We thank the reviewer for their comments on the paper. Our response to the specific points is given below in *italics* and proposed changes to the text in blue.

1) However, I have concerns regarding the novelty and broader implications of this work, particularly how it advances beyond previous factorial simulations.

A number of published studies have examined the modelled global impacts of climatic versus physiological CO_2 effects on LGM vegetation. Several have simulated LGM climate impacts on vegetation (and/or fire) with, or without, inclusion of the physiological effects of CO_2 on plants (Levis et al. 1999, Harrison and Prentice 2003, Martin Calvo et al. 2014). Others have performed factorial experiments to more formally separate the effects of climate and CO_2 (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). The strong influence of low LGM CO_2 (in addition to effects of a cold and dry global climate) in suppressing primary production is a consistent finding from both types of analysis. However, there are substantial differences in the relative importance of CO_2 and climate change effects attributed by different models.

*All these previous studies have used land ecosystem models based on the "plant functional type" (PFT) paradigm, which requires lists of parameter values to be specified separately for each PFT. This approach embeds uncertainty in the delimitation of PFTs and the parameter values assigned to them, because in reality trait variation within PFTs is substantially larger than variation between them (Kattge et al., 2011). In some cases, the PFT representation has resulted in an unrealistic simulation of LGM vegetation patterns (e.g. Woillez et al. 2011). Our approach here is intended to put the calculation of changes in GPP on a sounder basis by using a recently developed model, the P model, which is expressly designed to account for acclimation and adaptation to environment **independently** of PFTs (apart from the distinction between the C_3 and C_4 photosynthetic pathways). The P model has been subject to extensive evaluation against worldwide data from eddy-covariance flux towers. We use a newly published extension of the model which simulates foliage cover and its seasonal cycle, also independently of PFTs, and has been shown to do so more accurately than any state-of-the-art vegetation model (Zhou et al., 2025). We use a new process-based scheme to represent the relative competitive success of C_3 versus C_4 plants, which has been validated against worldwide soil carbon stable isotope data (Lavergne et al., 2024). This combination of parameter-sparse and independently validated models enables us, for the first time, to apply an eco-evolutionary optimality approach to simulate past vegetation function in a globally consistent way.*

Less attention has been paid to productivity changes since the MH, compared to the LGM. As the CO_2 and climate differences between MH and pre-industrial time are relatively small, it is likely that primary production changes as represented by conventional models would be dominated by uncertainties linked to PFTs. Here, we use the same consistent global methodology to estimate MH to pre-industrial changes in GPP. We include the effect of changes in the light regime, which are a 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.

In order to make it clear what the novel contribution of this paper is relative to earlier work, we propose to modify the Introduction as follows (line 62 et seq.):

Three sets of factors could potentially impact vegetation productivity changes between the LGM, MH and pre-industrial periods: changes in climate, atmospheric CO_2 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 CO_2 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 CO_2 (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-CO_2) 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 C_4 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 CO_2 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 ….

We will remove Bragg et al. (2013) from this section since that was not a global study, although it is referred to later on when we discuss regional patterns. We will add the following references:

Chen, W., Zhu, D., Ciais, P., Huang, C., Viovy, N., Kageyama, M., 2019. Response of vegetation cover to CO_2 and climate changes between Last Glacial Maximum and pre-industrial period in a dynamic global vegetation model. Quaternary Science Reviews 218, 293-305, https://doi.org/10.1016/j.quascirev.2019.06.003

Claussen, M., Selent, K., Brovkin, V., Raddatz, T. Gayler, V., 2013. Impact of CO2 and climate on Last Glacial maximum vegetation – a factor separation. Biogeosciences 10, 3593-360. https://bg.copernicus.org/articles/10/3593/2013/

Foley, J. A. (1994), The sensitivity of the terrestrial biosphere to climatic change: A simulation of the Middle Holocene, *Global Biogeochem. Cycles*, 8(4), 505–525, doi:10.1029/94GB01636.

Francois, L., Godderis, Y., Warnant, P., Ramstein, G., de Noblet, N., and Lorenz, S.: Carbon ´ 5 stocks and isotopic budgets of the terrestrial biosphere at mid-Holocene and last glacial maximum times, Chem. Geol., 159, 163–189, 1999. 972

Haas, O., Prentice, I.C., Harrison, S.P., 2023. Examining the response of wildfire properties to climate and atmospheric CO_2 change at the Last Glacial Maximum *Biogeosciences* 20: 3981-3995, https://doi.org/10.5194/bg-20-3981-2023

Harrison, S.P., Cramer, W., Franklin, O., Prentice, I.C., Wang, H., Brännström, Å., de Boer, H., Dieckmann, U., Joshi, J., Keenan, T.F., Lavergne, A., Manzoni, S., Mengoli, G., Morfopoulos, C., Peñuelas, J., Pietsch, S., Rebel, K.T., Ryu, Y., Smith, N.G., Stocker, B.D., Wright, I.J., 2021. Eco-evolutionary optimality as a means to improve vegetation and land-surface models. *New Phytologist* 231: 2125-2141, https://doi.org/10.1111/nph.17558

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., **Harrison, S.P.**, van Bodegom, P.M., Reichstein, M., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C., Blonder, B., Bond, W., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Durka, W., Elser, J., Enquist, B.J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R., Green, W., Gutierrez, A.G., Hickler, T., Higgins, S., Hodgson, J.G., Jalili, A., Jansen, S., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B., Messier, J., Moles, A., Müller, S., Nadrowski, K., Naeem, S., Niinemets, U., Nöllert, S., Nüske, A., Ogaya, R., Joleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado, B., Sardans, J., Shiodera, S., Shipley, B., Sosinski, E., Soussana, J-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., Wright, S.J., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935. doi:10.1111/j.1365-2486.2011.02451.x

Martin Calvo, M., Prentice, I.C., Harrison, S.P., 2014. Climate versus carbon dioxide controls on biomass burning: a model analysis of the glacial-interglacial contrast. *Biogeosciences*, 11, 6017–6027. doi:10.5194/bg-11-6017-2014

O'ishi, R. and Abe-Ouchi, A.: Influence of dynamic vegetation on climate change and terrestrial carbon storage in the Last Glacial Maximum, Clim. Past, 9, 1571–1587, https://doi.org/10.5194/cp-9-1571-2013, 2013

Levis S, Foley JA, Pollard D. CO_2, climate, and vegetation feedbacks at the Last Glacial Maximum. *J Geophys Res* 1999, **104**: 31191–31198.

We will also take the opportunity to update two references which are now published:

Cai, W., Zhu, Z., Harrison, S.P., Ryu, Y., Wang, H., Zhou, B., Prentice, I.C., 2025. A unifying principle for global greenness patterns and trends *Nature Communication and Environment* 6, 19, https://doi.org/10.1038/s43247-025-01992-0

Zhou, B., Cai, W., Zhu, Z., Wang, H., Harrison, S.P., Prentice, I.C., 2025. A general model for the seasonal to decadal dynamics of leaf area *Global Change Biology* e70125, https://doi.org/10.1111/gcb.70125

Previous studies used a variety of climate inputs and vegetation models. We will add a table in Supplementary (Supplementary Table 5) summarising these experiments and add text with a more detailed comparison between the various experiments in the Discussion, as follows:

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 5) 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 5) – 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. Despite the small change in CO_2 between the PI and MH (16 ppm), according to our simulations the lowering of CO_2 would have reduced GPP by about 3 PgC whereas the increase produced by the change in climate is only 2 PgC.

2) The impacts of changing CO_2 levels on plant growth have already been incorporated into many land surface models (LSMs) and Earth System Models (ESMs), though the

magnitude of physiological effects differs between models. The authors should clarify how this study advances prior work and explicitly discuss its implications for ecosystem modeling.

The impact of changing CO$_2$ levels on plant and ecosystem function is represented in most LSMs but its magnitude varies considerably among models, indicating uncertainty about how it should be implemented. The large number of PFT-specific parameters that need to be specified in state-of-the-art LSMs further increases uncertainty in model predictions of the response to CO$_2$. However, we have confidence in the response of the P model to changing CO$_2$ because (a) it arises naturally from the model's foundation in the biochemistry of photosynthesis (no additional parameters are needed) and (b) it is supported both by controlled-environment studies (Smith and Keenan, 2020), including plants grown at low CO$_2$ (Harrison et al., 2021), and FACE experiments (Wang et al., 2017). We will add sentences in the Methods (Section 2.1) to make this explicit:

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).

We included discussion of the realism of the other EEO components used in the paper when describing each component in the Methods (Section 2.1) but we realise that the statement about the evaluation of the seasonal cycle of GPP was rather brief (lines 131-133), so we will modify this text to be more explicit:

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).

3) A direct comparison with existing models (e.g., DGVMs, LSMs, and ESMs) would strengthen the study's contribution. How does the EEO-based approach improve upon these models in simulating GPP and C3/C4 competition?

We included an evaluation of the different EEO components in the Methods (section 2.1) and have expanded this (see response to point 2 above). In particular, we now make it clear (both in the Introduction and Section 2.1) that the EEO approach provides predictions of the seasonal cycle of LAI and its inter-annual variability that are better than the state-of-the-art biosphere models that participate in the TRENDY project. Since this comparison has been made in other papers, it does not seem necessary to include a direct comparison with these models here. However, we will add a paragraph in the discussion about the advantages of the EEO approach it terms of reduced uncertainty and highlighting the overall better performance of these models compared to existing models, as follows:

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).

Additional references

Lavergne, A., Voelker, S., Csank, A., Graven, H., de Boer, H.J., Daux, V., Robertson, I., Dorado-Liñan, I., Martınez-Sancho, E., Battipaglia, G. et al., 2020. Historical changes in the stomatal limitation of photosynthesis: empirical support for an optimality principle. New Phytologist 225: 2484–2497.

Xu, H., Wang, H., Prentice, I.C., Harrison, S.P., Wang, G., Sun, X., 2021. Predictability of leaf traits with climate and elevation: a case study in Gongga Mountain, China. Tree Physiology. doi: 10.1093/treephys/tpab003.

Wang, H., Atkin, O.K., Keenan, T.F., Smith, N.G., Wright, I.J., Bloomfield, K.J., Kattge, J., Reich, P.B., Prentice, I.C., 2020. Acclimation of leaf respiration consistent with optimal photosynthetic capacity. Global Change Biology 26: 2573–2583.

4) The study reports an LGM GPP estimate of 84 PgC, within the CMIP6/PMIP4 range of 61–109 PgC. There is large inter-model variability (spanning tens of PgC).

The CMIP6/PMIP4 range of GPP is indeed large, reflecting differences in the input data between the simulations (e.g. the ice sheet configurations used) as well as model-dependent differences in simulated climate and vegetation. As we pointed out in the Discussion (lines 338 to 342), attempts to constrain simulated GPP using oxygen isotope data from ice cores show an equally large range, because of large uncertainties in estimates of ocean productivity as well as model-dependent differences. We are not claiming that the estimate of 84 Pg is necessarily correct – only that the relative contribution of different factors to this reduction in GPP shown by the decomposition should be reasonable. We chose the MPI model because it has been shown to reproduce simulated climate better than most of the other models in CMIP6/PMIP4 (see lines 396-399). We did not use the simulated vegetation from this experiment because the EEO approach applies independentlky of vegetation types. We will expand the discussion of the LGM reduction to clarify that, while the absolute magnitude is uncertain, the partitioning of the causes of the reduction are more likely to be robust:

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.

5) The authors conclude that CO₂ effects led to a 3 PgC reduction in GPP during MH, while climate changes contributed to a 2 PgC increase, yielding a net difference of only 1 PgC. Given the large uncertainty in model estimates, is this difference statistically significant? Could this conclusion be influenced by model structural biases or sensitivity to parameter choices?

We are using a single model to derive climate inputs. The EEO-models used to estimate GPP have very few parameters (at least an order of magnitude less than most land surface or vegetation models) and the values of these parameters have been explicitly derived from observations and/or experiments. Thus, our estimates of the effect of different drivers to changes in GPP during the MH are not expected to be influenced by structural biases or sensitivity to parameters.

The changes between MH and pre-industrial times are small, but they are consistent with expectations: GPP is reduced by the lower CO_2 but increased by the generally warmer and wetter climate in the northern hemisphere. We will modify the text in the Discussion to acknowledge that the MH changes are small but that the partitioning is consistent:

The simulated overall change in GPP in the MH compared to the PI is small (< 1 PgC). Nevertheless, the changes in response to individual drivers are consistent with expecations: 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.