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Fire-derived ozone intensifies carbon loss in Amazon forests under extreme droughts



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The Amazon rainforest is a vital contributor to the removal of anthropogenic carbon dioxide from the atmosphere. Ozone (O_3) is an atmospheric pollutant that reduces carbon dioxide uptake by vegetation. Yet the degree to which variability in ozone, elevated by anthropogenic-derived fire activity, and climate contribute to changes in Amazon forest productivity remains poorly understood. Here, we employ a land surface model to quantify the interannual variability of fire-derived ozone damage across the Amazon and explore its coupling with extreme drought and stomatal responses. We estimate that fire-derived ozone damage increases carbon losses by approximately one quarter of direct fire emissions, revealing a potentially important indirect pathway by which may fires amplify carbon loss. Notably, our simulations suggest high fire activity during extreme droughts, such as in 2024, likely result in ozone damage despite extensive stomatal limitation, highlighting the urgency to reduce deforestation and forest fire as the climate changes.

Ground-level ozone (O_3) is an invisible threat to the Earth's biosphere^{1,2}. Each year, it drives billion-dollar losses of global agriculture^{2,3} and suppresses the land carbon sink through O_3 damage to vegetation^{4–6}. Tropical forests generate half of global gross primary productivity (GPP) and sustain one quarter of the land carbon sink⁷, thus their stability is critical to the Earth's climate. Yet, the traits that make tropical forests so productive: dense, evergreen canopies and high stomatal conductance, also render them uniquely vulnerable to O_3 damage by permitting a high flux of O_3 to enter leaves year-round⁶. The prospect of an Amazon “tipping point” has already raised global concern^{8–10}, and forests are becoming increasingly exposed to unprecedented human and climate stressors, from intensifying droughts to extreme fire events^{11–13}. However, O_3 , a pollutant capable of undermining tropical forest resilience, is rarely considered in carbon budgets or future scenarios, even as rising emissions of O_3 precursors are estimated to reduce present-day tropical forest land carbon sequestration by 14–27%⁶. The Amazon forest holds around 120 Pg of carbon, so any changes in this huge carbon stock have a global relevance in terms of climate change¹⁴.

NO_x emissions from fires are responsible for a large proportion of elevated O_3 in the Amazon and studies have estimated that fire-related O_3

damage decreases Amazon plant productivity by ~15%^{15,16} however the effect of fire-related O_3 damage on atmospheric CO_2 has not been explicitly quantified, preventing understanding of the effect on the Amazon carbon budget and the magnitude of this effect relative to direct CO_2 emissions from fire. These earlier studies critically lacked any data on tropical forest O_3 susceptibility. Recent experimental work has shown that tropical tree species exhibit O_3 susceptibility comparable to, or greater than, many temperate taxa⁶, suggesting studies that assumed a lower susceptibility based on temperate observations^{15,16} may underestimate O_3 -driven losses in the productivity of these ecosystems.

All studies to date report the impacts of O_3 under present-day climatic averages^{4,5,15,16}, yet the risk of O_3 damage in response to interannual variability and changing climate conditions remains poorly understood. The most recent Intergovernmental Panel on Climate Change (IPCC) report warns that the Amazon is likely to become drier in the future, with more frequent, more intense droughts and fires¹⁷ as global CO_2 concentrations rise. Drought stress can trigger stomatal closure, potentially shielding leaves from the increasing O_3 concentrations derived from higher fire emissions^{18,19}. Likewise, increasing atmospheric CO_2 and subsequent meteorological changes can suppress stomatal conductance²⁰, reducing the

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flux of O_3 into plants even as photosynthetic productivity is enhanced through CO_2 fertilisation²¹. Understanding how these interacting stressors—climate change, drought and fire—are currently jointly influencing O_3 damage is therefore critical for constraining present-day carbon budgets and projecting future vegetation–climate feedbacks.

Over the 1997–2024 period, droughts have occurred across the Amazon in 1997/98, 2005, 2007, 2010, 2015/16 and 2023/4. Among these, the 2015/16 and 2023/24 events rank among the most extreme on record²² with 2023/24 responsible for the highest fire emissions in recent times²³. Yet each event displays distinct spatial and temporal patterns, shaped by differing climatic drivers and human ignition sources.

Here, we assess how drought and fire regimes influence regional O_3 concentrations and how their interaction with stomatal physiology controls O_3 vegetation damage across the Amazon. Using a land surface model driven by observed meteorology, we investigate the interannual variability in O_3 damage in the period 1997–2024. We quantify the magnitude of indirect carbon emissions from fire-derived O_3 damage relative to direct fire carbon emissions, highlighting this pathway of fire–carbon exchange. To understand the drivers of trends and variability in O_3 damage in our model, we explore the contributions from meteorology, rising atmospheric CO_2 and fire emissions. Finally, we compare the temporal and spatial patterns of O_3 damage during major droughts to evaluate how climate extremes alter O_3 vulnerability, providing insight into future risks and potential mitigation pathways under a changing 21st-century climate.

Results

Drought, fire and climate change in the present-day Amazon

We first evaluate simulated stomatal conductance, gross primary productivity (GPP) and tropospheric NO_2 columns to validate the land surface model^{24,25} and its representation of drought responses and fire emissions in the Amazon.

Simulated stomatal conductance shows clear decreases during drought periods, however there is also a significant declining trend over time ($r^2 = 0.76$, $p < 0.001$, Supplementary Fig. 1). Site-level observations at the LBA-Km67 fluxsite in Santarém from 2002–2021 also find that the 2015–2016 period has the lowest stomatal conductance in this time range, and that the period 2015–2021 has lower stomatal conductance than earlier periods^{26,27}. Sensitivity tests reveal the modelled trend is due to approximately equal contributions from stomatal closure from increasing CO_2 and a long-term meteorological change (Supplementary Figs. 2, 3). Meteorological driving data (Supplementary Fig. 3) and observational studies^{28,29} reveal an increasing vapour pressure deficit (VPD) across the Amazon—due to the warming climate—which is known to reduce stomatal conductance^{20,30}. Despite this decline in stomatal conductance, simulated

evapotranspiration shows no significant change over the study period, in agreement with observations³¹.

Simulations of GPP in the Amazon with and without consideration of O_3 damage reproduce the general variability in annual GPP derived from two satellite products, but do not faithfully capture all interannual differences (Fig. 1). Compared to the satellite products, the simulations suggest smaller drought-related GPP declines in 2007 and 2010 but greater effects in later drought periods (2015/16, 2023/24). Satellite products and simulations diverge in 2020, and in the years following, there are substantial differences between satellite products. On average, seasonal patterns are well reproduced by the model (Supplementary Fig. 4).

Satellite observations of the O_3 precursor NO_2 show similar interannual variability to the model used to produce O_3 concentrations for this study (Supplementary Fig. 5). Tropospheric NO_2 columns are elevated in areas with fire activity, with consistent spatial patterns between satellites and models during drought years (Supplementary Fig. 6). Due to the non-linear relationship between O_3 precursor concentrations and O_3 production, accurate NO_2 variability does not necessarily result in accurate simulation of O_3 concentration.

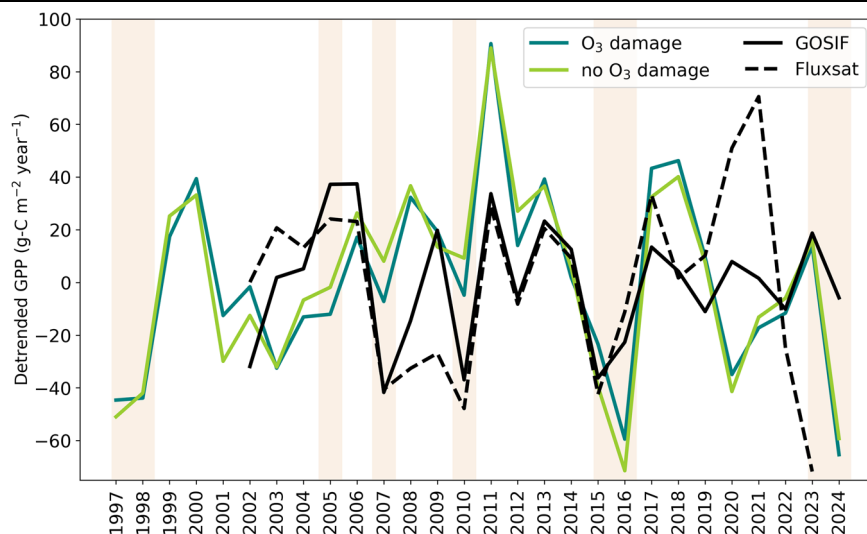
An evaluation of interannual variability of Amazon O_3 concentrations was not possible due to lack of long-term O_3 observations (e.g., decadal measurements), although the model has previously been evaluated against six measurement sites in the Amazon; the model was able to reproduce spatial, seasonal and daily surface O_3 variability³². We also evaluate against the TES surface O_3 product, which is indicative of boundary and lower free tropospheric O_3 concentrations, for the years 2005–2011. The seasonal cycle follows the same pattern in model and reference dataset, although the reference dataset shows higher concentrations and reduced variability, consistent with expected behaviour of lower tropospheric O_3 compared to the surface (Supplementary Fig. 7). The interannual patterns are reproduced ($r^2 = 0.62$), with higher O_3 during drought years apparent in both datasets (Supplementary Fig. 8). The same relationship is identified in August ($r^2 = 0.73$), the peak biomass burning season, but the modelled surface concentrations exhibit substantially greater variability than the satellite data.

Drought, fire and climate change contributions to O_3 damage

Fire activity emerges as the dominant correlate of interannual variability in surface O_3 concentration in the Amazon during the years 1997–2024 (Fig. 2a). All drought years except 2015 and 2023 show higher fire activity and above-average O_3 concentrations, with 2024 reaching record levels in both respects (Fig. 2a). There is a strong correlation between modelled surface O_3 and observed fire emissions each year ($r^2 = 0.72$, $p < 0.001$). Furthermore, the linear relationship is also produced by four additional Earth system models in the period 1997–2014, despite differences in their

Fig. 1 | Evaluation of annual gross primary productivity (GPP) over the Amazon region.

Detrended annual mean GPP for the Fluxsat satellite product (2002–2023; black dashed line), the GOSIF satellite product (2002–2024; black solid line), and model simulations with O_3 damage (blue solid line) and without O_3 damage (green solid line) during the period 1997–2024. Drought years are shaded brown.



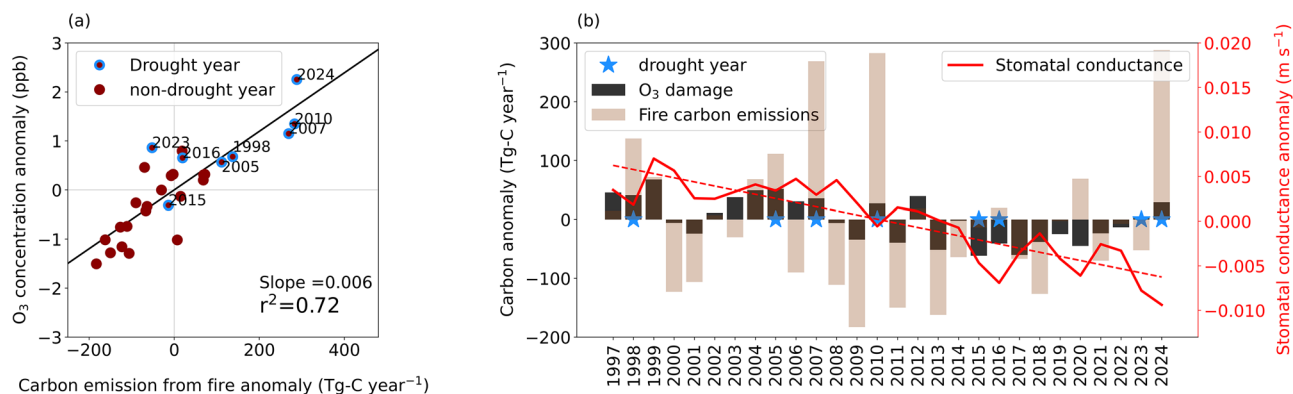


Fig. 2 | Annual mean variability in O₃ concentration, O₃ damage, fire carbon emissions and stomatal conductance. **a** The relationship between observation-based fire carbon emission anomalies and simulated O₃ concentrations. Drought year markers are outlined in blue and labelled with the year. A linear fit is calculated

(black solid line). **b** Annual mean anomalies in direct fire carbon emissions (brown bars), carbon emissions from O₃ damage (black bars) and stomatal conductance (red solid line). **b** contains the linear trend in stomatal conductance (red dashed line) and highlights drought years (blue star markers).

meteorology, structural complexity and representation of O₃ chemistry³³, indicating a robust relationship between fire and O₃ in the Amazon (Supplementary Fig. 9).

A timeseries of simulated O₃ damage shows that drought years frequently experience O₃ damage greater than preceding non-drought years, however there is also a trend towards reduced damage over time (Fig. 2b). For example, while O₃ damage during the 1998 El Niño was 50 Tg-C above average, O₃ damage in 2024 is lower despite higher O₃ concentrations and fire emissions (Fig. 2a). Nonetheless, 2024 stands out as overturning a pattern of reduced damage in the previous 10 years (Fig. 2b). The carbon loss to O₃ damage represents the reduction in total net carbon accumulated over the year by both vegetation and soil.

We use multiple linear regression to evaluate the predictive skill of environmental variables for simulated carbon loss associated with O₃ damage. A regression including stomatal conductance and O₃ concentration explains 70% of the temporal variance in carbon loss, suggesting equal predictor contributions from each effect, but this includes temporal autocorrelation and drivers that are likely physically related. After detrending to isolate variability, explanatory power decreased to 50%, with O₃ concentration emerging as the dominant predictor (standardised importance = 0.8) compared to stomatal conductance (0.4) (Supplementary Table 1). This indicates that O₃ concentrations are more closely associated with year-to-year variability in carbon loss, whereas stomatal conductance includes longer-term variability. Whilst fire-related O₃ variability is strongly associated with drought conditions (Fig. 2a), stomatal conductance is shaped not only by episodic drought events but also by a long-term declining trend (Fig. 2b) as a result of the changing climate and increasing atmospheric CO₂ (Supplementary Figs. 2, 3). As these drivers are connected by meteorology, and the apparent contribution of stomatal conductance to longer term trends may partly reflect parallel temporal trends rather than a direct mechanistic linkage, sensitivity tests are required to explicitly partition the underlying O₃ and meteorological contributions to carbon loss.

We perform sensitivity tests in which drivers are fixed at 1997 baseline values to isolate the effect of interannual variability in O₃ concentration and stomatal conductance (affected by meteorology and CO₂) on carbon loss relative to the simulation start (Fig. 3 and Supplementary Table 2). These experiments diagnose individual pathway contributions, but do not include all non-linear interactions present in the fully transient simulation. Therefore, the sum of individual contributions does not exactly reproduce the total simulated carbon loss (Fig. 3c). Nevertheless, the combined contributions to carbon loss from O₃ concentration and stomatal conductance reproduce the interannual variability in total O₃ damage in a 1:1 relationship with an RMSE of 10 Tg year⁻¹ and $r^2 = 0.93$ (comparing black bars with grey crosses in Fig. 3c) suggesting they independently describe the majority of the simulated O₃ damage. The variability in carbon losses attributed to each

pathway is of the same magnitude, in agreement with the linear regression that both pathways are equally important contributors to variability (Fig. 3c). Note that the regression-based coefficients above reflect statistical association, whereas sensitivity experiments provide mechanistic attribution within the model.

The potential reduction in net annual carbon uptake (to vegetation and soil) from fire-related O₃-plant damage is 24% the magnitude of direct carbon emissions from fires ($r^2 = 0.66$, $p = 0.001$). An uncertainty range of 18 to 35% is derived from observed variability in the susceptibility of tropical tree species to O₃ damage (Fig. 3a), however, additional uncertainties in the model representation of land surface processes, such as stomatal behaviour and indeed the O₃ damage scheme employed, have not been explored. Therefore, the contribution to carbon emissions should be interpreted as an order-of-magnitude estimate. Even so, these findings highlight a large potential contribution of O₃ damage to indirect carbon emissions from fire, climate extremes and shifts in Amazon carbon cycle dynamics.

The effect from O₃ exposure is strongly modulated by stomatal conductance, which reduces O₃ damage when stomatal conductance is lower ($r^2 = 0.80$, $p < 0.001$; Fig. 3b). Sensitivity tests isolating CO₂ effects show a strong reduction in stomatal conductance correlates with reduced O₃ damage ($r^2 = 0.84$, $p < 0.001$; Supplementary Fig. 10a), leading to increasingly avoided damage over time (approx. 2 Tg-C year⁻¹; Fig. 3c, yellow bars). Drought-induced reductions in stomatal conductance also show greater suppression of O₃ damage in the second half of the simulation period (Fig. 3c, red bars; Supplementary Fig. 10b). Combined, this has resulted in a weakening effect of O₃ damage on vegetation despite several recent extreme fire events. In particular, reduced stomatal conductance relative to 1997 has likely led to substantial prevention of O₃ damage in recent years (Fig. 3c).

Ozone damage during drought events

On average, drought results in a marginal increase in O₃ concentrations in the northern Amazon (11°N–0°N) during January–April, contemporaneous with a decrease in O₃ flux (Fig. 4a). In the southern Amazon (0°S–21°S) drought drives much stronger increases in O₃ during July–October, instead associated with a significant increase in the flux of O₃ through the stomata compared to non-drought years (Fig. 4b).

The O₃ flux change during drought is reflected in the resulting O₃ damage to plant productivity (Figs. 4c, 4d). There is no statistically significant difference between O₃ damage during drought and non-drought years in the northern Amazon (Fig. 4c), although at a more detailed spatial scale drought significantly decreases O₃ damage in the northernmost region (Supplementary Fig. 11a). Conversely, O₃ damage during drought in the southern Amazon is, on average, ~10–30 Tg-C month⁻¹ greater in July–October compared to the average monthly O₃ damage in non-drought years (Fig. 4d). However, we note that there is substantial variability between

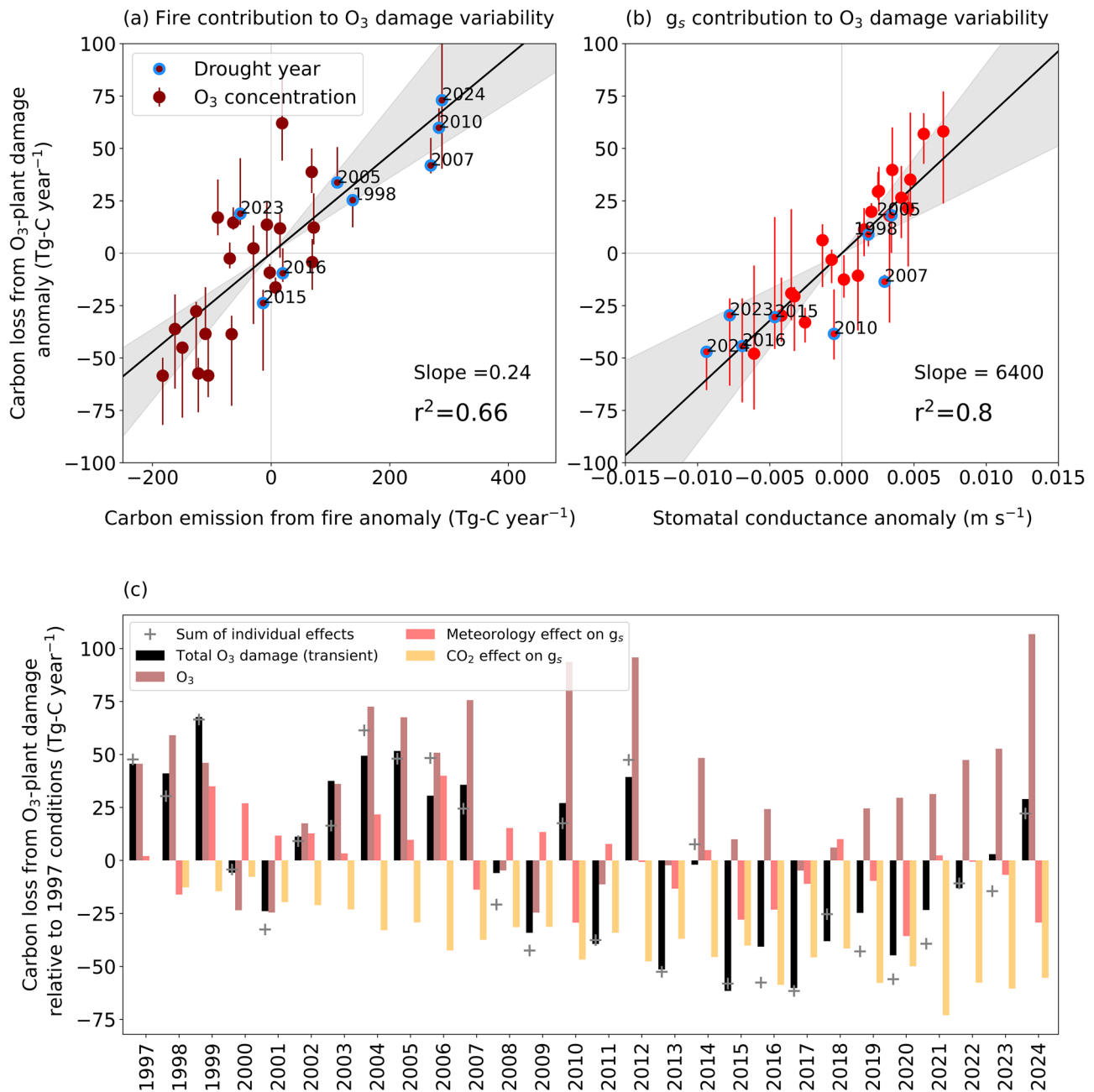


Fig. 3 | Fire emissions and stomatal conductance and their contributions to O₃ damage. The relationship between **a** fire carbon emissions and simulated loss of land carbon storage due to O₃ damage (removing effects of changing stomatal conductance) and **b** stomatal conductance and simulated loss of land carbon storage due to O₃ damage (removing effects of fire emissions). Drought year markers are outlined in blue and labelled with the year. A linear fit is calculated (black solid line) and simulations with higher and lower O₃ sensitivities are indicated by vertical bars with

corresponding linear fits (grey shading). **c** Annual mean anomalies in carbon emissions from O₃ damage (black bars) and contributions to this damage attributed to O₃ concentration (brown bars), changing meteorology (red bars) and atmospheric CO₂ (yellow bars) relative to 1997 values. The sum of individual effects (grey crosses) does not exactly sum to the total damage as the interactive effects are not included.

droughts. This damage primarily occurs in the Arc of Deforestation (Supplementary Fig. 11b), where the agricultural borders are advancing into the primary rainforest and where there is also substantial degraded and transitional forest that is flammable³⁴. Almost all fires in the Amazon are human-initiated, associated with deforestation, or when fires from clearing or agriculture escape into adjacent forest³⁵. The increase in fire emissions in the Arc of Deforestation currently outweighs any ‘protective effect’ of drought against O₃ damage in the dry season.

Compared to the direct impacts of drought weather in the simulations, O₃ only has a modest effect on NPP in the northern Amazon (Fig. 4c). Areas

that experience drought-related protection from O₃ damage are highly affected by drought stress directly, resulting in significant losses of productivity from the drought itself (Supplementary Fig. 11c). In the southern Amazon, O₃ substantially compounds drought-driven declines in NPP, amplifying the loss of productivity during the fire season (Fig. 4d). During August, the average decrease in NPP resulting from drought-related O₃ damage is 50% of the magnitude of NPP loss directly from drought meteorology (Fig. 4d). Among simulations of individual drought years, this varies substantially from years with reduced O₃ damage compared to average (2016) to years in which O₃ damage is greater than the effect of

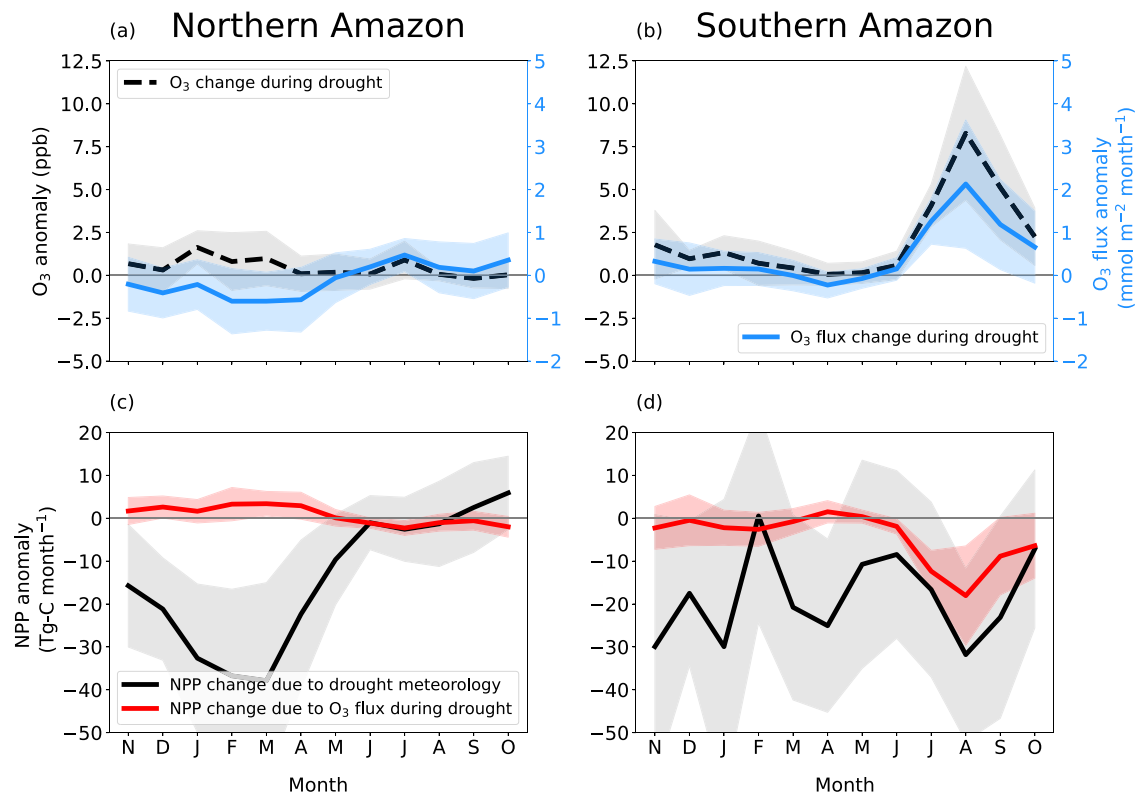


Fig. 4 | Monthly comparison of O₃ concentrations, stomatal flux and O₃ damage in drought years relative to non-drought years. Anomalies during drought years relative to non-drought years for (a,c) the northern Amazon and (b,d) the southern Amazon. a,b: O₃ concentration (black dashed line) and simulated flux of O₃ through the stomata (blue solid line). c,d: simulated Net Primary Productivity (NPP) change

due to O₃ damage during drought (red solid line) and due to the drought meteorology (black solid line). Standard deviations (shading) are calculated from individual drought years (1998, 2005, 2007, 2010, 2015, 2016, 2023, 2024) relative to the non-drought year mean.

drought stress (2010). This highlights that O₃ can amplify drought stress where seasonal fires are most prevalent.

Ozone damage during individual extreme droughts

The spatial and seasonal characteristics of each drought are distinct and occur against the backdrop of long-term climate change, affecting fire activity and O₃ flux into leaves through stomata. Recent drought events in our simulations show a transition towards lower stomatal O₃ fluxes even with higher O₃ concentrations (Supplementary Fig. 13). Here, we look at the most extreme droughts occurring in 1997/98, 2015/16, and 2023/24, which were all associated with El Niño events. We highlight that this event-level analysis depends strongly on the spatial distribution and magnitude of simulated O₃ concentrations, which remain challenging to validate. Confidence is particularly limited for the 2023/24 event, when observational coverage and independent model estimates of surface O₃ are sparse.

El Niño events tend to span 2 years because they occur in the transition from one year to the next. They can affect the Amazon at the end of the first year, although the largest meteorological and fire impacts occur in the following year³⁶. At the onset of El Niño, the dry seasons of 1997 and 2023 already showed higher fire activity and elevated O₃ concentrations (Fig. 5a, g). However, whilst O₃ concentrations in 1997 led to a significant increase in O₃ flux, our simulations suggest there was a lower O₃ flux than average in 2023 attributed to drought- and climate change-related stomatal exclusion. In the years that follow the onset (1998 and 2024), elevated O₃ concentrations are higher and more widespread, with above-average O₃ fluxes during both events (Fig. 5c, i). The extreme drought in 2024 was also associated with the highest fire activity of the recent period (Fig. 2b), likely overwhelming protection from stomatal closure and resulting in significantly higher O₃ fluxes in the south and southwest (Fig. 5i). Droughts in 2005 and 2010 also demonstrate higher O₃ fluxes in areas that are rarely

exposed to elevated O₃ (Supplementary Fig. 12d, h). These remote areas are not usually considered ‘at risk’ from stressors, and we hypothesise that vegetation here may be more sensitive to O₃ damage due to lack of historical exposure.

The drought event in 2015/16 is the only drought event in the recent period that does not show significant O₃ damage during the southern Amazon dry season (Fig. 5f). Fire activity in 2016 remained relatively low despite drought conditions^{37,38} so O₃ concentrations did not increase as in other recent droughts (Fig. 2a).

All three El Niño-related droughts show similar responses in the northern Amazon during November–April; there are significant reductions in O₃ fluxes despite increased O₃ concentrations due to fire activity (Figs. 5b, 5e, 5h). This indicates that the northern Amazon is more likely to experience a ‘protective’ effect from drought, even when fire activity is higher than usual for the season. The most intense period of the 2015/16 drought stress occurred during this season^{37,38}, avoiding high fire activity in the Arc of Deforestation later in the year and thus minimising O₃ damage. Other droughts, for example, those triggered by Atlantic Multidecadal Oscillation (AMO) events, tend to begin later in the year^{37,39} with a smaller increase in fire anomalies in November–April (Supplementary Fig. 12).

Discussion

Fire, climate change and extreme events drive considerable interannual variability in O₃ damage in the Amazon. Previous studies have quantified present-day mean GPP losses of 137 Tg-C year⁻¹ in fire-related O₃ damage in the Amazon¹⁵. We now quantify a standard deviation in net carbon loss of 38 Tg-C year⁻¹ with a total range of 129 Tg-C year⁻¹ for the period 1997–2024 (Fig. 2b). Variability in our simulations is affected equally by fire activity (which impacts O₃ concentrations), and drought and CO₂ (which modify stomatal conductance). Although it has been suggested that drought can offer

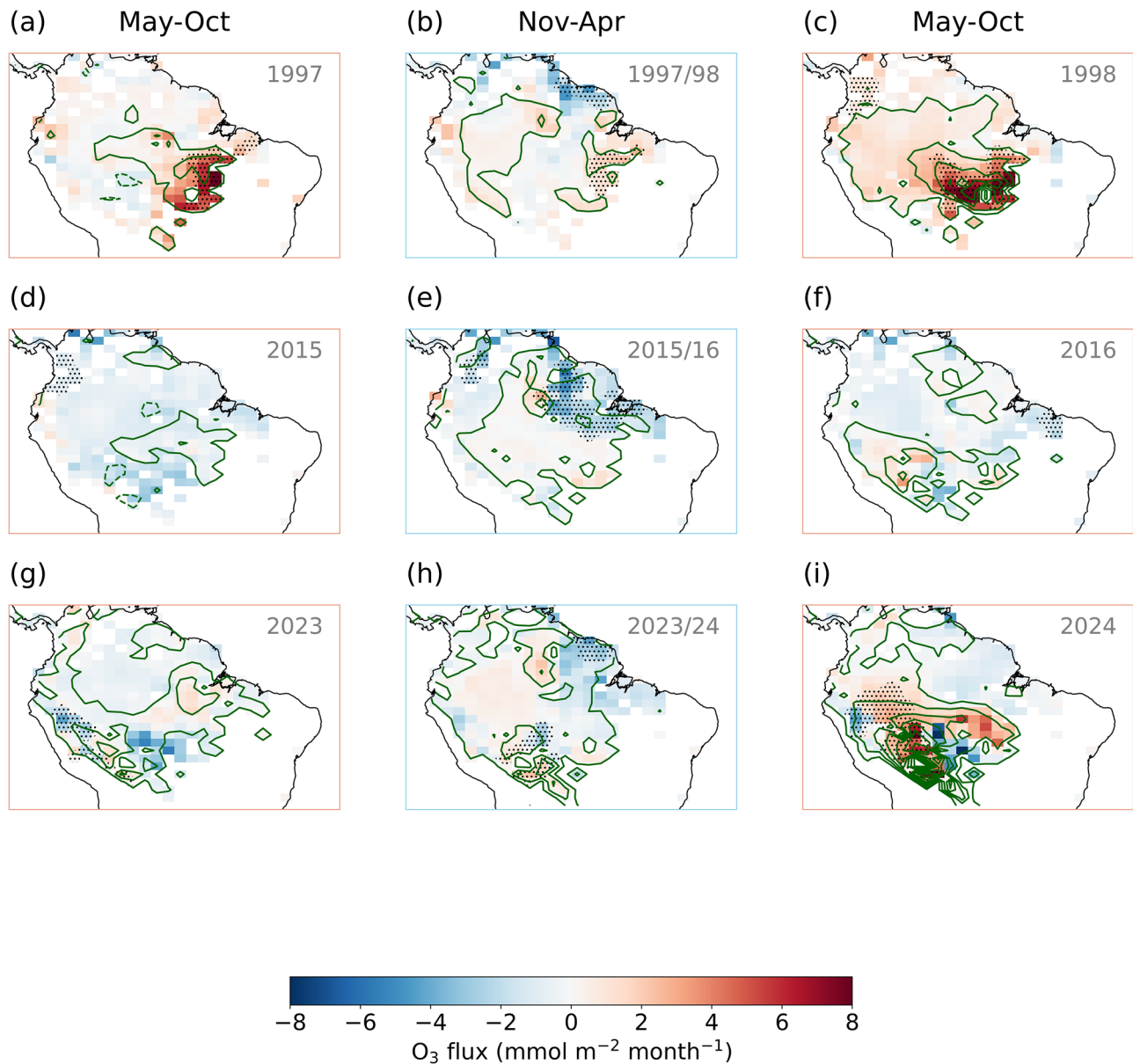


Fig. 5 | Simulated flux of O₃ through the stomata and O₃ concentration anomalies compared to non-drought years. Seasonal anomalies in O₃ flux (shading) and O₃ concentration (green contours) are shown for droughts in (a–c) 1997/98, (d)–(f) 2015/16 and (g–i) 2023/24. O₃ concentration is in intervals of

3.75 ppb (positive change = solid line, negative change = dashed line). Stippling indicates clusters of 5 or more gridcells where the O₃ flux is significantly different ($p < 0.05$) to a non-drought year using a one-sided student's *t*-test.

a protective effect against O₃ damage¹, we propose that, whilst the past decade has experienced a reduction in O₃ damage in response to decreasing stomatal conductance, significant productivity losses are still possible during years with high fire activity (such as 2024; Fig. 2b). Our simulations suggest that extreme drought events affect both fire activity and stomatal behaviour to result in O₃ damage that is a balance between the magnitude and locations of fire emissions and drought severity. Contrasting events in 2016 and 2024 demonstrate two ways that drought-related O₃ damage can be affected by fire activity in the dry season; a lack of human-initiated ignition in the Arc of Deforestation in 2016 likely protected large areas of the south and south-east Amazon from O₃ damage, but this was not the case in simulations of 2024.

We show that, in response to Amazon fire, indirect carbon emissions from O₃ damage are an important component of the Amazon carbon budget, which therefore merits further work to reduce current uncertainties. As there remain limited observations of surface O₃ in the Amazon, model data provide an opportunity to understand O₃ distribution and its effects, especially over annual and longer-term timescales. However, continued O₃

monitoring is essential to improve confidence in model output and to validate long-term patterns. Modelling of stomatal conductance and O₃ uptake remains a highly parameterised process and experimental work and model design must urgently focus on developing more process-based representations of O₃ impacts on vegetation (via its effect on stomatal conductance, changes to respiration and carbon partitioning).

This study attributes an average reduction in O₃ damage of 2 Tg-C per year due to increasing CO₂ concentrations over the simulation period (Fig. 3c). As atmospheric CO₂ concentrations continue to respond to emissions changes, the resulting effect on future O₃ damage must also be considered, including near-term protection from rising CO₂ but also the long-term possibility of increasing damage in a low-carbon future.

As Earth system models predict intensifying Amazon drying in the future, drought events of comparable magnitude are likely to reoccur⁴⁰. Climate change is likely to continue increasing VPD and CO₂, thereby reducing stomatal conductance further⁴¹, but this also risks increasing forest flammability¹¹. The extreme droughts of 2015/16 and the recent 2023/24

event have both been at least partly attributed to anthropogenic climate forcing^{12,43}, with changes in dry season length and fuel availability also contributing to increased fire risk¹³. Critically, our simulations of 2005 and 2024 (Supplementary Fig. 12) suggest widespread drought can lead to fire in primary and remote Amazon forest^{37,44}, shifting elevated O₃ episodes away from the Arc of Deforestation. Future observations of O₃ concentrations in remote Amazonia will be essential to determine whether O₃ pollution occurs under severe drought conditions. Already, 2024 reached unprecedented scales of forest disturbance due to fire despite a reduction in deforestation²³. Such a shift endangers remote and protected areas, and highlights that decreasing deforestation must be combined with decreasing degradation to reduce drought-related fires^{44,45} and mitigate against carbon losses from O₃ damage.

Methods

The UK land surface model (JULES) description

The Joint UK Land Environment Simulator, JULES, is a land surface model designed to simulate the processes occurring in the Earth's land areas^{24,25}. Developed by institutions in the UK, JULES integrates representations of land-atmosphere interactions, incorporating heat and energy exchanges, vegetation dynamics, soil processes, and hydrology to provide a comprehensive representation of land-atmosphere interactions.

The model calculates the energy balance at the land surface, considering incoming solar radiation, outgoing longwave radiation, sensible heat flux, and latent heat flux²⁴. This study used JULES to model the growth, development, and competition between different vegetation types. It represents photosynthesis, plant and heterotrophic respiration, and the influence of environmental conditions on plant growth²⁵. JULES has a multilayer canopy radiation interception and photosynthesis scheme that accounts for direct and diffuse radiation, sun fleck penetration through the canopy, inhibition of leaf respiration in the light and change in photosynthetic capacity within the canopy. It considers soil moisture dynamics and their impact on plant water uptake, which affects photosynthesis and stomatal conductance during water limitation²⁵. JULES accounts for hydrological changes through evaporation, transpiration, and runoff²⁴. These processes collectively allow JULES to simulate the dynamic interactions between the land surface and the atmosphere.

JULES uses the Medlyn optimality-based stomatal conductance scheme, which is calculated from prognostic photosynthesis, VPD and internal CO₂. Net photosynthesis is simulated using the Farquhar model and includes thermal acclimation. Evaluation at tropical sites showed thermal acclimation improved model skill compared to fluxsite measurements⁴⁶. Soil moisture responses remain a significant uncertainty in simulating stomatal behaviour; JULES applies an empirical beta parameter to limit stomatal conductance when soil is dry.

The UK Earth System model (UKESM1) description

UKESM1 was used to produce modelled O₃ concentrations and NO₂ columns. UKESM1 is a composite model incorporating the physical climate model HadGEM-GC3.1⁴⁷ with additional Earth system components encompassing land processes and atmospheric chemistry⁴⁸. The UK Chemistry and Aerosol scheme (UKCA) integrates both stratospheric and tropospheric chemistry components⁴⁹ and is coupled with the GLOMAP-mode aerosol microphysics scheme^{50,51}. The model's lowest vertical level covers an altitude range of 0 to 40 m, with a midpoint height of 20 m above orography, while its spatial resolution is 1.25° latitude by 1.875° longitude (approximately 200 km at the equator).

UKCA includes 84 chemical species used to simulate chemical cycles of O_x, HO_x, and NO_x, as well as oxidation reactions of CO, CH₄, and NMVOCs.

Datasets

Simulated O₃ concentration data

Hourly O₃ concentration data is used as driving data in JULES and to establish a relationship between annual mean O₃ concentrations and fire

emissions in the Amazon. We use O₃ concentrations from the UKESM1 CMIP6 historical simulation⁵², which is publicly available until the year 2014, and extend the simulation to the end of 2024. UKESM1 was selected for our simulations of O₃-plant damage as it has been validated against observed O₃ in the tropics and was shown to accurately capture changes in O₃ in response to environmental and emissions changes at a range of time resolutions³².

The CMIP6 historical simulations are core experiments from CMIP6 that cover the historical period from 1850 to 2014, including anthropogenic, solar and volcanic forcings. Forcings included prescribed and interactive components. Anthropogenic and biomass burning emissions (from GFED4s), encompassing O₃ precursors such as VOCs, NO_x, and CO, were specified with a monthly resolution. Lightning NO_x was calculated through a parameterisation that factors in lightning flash density based on cloud-top height⁵³. Soil-derived NO_x was prescribed from a spatially explicit model output provided by Yienger and Levy⁵⁴, adjusted to yield an annual flux of 12. Methane (CH₄) levels were set as annual mean surface concentrations, relying on observations throughout the historical period. Isoprene and monoterpene emissions were generated by the interactive biogenic VOC (iBVOC) emission model⁵⁵. Meanwhile, other biogenic emissions were prescribed as monthly mean climatologies based on data from the years 2001–2010^{56,57}.

The coupled, free-running simulation extended to 2024 was initialised from the end of the UKESM historical free-running ensemble member. Anthropogenic emissions, crop and pasture fractions, nitrogen deposition and prescribed greenhouse gas concentrations followed the SSP3-7.0 scenario⁵². Biomass burning emissions were from GFED4s.

O₃ in UKESM1 has been evaluated at six Amazon sites and 11 remote tropical sites and found to accurately represent variability in O₃ concentrations at time resolutions from hourly to seasonal, but with a systematic positive bias³². Our study evaluates anomalies (changes from the mean) to reduce the impact of systematic bias. At a monthly resolution, variability in O₃ concentration at the three sites is driven by changes in O₃ chemical production rather than transport and loss processes. These sites are NO_x-limited so O₃ production and O₃ concentration increase with NO_x concentration, suggesting that good representation of NO_x is essential for simulation of O₃ concentrations. However, accurate representation of NO_x does not necessarily confirm accurate O₃ concentrations, as the effect of changing precursors is non-linear, and O₃ concentrations also depend on transport and loss processes (both chemical and depositional). Evaluation of isoprene columns, the dominant VOC precursor in the region, shows a positive bias in UKESM1 in the wet season but reasonable agreement in the dry season⁵⁸, the period with the highest O₃ and therefore most relevant for this study.

The lack of long-term interannual measurements of O₃ concentration in the Amazon remains a limitation to our understanding of O₃ trends and patterns, yet modelling studies give valuable insight based on best understanding of chemical and meteorological processes.

Meteorology in the UKESM1 simulation is internally generated, so it does not correspond to the observed meteorology in each year. This was the only CMIP6 UKESM1 historical ensemble member to include output of hourly O₃, considered essential for accurate calculation of stomatal fluxes. Here, we consider the possible effects of this on O₃ concentrations and the implications for event-specific attribution.

To demonstrate the robustness of the relationship between simulated O₃ and fire activity in the Amazon (Fig. 2a), we compare the identified trend to the UKESM1 AMIP simulation 1997–2014, which is forced with observed meteorology, as well as consider variability among 12 UKESM1 historical ensemble members, which have identical emissions, but meteorology evolves independently. Additionally, a single ensemble member from the CMIP6 historical simulation was taken from each of four additional Earth system models (GISS, MRI, CESM, GFDL). The choice of models was based on data available from the Earth System Grid Federation (ESGF). The models represent a range of complexity, including fixed and interactive isoprene emissions, as well as showing substantial differences in

their average O_3 concentrations in the Amazon and trends over time³³. We find a consistent trend between AMIP simulations and transient simulations, with some differences among individual years (Supplementary Fig. 13). We also find the same linear relationship in all other Earth System models (Supplementary Fig. 9).

To evaluate uncertainty in O_3 concentration spatial maps, we compare the AMIP concentration fields in drought years 1998, 2005, 2007, and 2010 to those of our simulation. We find our simulation may underestimate the increase in O_3 concentration in drought years by a few ppb in the southern Amazon dry season (May–Oct) compared to the simulation with observed meteorology (Supplementary Fig. 14). We also compare the standard deviation in O_3 concentration among the ensemble members during these drought years. We find that standard deviations are greatest downwind of the fire activity, reaching up to 3 ppb in the southern Amazon during the May–Oct season (Supplementary Fig. 15). At this spatial and seasonal resolution, variability in O_3 distribution between ensemble members is small compared to the effect of the emissions on the O_3 concentrations (Supplementary Fig. 15). We conclude that meteorology is only a small contribution to O_3 concentration variability.

Boundary layer O_3 concentration data

An alternative approach for evaluating variability in simulated surface O_3 is to use satellite-derived estimates of lower-tropospheric O_3 . We use the TES lowermost-tropospheric O_3 product, which provides an estimate of O_3 concentrations across the boundary layer and lower free troposphere, with sensitivity that may extend between 900–700 hPa. These retrievals do not represent O_3 concentrations at the model surface layer or forest canopy level, and therefore typically exhibit higher concentrations and reduced temporal variability relative to canopy-level O_3 . The weaker variability in TES likely reflects the broader vertical sensitivity of the retrieval compared with modelled surface concentrations.

TES data were analysed for 2005–2011. We calculated a monthly climatology, annual means, and August monthly means, weighted by tropical broadleaf tree fraction, and compared these with UKESM1 surface O_3 concentrations.

As the TES retrieval and modelled surface O_3 are not directly equivalent variables, this evaluation is intended only to assess whether large-scale temporal variability, approximate seasonality and interannual variability are reproduced, rather than to evaluate absolute magnitude or spatial accuracy.

NO_x data

As interannual variability in modelled O_3 concentrations is difficult to validate due to lack of observations^{32,59}, evaluation of simulated tropospheric NO₂ columns was used to identify whether spatial and annual variability in precursor concentrations were reproduced by UKESM1.

Satellite-derived atmospheric NO₂ columns were taken from the OMI instrument on the Aura satellite, which provides daily tropospheric NO₂ columns from July 2004–2023 from an overpass time of 13:30. The daily coverage and high spatial resolution reduce uncertainty and contamination by cloud cover. In source regions, the majority of the NO₂ originates in the boundary layer, making tropospheric NO₂ columns a good proxy for surface NO_x⁶⁰.

Modelled NO₂ columns were obtained for UKESM1 by summing all NO₂ below the modelled tropopause height. The NO₂ concentrations are a result of chemical and physical processes modelled by UKESM1 as a result of prescribed NO_x emissions. Satellite NO₂ columns were regridded to match the model resolution, and both datasets were converted to annual and seasonal means from 2005 to 2023.

Fire emissions data

The Global Fire Emissions Database 4, including small fires (GFED4s) was used for fire carbon emissions. These direct carbon emissions data were used for comparison with O_3 concentrations and indirect carbon emissions that

are a consequence of O_3 damage. The GFED4s data were provided as monthly mean data from 1997–2024^{61,62}. The product used satellite-detected burned area, boosted to account for small fires that were below the detection limit of the satellite. The carbon emissions from all fire types were calculated from dry matter burnt multiplied by an emission factor specific to the fire type (e.g., 0.491 for tropical trees).

Gross primary productivity data

Two satellite-derived Gross Primary Productivity (GPP) datasets were used to evaluate modelled GPP and compare the performance of simulations with and without O_3 damage. Annual mean GPP were obtained from GOSIF, the Global OCO-2 based SIF product, which used sun-induced fluorescence (SIF) to infer GPP⁶³, and from Fluxsat, a satellite product using enhanced vegetation index (EVI) from MODIS and trained on the FLUXNET2015 eddy covariance dataset to estimate GPP⁶⁴. SIF is a direct physiological proxy for GPP due to its sensitivity to both Light use efficiency (LUE) and absorbed photosynthetically active radiation (APAR). This product is considered to be one of the most accurate methods to monitor GPP across a broad range of ecosystems^{65,66}. It is likely to be more sensitive at detecting variability than other products, as variability is not solely produced by variability in climate but also by the biomechanical responses affecting photo efficiency. FluxSat is chosen as an additional comparison using a different method of obtaining GPP. This product employs neural networks to upscale eddy flux tower observations of GPP using MODIS bands⁶⁵.

Both datasets were available at a 0.5° resolution and were regridded to the model resolution. Monthly and annual mean anomalies were calculated over the Amazon from 2002–2023 for Fluxsat and 2002–2024 for GOSIF, based on available data.

Satellite products have a degree of uncertainty, especially as they do not observe GPP directly. Interannual variability in GPP calculated by satellite products has demonstrated similar global patterns, although there are often regional differences between products⁶⁷. Furthermore, observations are affected by the presence of clouds, which over the Amazon, especially during the wet season, can obscure the land surface, decreasing data quantity and increasing uncertainty⁶⁴.

Model set-up and the O_3 damage scheme

This study used the Joint UK Land Environment Simulator (JULES) v1.5.6 at a spatial resolution of 1.25° latitude by 1.875° longitude^{25,68}. We included updates to plant functional types and physiology⁶⁹, photosynthetic and stomatal functional traits⁴⁶ and updates to the O_3 damage scheme⁶.

The driving data across simulations included prescribed annual CO₂ and land-use land-cover change as used in the Global Carbon Budget 2024⁷, with meteorology and forcing data from CRU-JRA v1.3 reanalysis⁷⁰ and hourly O_3 concentrations for the 1990–2024 period modelled by the UK Earth System Model, UKESM1⁴⁸. The land cover fraction of tropical broadleaf tree cover is prescribed from the 2015 land cover map produced by Harper et al.⁷¹, while crop and pasture fractions vary annually based on observations and therefore capture the expansion of agricultural land over the analysis period. As a result, the simulations represent major land-use transitions associated with cropland and pasture formation, although they do not fully capture interannual changes in tropical broadleaf forest extent, forest degradation, or shifts in forest edges associated with fire and deforestation. This simplification may introduce regional biases in areas of rapid land-cover change, particularly along active deforestation frontiers, and may underestimate tropical broadleaf cover prior to 2015.

The O_3 damage scheme employed in JULES modifies net photosynthesis (A_{net}) and stomatal conductance (g_s) by an O_3 damage factor (F , Eq. 1). F is controlled by an O_3 sensitivity parameter (α) and the flux of O_3 above a threshold (y) so that A_{net} declines linearly as O_3 flux increases above the threshold (Eq. 2) and the rate of decline (Eq. 1) depends on the O_3 sensitivity, α . The decline in A_{net} affects NPP, and the model assumes that (i) O_3 damage is instantaneous at the point of uptake and (ii) results in a

coordinated reduction in g_s (Eq. 3).

$$F = 1 - \alpha(\text{Flux } O_3 > y) \quad (1)$$

$$A_{\text{mod}} = A_{\text{net}} \times F \quad (2)$$

$$g_{\text{mod}} = g_s \times F \quad (3)$$

This instantaneous damage scheme does not consider that damage may be delayed (e.g., as a result of early leaf senescence) and therefore represents a simplistic representation of the possible changes to the forest ecosystem based on available observations of tropical vegetation. However, the parameters are calibrated based on observed reductions in NPP over longer timescales (growing seasons) such that these effects should be implicitly accounted for at the timescales considered in this work. The scheme applies damage directly to photosynthesis, which indirectly decreases stomatal conductance⁴. However, there are several physiological responses to O_3 that are not observed extensively enough to be included in current O_3 damage schemes. Among these observations is a decoupling between photosynthesis and stomatal conductance⁷¹, including that stomata can become sluggish and respond more slowly to changes in environmental conditions such as drought⁷². In this case, our simulations would represent a more conservative estimate of O_3 damage. Additional mechanistic developments that may arise in future include O_3 -driven changes to respiration and antioxidant capacity⁷³. Antioxidant response is currently implicitly included via the fixed threshold, although it likely varies by species and environment. Similarly, changes to carbon partitioning within the vegetation is not included. To implement these mechanistic changes for tropical trees, further observations and significant model development and calibration is needed.

Simulations

To isolate the effect of O_3 damage, we conducted simulations for the period 1997–2024: one with no O_3 damage (i.e., $\alpha = 0$) and one using an average O_3 susceptibility of tropical trees ($\alpha = 0.05$)⁶. Uncertainty in O_3 susceptibility is investigated by using values of α of 0.03, 0.05, and 0.12 based on the range of responses observed in tropical trees⁶, alongside a standard $y = 1 \text{ nmol } O_3 \text{ m}^{-2} \text{ PLA s}^{-1}$. The fixed threshold $y = 1$ is the recommended threshold used across studies and derived from sensitivity tests in existing literature^{6,74}. All simulations underwent separate 1000-year spin-ups (cycling 50 times over a 20-year period from 1975–1995) in which O_3 was fixed at mean 1990 concentrations. Only changes during the period 1997–2024 were evaluated due to the availability of fire emissions (beginning in 1997). The difference in total accumulated carbon in each year in simulations with and without O_3 damage gives the carbon loss due to O_3 damage.

We conducted sensitivity tests (Supplementary Table 3) to isolate the contributions of changes in O_3 meteorology and CO_2 to simulated damage. To quantify the effect of O_3 variability, we performed a simulation in which O_3 concentrations were fixed at 1997 levels throughout the simulation period. The resulting damage was compared with the fully transient simulation, in which O_3 concentrations varied over time. The difference between these simulations isolates the effect of changing O_3 concentrations on damage. To isolate the influence of meteorological variability, we conducted simulations with meteorological conditions fixed at 1997 values while allowing O_3 concentrations to vary transiently. We then compared these results with a corresponding simulation that used fixed 1997 meteorology but excluded O_3 damage. The difference between this estimate and the O_3 damage from the fully transient simulation represents the contribution of meteorological variability. Finally, to isolate the effect of CO_2 on stomatal conductance, we could not directly compare simulations with fixed versus transient CO_2 , because changes in CO_2 also alter GPP through CO_2 fertilisation, making the simulations non-comparable. Instead, we compared simulations with fixed 1997 O_3 concentrations and fixed 1997 meteorology, performed with and without O_3 damage. Under these conditions, CO_2 is the only variable that changes over the simulation period, allowing us to isolate its effect on stomatal conductance. Simulations were performed across the three values of α .

To attribute stomatal conductance changes to changing meteorology or increasing CO_2 , we use two sensitivity simulations without O_3 damage. To isolate the effect of increasing CO_2 , we use stomatal conductance output from the control simulation with meteorology fixed at 1997 values. To isolate the effect of changing meteorology, we fix CO_2 concentration at 1997 values.

Analysis

All datasets were regridded to the resolution of the JULES simulation (1.25° latitude by 1.875° longitude), if they were not already available at that resolution, and the Amazon region was selected. This was defined by the tropical broadleaf tree fraction from the 2015 land cover map produced by Harper et al.⁷¹. Analysis was limited to the period 1997–2024, constrained by GFED4s fire data beginning in 1997. To analyse the data, Python 3 with Jupyter notebooks was used.

For comparison to GPP satellite products, GPP from simulations and satellite data was masked to exclude gridcells with less than 90% tropical tree cover. Annual means were detrended to remove impacts of CO_2 fertilisation that were included in the JULES simulations but cannot be detected by the EVI product. For evaluation of seasonality, JULES GPP was compared to satellite-derived GPP in the central, less seasonal part of the Amazon (4°S–4°N) and the outer, more seasonal part of the Amazon (>4°S, >4°N) as well as separating into drought and non-drought years.

To obtain correlations between variables (O_3 concentrations, fire activity, total land carbon storage changes), annual mean gridded data were averaged over the Amazon region, weighted by the fraction of tropical broadleaf tree plant functional type and grid cell area. These values were presented as anomalies relative to the 1997–2024 mean. Annual means begins in January. Statistical metrics (r^2 and p-values) of the correlations were obtained from the *scipy* package Pearson's r formula in Python. We also perform a multiple linear regression to separate the effects of O_3 concentration and stomatal conductance on net carbon losses from O_3 damage and assign feature importance. We normalise the variables and use the *statsmodels* package multiple linear regression function in Python. Confidence intervals and p-values are provided in Supplementary Table 1.

To establish drought effects, monthly means were calculated for the northern and southern Amazon by dividing datasets at the equator, weighted by the fraction of tropical broadleaf tree and grid cell area. Data are then divided into drought years (1998, 2005, 2007, 2010, 2015, 2016, 2023, 2024) and non-drought years. The average of drought years was compared to the average of non-drought years. Standard deviations are calculated from individual drought years compared to the average non-drought year.

Further analysis of individual drought years was presented as spatial maps, as there is considerable variation between drought years that is hidden by the drought composite analysis. Seasonal responses were presented for November–April (the northern Amazon dry season) and May–October (the southern Amazon dry season). We performed a one-sided Student's *t* test at each grid cell to assess whether the observed values during each drought season were significantly greater than those in non-drought years ($n = 20$). To account for spatial noise and to reduce the influence of isolated or spurious significant pixels, we applied a cluster-based filtering step. We identified connected regions of significant grid cells ($p < 0.05$) and removed all clusters smaller than five grid cells in area. This ensured that only spatially coherent regions of significance were retained to adjust for multiple comparisons.

Data availability

This dataset⁷⁵ relates to simulated data produced using a land surface model. The study used the Joint UK Land Environment Simulator (JULES) v. 5.6 at a spatial resolution of 1.25° latitude by 1.875° longitude. The netCDF files used to produce results and figures in this manuscript are available at: <https://doi.org/10.5281/zenodo.12820514>.

Code availability

Jupyter notebooks that can be used to recreate figures from the publication in Python are available at: <https://doi.org/10.5281/zenodo.12820514>. (ref. 75).

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Competing interests

The authors declare no competing interests.

Additional information

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