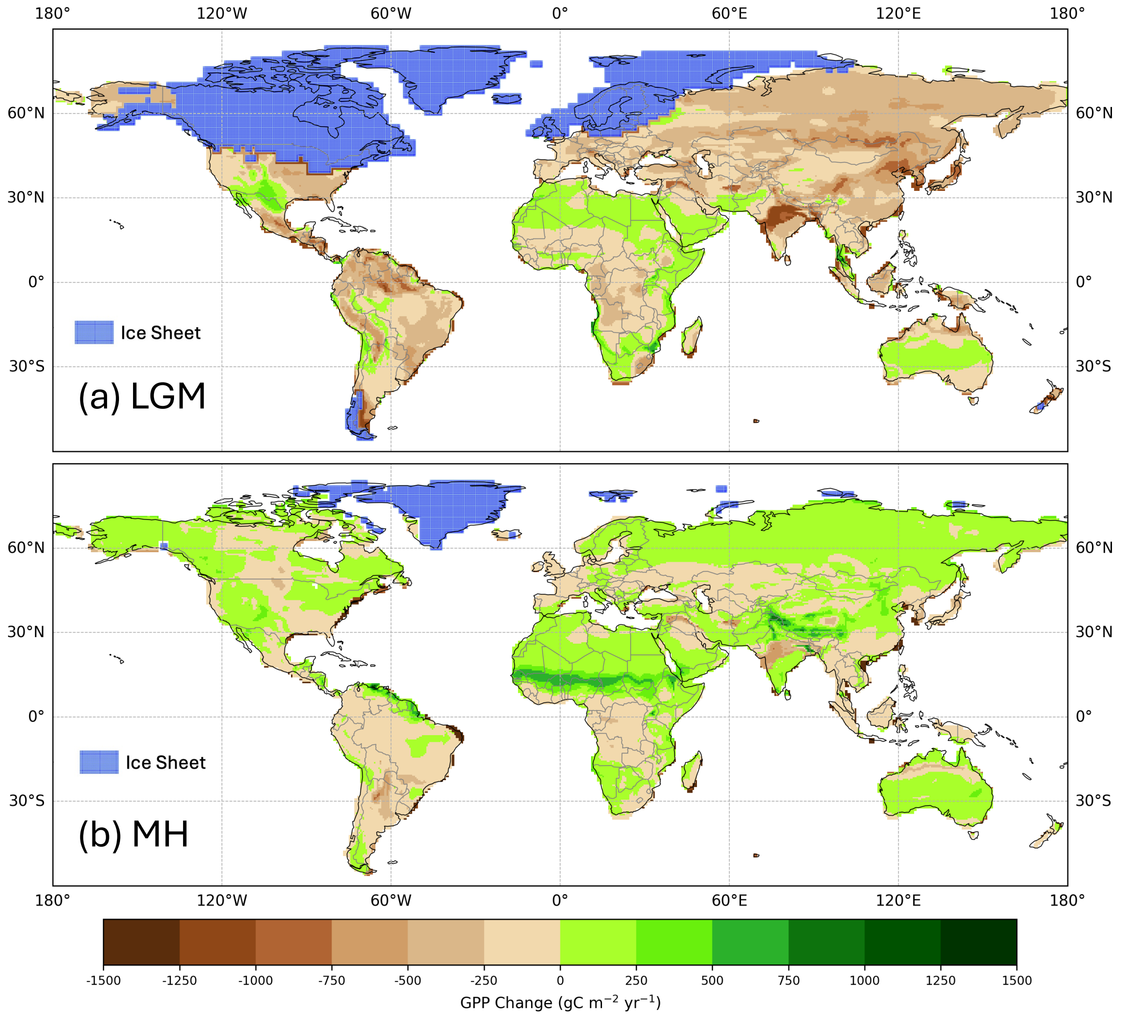

**Figure 3**: *Simulated change in total annual gross primary production (GPP) between the pre-industrial (PI) and (a) the Last Glacial Maximum (LGM) and (b) the mid-Holocene (MH).*

These changes in GPP were accompanied by a shift in the relative importance of $C_3$ and $C_4$ plants (Table 3, Figure 4). $C_4$ plants represented 23% and 25% of the vegetation fraction in the PI and MH experiments respectively, but 40% of the vegetation fraction at the LGM. $C_4$ plants were responsible for 56% of the total GPP at the LGM compared to 25% and 21% in the MH and PI respectively. The fraction of $C_4$ plants increased across most regions of the world at the LGM (Supplementary Figure 1), but in some regions including the Central Great Plains of North America, the northern Sahel, and the Tibetan Plateau and part of the Loess Plateau in northeastern China $C_4$ plants were less abundant than in the PI. The areas where $C_4$ plants were less abundant in the MH than in the PI were more extensive (Supplementary Figure 1) and are primarily in regions of northern Africa and Asia influenced by the expansion of the monsoons.

**Table 3**: *Changes in $C_3$/$C_4$ fraction and contribution of $C_3$/$C_4$ vegetation to total GPP*

| | **LGM** | **MH** | **PI** |
|---|---|---|---|
| Global average $C_4$ fraction | 40% | 25% | 23% |
| Global average $C_3$ contribution of total annual GPP (gC $m^{-2}$ $yr^{-1}$) | 281.4 | 608.9 | 618.6 |
| Global $C_3$ contribution to total GPP (PgC **$yr^{-1}$**) | 37.1 | 82.8 | 86.2 |
| Global average $C_4$ contribution of total annual GPP (gC $m^{-2}$ $yr^{-1}$) | 297.7 | 166.3 | 140.5 |
| Global $C_4$ contribution to total GPP (PgC **$yr^{-1}$**) | 46.8 | 27.5 | 23.4 |

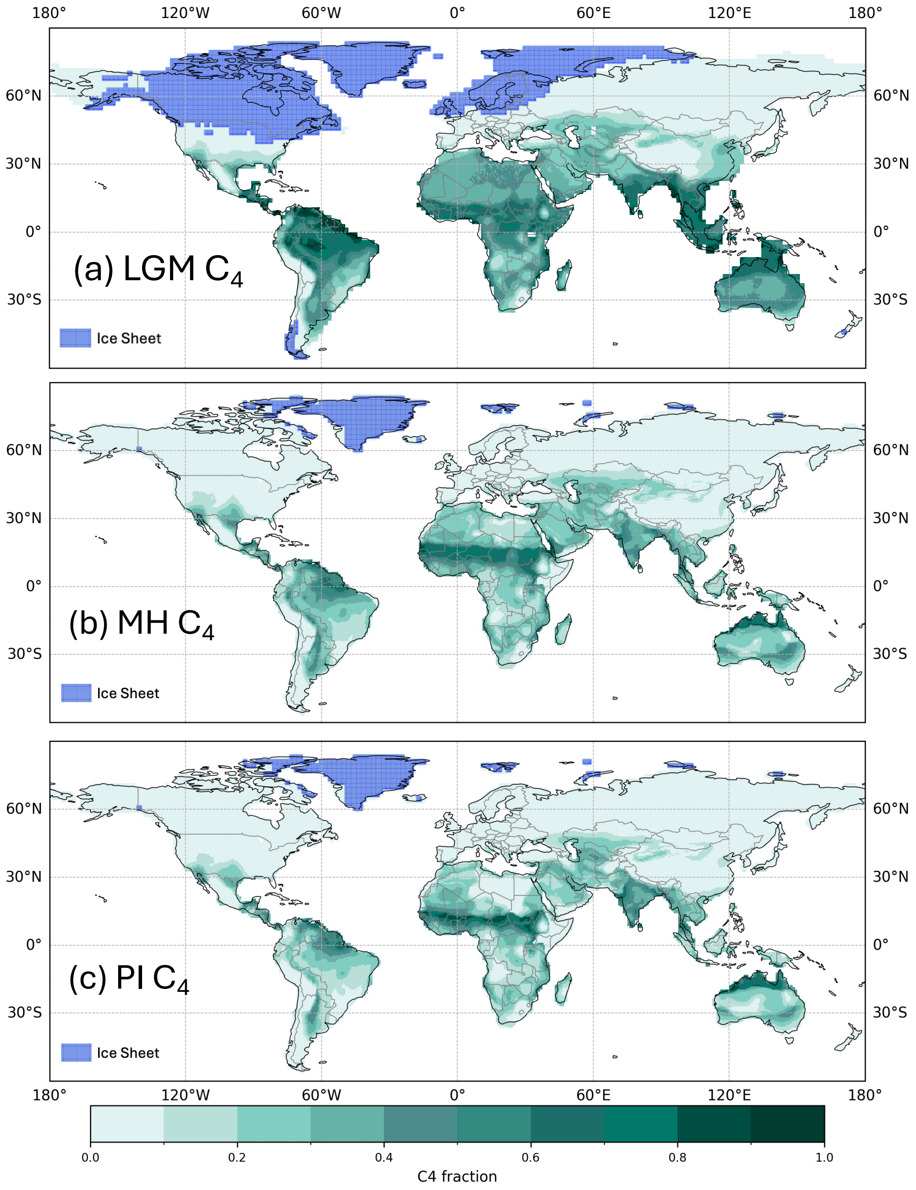

**Figure 4**. *Global $C_4$ fraction distribution for (a) the Last Glacial Maximum (LGM), (b) the mid-Holocene (MH), and (c) the pre-industrial (PI).*

The factorial experiments showed that the changes in climate and $CO_2$ had a large negative effect on GPP at the LGM, while light (PPFD) had a small positive effect (Table 4, Figure 5). The shift to a colder, drier climate had a somewhat larger negative effect on plant productivity (–14.8 PgC yr$^{-1}$) than the reduction in $CO_2$ (–12.2 PgC yr$^{-1}$). Climate has a major impact on reducing GPP in the high- to mid-latitudes of North America and Eurasia (Figure 6a, Supplementary Figure 2) but changes due to the lowering of $CO_2$ were almost as important (Figure 6b, Supplementary Figure 3). Changes in climate (Supplementary Figure 2: Supplementary Table 2), most likely the overall reduction in precipitation (Supplementary Figure 5), was the most important factor causing reduced GPP in northern Amazonia, India and north-western China. However, the cooler climate had a positive effect on GPP in regions that are semi-arid today (Supplementary Figure 2, Supplementary Figure 5). Changes in PPFD were the dominant factor in increasing GPP at the margin at the northernmost edge of the vegetated zone downwind of the Scandinavian ice sheet and into Beringia (Supplementary Figure 4).

The two-way synergy between climate and $CO_2$ was positive (Table 4, Figure 5), i.e. the change in GPP is less than would be expected if the impacts were additive. This reflects the fact that, whereas lower temperatures favour $C_3$ plants, lower $CO_2$ offsets this and promotes the expansion of $C_4$ plants over much of the globe (Supplementary Figures 6, 7). $C_4$ plants were especially favoured in tropical regions, where the climate changes were relatively muted, and the changes in $CO_2$ correspondingly more influential. The synergies of both climate and $CO_2$ with PPFD, although small (0.9 and 0.2 PgC yr$^{-1}$ respectively) are negative. The synergy between climate and PPFD probably reflects the fact reduced cloud cover in drier climates (Supplementary Figure 6, 8). The synergy between $CO_2$ and PPFD stems from the fact that both low $CO_2$ and high PPFD favour $C_4$ plants, increasing GPP particularly in the extratropics (Supplementary Figure 7, 8).

Climate changes had a positive effect on GPP in the mid-Holocene (Table 4, Figure 5). This likely reflects the impact of increased precipitation in now semi-arid regions due to monsoon expansion combined with warmer growing seasons in the high northern latitudes, both consequences of the orbitally-induced changes in solar radiation (Supplementary Figure 5). These experiments also show that changes in PPFD have a positive effect on plant growth, particularly in the northern mid- to high latitudes and in now-arid regions (Supplementary Figure 4). The positive impact in northern mid- to high latitudes appears to be due to enhancement of growing season conditions for $C_3$ plants, while the positive impact in now-arid regions reflects an increase in $C_4$ plants (Supplementary Figure 8). However, the reduction of $CO_2$ compared to the PI state (16 ppm) resulted in a much larger overall reduction in GPP than the enhancements due to climate or PPFD changes (Supplementary Figure 3). The impact of the lower $CO_2$ in the mid-Holocene is the dominant factor causing reductions in GPP in southern China, the southern hemisphere tropical and savanna regions in Africa, and in the cerrado of South America (Figure 6). The two-way synergies between the three drivers are all positive, but small (Table 4, Figure 5).

**Table 4**. *Stein-Alpert decomposition of the impact of changes in climate, $CO_2$ and light* (photosynthetic photon flux density, PPFD), *and their synergies, on gross primary production (GPP) at the Last Glacial Maximum (LGM) and in the mid-Holocene (MH) compared to the pre-industrial (PI) simulations. Note that the baseline GPP value for the LGM is for the common land area between this experiment and the PI simulation and is therefore smaller than the baseline GPP value for the MH decomposition.*

| Experiment | Stein-Alpert decomposition | Climate | $CO_2$ | PPFD | GPP ($PgC\ yr^{-1}$) |
|---|---|---|---|---|---|
| LGM | f0 | PI | PI | PI | 99.1 |
| | f1, LGM | LGM | PI | PI | 84.3 |
| | f2, LGM | PI | LGM | PI | 86.9 |
| | f3, LGM | PI | PI | LGM | 100.3 |
| | f12, LGM | LGM | LGM | PI | 75.4 |
| | f13, LGM | LGM | PI | LGM | 84.6 |
| | f23, LGM | PI | LGM | LGM | 87.8 |
| | f123, LGM | LGM | LGM | LGM | 75.7 |
| MH | f0 | PI | PI | PI | 109.6 |
| | f1, MH | MH | PI | PI | 111.5 |
| | f2, MH | PI | MH | PI | 107.0 |
| | f3, MH | PI | PI | MH | 110.6 |
| | f12, MH | MH | MH | PI | 109.1 |
| | f13, MH | MH | PI | MH | 112.5 |
| | f23, MH | PI | MH | MH | 108.1 |
| | f123, MH | MH | MH | MH | 110.1 |

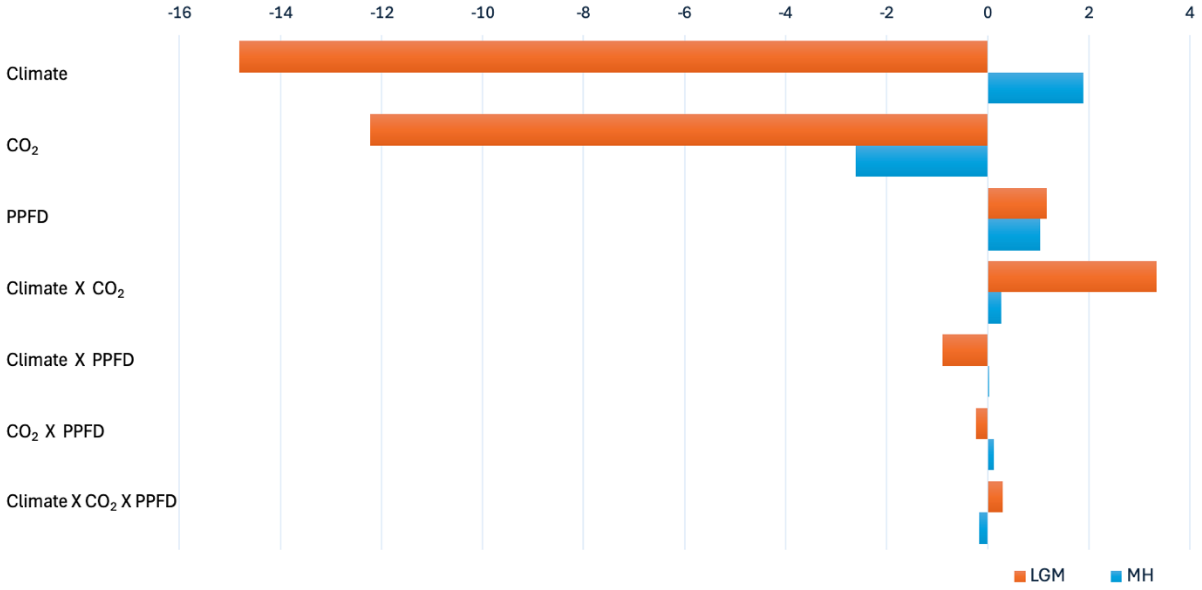

*Figure 5. Impact of climate, light and $CO_2$ on the changes in gross primary production (GPP, PgC) at the Last Glacial Maximum (LGM) and the mid-Holocene (MH) compared to the pre-industrial (PI) period. Note that the results are based on the common land area between each experiment and the PI simulation.*

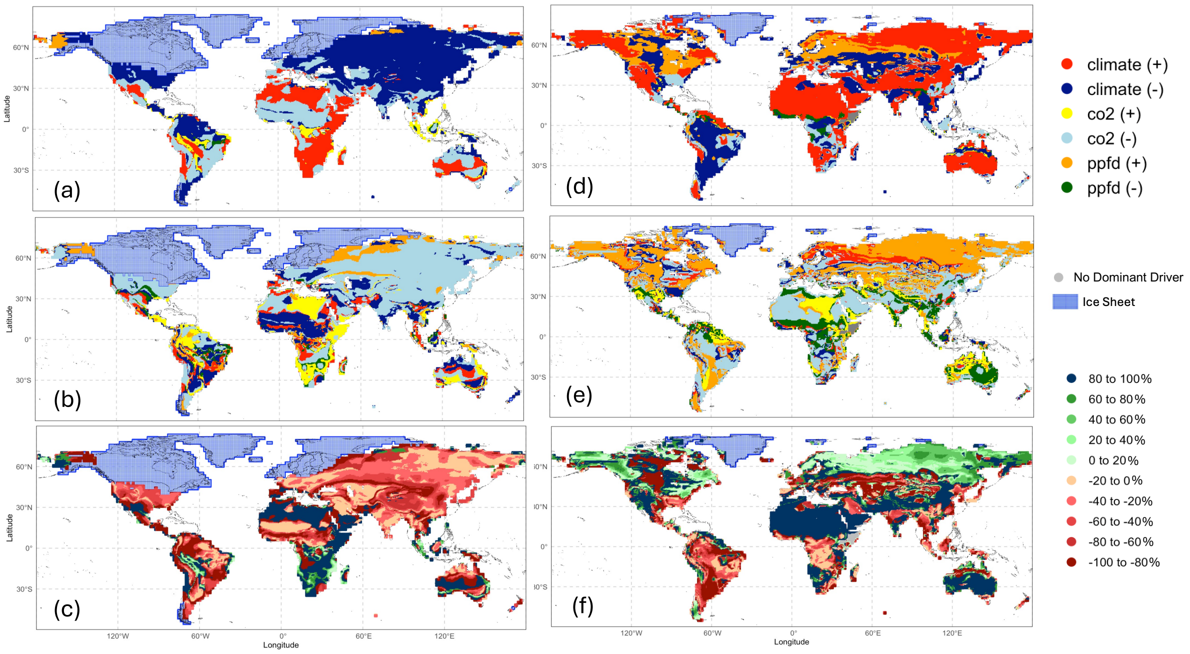

*Figure 6. Global distribution of (a) main drivers and constraints (b) secondary drivers and constraints and (c) the proportional difference (percentage) of total change between the main and the secondary driver on gross primary production (GPP) at the Last Glacial Maximum (LGM) compared to the pre-industrial (PI) experiment; and (d) main drivers and constraints (e) secondary drivers and constraints (f) the proportional difference (percentage) of total change between the main and the secondary driver on gross primary production (GPP) in the Mid-Holocene (MH) compared to the pre-industrial (PI) experiment.*

## 4. Discussion

We have shown that the LGM was characterised by a large reduction in modelled GPP, while the mid-Holocene was characterised by a small increase in GPP compared to the pre-industrial state. The simulated reduction at the LGM is consistent with previous model-based estimates (e.g. Francois et al., 1998; Prentice et al., 2011; Hoogakker et al., 2016), including those from the latest phase of the Couple Model Intercomparison project (CMIP6/PMIP4: Supplementary Table 3). However, there is a considerable range in the magnitude of these modelled estimates, reflecting differences in both the simulated LGM climate and in the vegetation model used. Our estimate of the GPP at the LGM (84 PgC yr$^{-1}$) is in the middle of the range of the CMIP6/PMIP4 models (61-109 PgC yr$^{-1}$). There have been a limited number of studies that have estimated GPP at the LGM by constraining model estimates using oxygen isotope records from ice core (Landais et al., 2007; Ciais et al., 2011; Yang et al., 2022). These show a similarly large range in simulated GPP (40-110 PgC yr$^{-1}$), in part because of the uncertainties associated with estimating ocean productivity and respiration fractionation rates. Thus, although there is a consensus that GPP was considerably lower at the LGM than during pre-industrial times, and this is consistent with pollen evidence for a very large reduction in tree cover over much of the world (Prentice et al., 2000; Williams, 2003; Pickett et al., 2004; Marchant et al., 2009), the absolute magnitude of this change is uncertain. Nevertheless, since the climate simulated by the MPI ESM has been shown to reproduce pollen-based climate reconstructions better than most other CMIP6/PMIP4 models (Kageyama et al., 2021) and we use robust EEO-models to estimate the change in GPP, the partitioning of the impacts of different factors in the simulated reduction of GPP is likely to be robust.

The modelled abundance of $C_4$ plants was nearly double at the LGM compared to the pre-industrial era (40% versus 23% of the vegetation fraction) and that $C_4$ vegetation was responsible for 56% of the total modelled GPP at that time. These changes are broadly consistent with pollen-based reconstructions, indicating a substantial reduction in tree cover at the LGM (Prentice et al., 2000). However, while pollen data can be used discriminate between trees (virtually all $C_3$) and grasses, it cannot be used to infer changes in the importance of $C_3$ and $C_4$ grasses. Compound-specific $\delta^{13}C$ analyses of leaf wax biomarkers provide evidence of the relative contribution of $C_3$ and $C_4$ plants (Eglinton & Eglinton, 2008; Diefendorf et al., 2010) and have shown that $C_4$ plants were more abundant at the LGM than during the Holocene in many regions of the world (e.g. in southern Africa: Rommerskirchen et al., 2006; Vogts et al., 2012; eastern Africa: Sinninghe Damsté et al., 2011; Himalayan Basin: Galy et al., 2008; southern China: Jiang et al., 2019; south-western North America: Cotton et al., 2016; northern South America: Makou et al., 2007), consistent with our simulations. There are a few regions where $C_4$ plants were less abundant at the LGM than during the Holocene, including the Chinese Loess Plateau and the Great Plains of North America (Cotton et al., 2016). Both of these regions are identified as characterised by reduced $C_4$ abundance in our simulations. A number of modelling studies have shown that $C_4$ plants were globally more abundant at the LGM (e.g. Harrison & Prentice, 2003; Bragg et al., 2013; Martin Calvo & Prentice, 2015) but did not quantify the relative contribution of $C_4$ plants to global GPP. Thus, our analyses are consistent with previous studies of the nature of the shift in vegetation composition at the LGM and provide, for the first time, a quantitative estimate of the magnitude of this change.

Climate has a negative effect on GPP at the LGM but a positive effect in the MH. The LGM climate was globally colder and drier, although the largest changes in both temperature and precipitation were in the northern mid- to high-latitudes (Kageyama et al., 2021). This is reflected in our simulations; the overall reduction in GPP compared to the pre-industrial baseline in the northern extra-tropics was 52%, far larger than the reductions in the southern extra-tropics (13%) or the tropics (3%). The cooling in the ice-free regions of the northern extra-tropics reflects advection of cold air temperatures downwind from the ice sheets, while the drying largely reflects the temperature-induced reduction in evaporation and precipitation recycling (Izumi et al., 2013; Li et al., 2013; Kageyama et al., 2021). The positive effect of climate on GPP in the MH reflects changes in precipitation in now semi-arid regions of the sub-tropics as a result of the expansion of the northern hemisphere monsoons and a lengthening of the growing season in the northern mid- to high-latitudes as a result of increased solar radiation in summer (Brierley et al., 2020). These changes in climate are reflected in our simulations; although the northern extra-tropics are the only region to show an overall increase in GPP compared to the pre-industrial (4%), regions influenced by monsoon expansion, such as the Sahel and parts of Asia, also show increased GPP.

The modelled reduction of GPP by low LGM relative to pre-industrial $CO_2$ was of similar magnitude (12%) to that of LGM climate (15%). Some other factorial model experiments (e.g. O'Ishi and Abe-Ouchi, 2013; Claussen et al., 2013; Martin Calvo and Prentice, 2015; Chen et al., 2019; Haas et al., 2023; see Supplementary Table 4) have shown a larger impact of $CO_2$ on primary production (either GPP or net primary production, NPP) relative to climate. For example, Claussen et al. (2013) showed reductions in NPP of 4% due to climate and 45% due to $CO_2$ and Martin Calvo and Prentice (2015) showed reductions in NPP of 2% due to climate and 23% due to $CO_2$. Some of differences among experiments may have been caused by difference in modelled climate (Haas et al., 2023); but changes in PFT abundance are likely to be an important additional source of uncertainty. Woillez et al. (2011) also indicate a dominant role for low glacial $CO_2$ in reducing NPP at the LGM. In that analysis, however, a greater sensitivity of needleleaf PFTs to low $CO_2$ compared to brodleaf PFTs was implied by choices of parameter values that were not necessarily well-founded, and led to an unrealistically large simulated extent of broad-leaved forests at the LGM.

In addition to the fact that these various experiments were based on different models of the LGM climate, they were also made using different biosphere models (Supplementary Table 4) – which may have different sensitivities to $CO_2$ changes. Thus, although models agree that changes in $CO_2$ contributed to the large observed differences between LGM and pre-industrial vegetation patterns, the magnitude of the impact of low $CO_2$ on primary production is still uncertain. The modelled impact of lowered $CO_2$ on GPP in the MH here is larger than the impact of climate, offsetting the positive impacts of climate change in the MH experiment. The importance of $CO_2$ in driving vegetation changes has been widely commented on for the LGM (Polley et al., 1993; Jolly & Haxeltine,1997; Cowling & Sykes, 1999; Harrison & Prentice, 2003; Flores et al., 2009; Prentice et al., 2011; Bragg et al., 2013; Martin Calvo & Prentice, 2015) and in the context of ongoing and future climate changes (Piao et al., 2006; Keenan et al., 2014; Archer et al., 2017; Haverd et al., 2020: Piao et al., 2020) but its role in offsetting the positive impacts of climate change in the MH has not been widely noted. The simulated overall change in GPP in the MH compared to the PI is small (< 1 PgC $yr^{-1}$). Nevertheless, the changes in response to individual drivers are consistent with expectations: changes in climate and PPFD had a positive impact on GPP while the reduction in $CO_2$ in the MH compared to the PI had a negative impact on GPP. The positive effect of climate on GPP in the MH reflects changes in precipitation in now semi-arid regions of the sub-tropics, as a result of the orbitally induced expansion of the northern hemisphere monsoons and the lengthening of the growing season in the northern mid- to high-latitudes (Brierley et al., 2020). These changes in climate are reflected in our simulations. The northern extratropics are the only region to show an overall increase in GPP compared to the pre-industrial (4%) when $CO_2$ effects are included, but regions influenced by monsoon expansion, such as the Sahel and parts of South and East Asia, also show a tendency to increased GPP due to the MH climate.

We have derived climate inputs from the MPI ESM. When compared to reconstructions of both marine and terrestrial climate variables, the MPI ESM has been shown to be among the best-performing models both for the LGM and the mid-Holocene (Brierley et al., 2020; Kageyama et al., 2021). Nevertheless, the use of a single climate model is a limitation of this study. It would be useful to repeat these analyses with a wider range of models that have made palaeoclimate simulations of these two key periods, but the constraint is that most of these models do not provide information on changes in tree cover that is to run the $C_3$/$C_4$ competition model.

We have used a sequence of EEO-based models to simulate GPP and the relative contribution of $C_3$ and $C_4$ plants to overall productivity. Haas et al. (2023) also used the P model to simulate GPP at the LGM. Other studies of past vegetation changes have used models that simulate changes in past vegetation on the basis of the competition between PFTs. PFT-based models require key physiological parameters to be specified separately for each PFT. The EEO modelling approaches used here avoid this complexity, considerably reducing uncertainties due to model parameterisation (Harrison et al, 2021) while at the same time representing the key processes of photosynthesis and plant growth accurately (Wang et al., 2017; Smith et al., 2019; Jiang et al., 2020; Lavergne et al., 2020; Peng et al., 2020; Smith & Keenan, 2020; Wang et al., 2020; Xu et al., 2021; Zhu et al., 2022). Furthermore, they capture recent trends in vegetation growth more accurately than the land-surface models used to predict the terrestrial carbon cycle (Cai et al., 2025; Zhou et al., 2025).

## 5. Conclusions

Eco-evolutionary optimality approaches provide a robust way of modelling vegetation changes under different climate regimes. We compared simulated changes in GPP and $C_3$/$C_4$ plant abundance in a cold glacial and a warm interglacial period relative to the pre-industrial state. We showed that the colder, drier climate at the LGM substantially decreases GPP and the warmer, wetter climate of the MH increases GPP. Changes in vegetation productivity caused by the lower $CO_2$ in both intervals compared to the pre-industrial contributed to the reduction of GPP at the LGM and was sufficient to annul the positive impacts of climate on GPP during the MH. These results point to the importance of a realistic treatment of the direct physiological impacts of $CO_2$ on plant growth to simulate realistic ecosystem changes, both in the past and in the future.

## Data Availability

The CMIP6 MPI-ESM1-2-LR outputs are accessible via the Earth System Grid Federation (ESGF) at http://esgf-node.llnl.gov/search/cmip6/ (last accessed: 2 December 2024). Interpolated input data and derived outputs related to this study are available at DOI: 10.5281/zenodo.14257604. The documentation for the P model, the C3/C4 competition model, and the SPLASH model can be found at DOI: 10.5281/zenodo.8366848 (Orme and Marion, 2023). The codes used for model coupling and experiment analysis used in this paper is available at DOI: 10.5281/zenodo.14257604.

## Supplement.

Supplementary Information is available for this paper.

## Author Contributions

JZ, SPH and ICP designed the study. BZ provided model code. JZ ran the experiments. JZ and SPH conducted the analyses. SPH wrote the first version of the manuscript and all co-authors contributed to the final version.

## Competing Interests

None of the authors has any competing interests.

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