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LETTER

The uncertain impacts of an 1.5 °C overshoot-and-decline scenario on carbon stocks and productivity in terrestrial ecosystems

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Abstract

Overshoot scenarios, in which global temperatures peak and then decline through emission reductions and CO_2 removal, are increasingly central to climate policy as we are already approaching 1.5 °C warming. Yet the ecological reversibility of such pathways remains poorly understood, even though the trajectories of productivity and carbon stocks in terrestrial ecosystems have major implications for land-based carbon sink projections. Here we draw on four complementary lines of research to study the land carbon sink under overshoot: (i) CMIP6 models project declines in net ecosystem productivity (NEP) after peak warming. Nevertheless, NEP remains positive, leading to a stabilisation of the carbon stocks in terrestrial vegetation (cVeg). The CO_2 ramp up-down model experiment by CDRMIP underscores that these models predict near-reversibility of the vegetation carbon stock. (ii) A systematic review on global change experiments identified 256 papers

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(warming, drought, irrigation or elevated CO_2, all elements of an overshoot scenario). However, only 15 included a recovery phase following treatment. This reveals a gap in experimental design for understanding ecosystem responses under overshoot conditions. Where recovery was assessed, responses were mixed, with persistent legacy effects documented after drought. (iii) Modern-day overshoot analogues, including two El Niño events and the 2018–2020 European droughts, show that compound heat and drought can cause carbon losses that recover slowly, with repeated extremes progressively reducing ecosystem resilience. (iv) Paleoclimate records from the Holocene Climatic Optimum and the Paleocene–Eocene Thermal Maximum demonstrate that exceeding ecological thresholds can trigger vegetation changes and carbon cycle feedbacks that long outlast the climatic perturbation itself. Together, these findings show that the trajectory of the terrestrial carbon sink during climate overshoot is uncertain, because ecosystem responses are often delayed, nonlinear, and threshold dependent.

1. Introduction

As global mean temperatures approach 1.5 °C above pre-industrial levels (Cannon 2025, Forster *et al* 2025), overshoot scenarios are increasingly considered as plausible climate pathways for eventually meeting the Paris Agreement targets (Schleussner *et al* 2016, Hoegh-Guldberg *et al* 2019, Meyer and Trisos 2023, Van Vuuren *et al* 2026). In such scenarios, temperatures peak, temporarily exceeding a target (such as 1.5 °C or 2 °C) before declining through a combination of strong emissions reductions and large-scale carbon dioxide removal (figure 1; Moustakis *et al* 2024, Mendez *et al* 2025, Reisinger *et al* 2025). This temperature peak is likely accompanied by drastic changes in precipitation and extreme weather events (IPCC 2021, Pfleiderer *et al* 2024). Although integrated assessment models often treat these pathways as largely reversible, growing evidence suggests that overshoot raises the risk of crossing critical tipping points in the Earth system (Ritchie *et al* 2021, Armstrong McKay *et al* 2022, Winkelmann *et al* 2025). This risk is particularly pronounced as the overshoot period gets longer, which increases the likelihood of triggering irreversible changes (Pfleiderer *et al* 2024, Schleussner *et al* 2024).

Understanding the impact of overshoot on terrestrial ecosystems is critical. They absorb roughly a quarter of anthropogenic CO_2 emissions, making them a crucial carbon sink (Friedlingstein *et al* 2025), yet they also represent the largest source of uncertainty in future climate projections (Canadell *et al* 2021, Gier *et al* 2024). How a cooling phase of declining temperatures and CO_2 concentrations would affect this sink remains poorly understood. The core concern is hysteresis: rather than recovering symmetrically after peak warming, terrestrial ecosystems may carry persistent legacy effects or be pushed past tipping points from which recovery is impossible (Albrich *et al* 2020, Wigneron *et al* 2020, Meyer and Trisos 2023, Swann *et al* 2026). Dedicated modelling efforts focussed on the phase of negative emissions, such as through the Carbon Dioxide Removal Model Intercomparison Project (CDRMIP), indeed showed hysteresis in the land carbon sink, with higher terrestrial carbon uptake during cooling than during the preceding warming phase (Koven *et al* 2022, Asaadi *et al* 2024, Sanderson *et al* 2025). However, these studies also revealed a strong disagreement among land models under overshoot scenarios (Koven *et al* 2022, Asaadi *et al* 2024), underscoring how little is known about the underlying mechanisms and geographic patterns of carbon-cycle feedbacks. This risk of hysteresis is reinforced by regional climate change, as the changes in regional precipitation and climatic extremes are likely to reverse only partially after global temperatures peak (Pfleiderer *et al* 2024, Liu *et al* 2025). Moreover, the intensification of extreme events (droughts, storms) during peak warming may drive ecosystems past tipping points before regional cooling can take effect (Armstrong McKay *et al* 2022, Möller *et al* 2024, Ritchie *et al* 2026), though tipping of slow-onset elements may be avoided if the magnitude and duration of the overshoot remain limited (Ritchie *et al* 2021, 2026). Therefore, ecological reversibility during overshoot cannot be assumed, yet it remains a critical gap in the literature.

Studying the impact of overshoot on ecosystems is challenging however, as observations of recovery following peak temperatures remain scarce. We therefore consider complementary sources of information in this study. First, Earth System Models (ESMs) offer a global, multi-decadal perspective on land carbon dynamics. However, they were not designed for overshoot trajectories and poorly represent legacy effects and disturbance-recovery dynamics (Armstrong McKay *et al* 2022). We can also look at manipulation experiments on global change, which offer mechanistic precision (De Boeck *et al* 2015). However, these are typically restricted to single drivers, limited spatial scales and number of species, and short timeframes, meaning slow processes such as species turnover may go undetected (Luo *et al* 2011). Modern-day analogues of extreme climatic events provide observational validation but

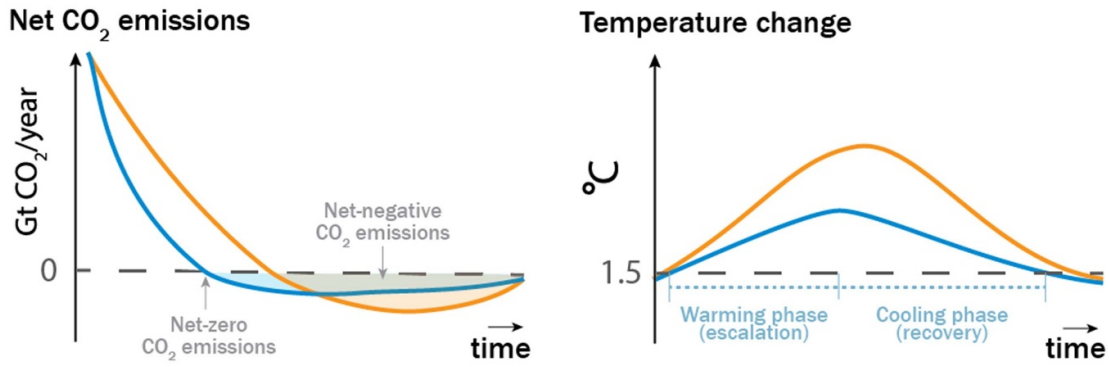


Figure 1. Schematic of net CO_2 emission pathways and their respective global temperature outcomes. The left panel displays two illustrative emission trajectories of mitigation pathways (blue and orange lines) that achieve net-zero and subsequently net-negative CO_2 emissions. The right panel depicts the resulting temperature change over time relative to a 1.5 °C target (horizontal dashed line), representing overshoot scenarios where global temperatures rise beyond the target, peak, and then decline.

are similarly constrained in duration and scope. Lastly, Paleoclimate records extend the temporal frame to periods of substantial temperature change (Fordham *et al* 2020), but no past interval closely mirrors the pace of contemporary warming, and proxies such as pollen and stable isotopes only capture some elements of past vegetation dynamics. Nevertheless, because these limitations are largely non-overlapping, the four approaches together offer a broader picture of what terrestrial ecosystems may face under an overshoot scenario.

Our primary focus in this comparison is on carbon stocks and productivity in terrestrial ecosystems. This is not to diminish the importance of biodiversity or shifts in species composition (Chapin *et al* 1995, Meyer and Trisos 2023, Metz *et al* 2026), which can themselves have substantial impacts on productivity (Morin *et al* 2018). However, ESMs represent vegetation through fixed plant functional types that preclude ecotone shifts or novel ecosystems, and manipulation experiments and modern-day analogues are too short-lived or coarse to capture compositional turnover. We therefore restrict our primary scope to carbon-related responses, though we draw on paleoclimate records to reflect on longer-term compositional change.

In this study, we synthesise current knowledge to examine how terrestrial ecosystem productivity and carbon stocks respond under climate overshoot scenarios, with focussing on the trajectory during the cooling phase. We integrate evidence from four complementary sources. First, we assess global ESM simulations, while also zooming in on Europe, where extensive observational records and experiments are available, and Africa, where limited data availability makes models the primary tool for evaluating climate change impacts. Second, we conduct a systematic review of global change manipulation experiments to determine whether studies include recovery phases following warming, altered precipitation, or elevated CO_2 treatments, and to assess how ecosystems respond during recovery. Third, we analyse modern-day analogues, studying ecosystem responses to recent climate extremes. We include the 2015–2016 and 2023–2024 El Niño events in tropical forest regions and the 2018–2020 European droughts. Fourth, we examine paleoclimate reconstructions from pollen records and geological archives, which provide a longer-term perspective on ecosystem responses than contemporary observations and experiments alone can capture.

2. Methods

2.1. CMIP6 model and scenario selection

To assess terrestrial carbon cycle responses under overshoot scenarios, we analysed output from the CMIP6 multi-model ensemble of ESMs. We selected ten models for which output was available for at least three of the four following scenarios: SSP1-1.9, SSP1-2.6, SSP5-3.4-OS, and SSP5-8.5. These emission-driven scenarios combine the three types of processes that govern the land carbon sink response to climate change: processes that regulate how ecosystems respond to changes in CO_2 concentrations, to changes in climate, and to anthropogenic land use change (Palazzo Corner *et al* 2023) (see table S1 for included models and scenarios).

SSP1-1.9 and SSP1-2.6 were selected because they show a temperature overshoot pathway in most models, which we define as a scenario in which the end-of-century temperature is lower than the maximum temperature reached before 2100 (see figure S1 for temperature projections per model and table S2 for overshoot details). This does not mean that the temperature falls below the Paris Agreement thresholds of 1.5 or 2 °C by 2100, but they all include a temperature increase and decrease around a variable peak. The multi-model mean of SSP1-2.6 only shows a very limited overshoot trajectory, representing almost a stabilisation scenario, while SSP1-1.9 shows a stronger overshoot. SSP5-3.4-OS is specifically designed to produce a sharp rise followed by a

decline in atmospheric CO_2, resulting in a strong temperature overshoot across models. Lastly, SSP5-8.5 was included as a reference high-end scenario and comparison to SSP-3.4-OS: it follows the same trajectory as SSP5-3.4-OS until 2060, after which CO_2 concentrations continue to rise rather than decline.

To complement these emissions-driven scenarios with an idealised benchmark of carbon cycle reversibility, we additionally analysed the concentration-driven 1pctCO2-cdr experiment from CDRMIP (Keller *et al* 2018). In this experiment, atmospheric CO_2 is increased at a rate of 1% yr^{-1} from pre-industrial conditions (1pctCO2) until quadrupling, followed by a symmetric decline of 1% yr^{-1} back to pre-industrial CO_2 concentrations, which are then held constant for a minimum of 60 years. Unlike the SSP overshoot scenarios, 1pctCO2-cdr isolates the carbon cycle response to a CO_2 ramp-up/ramp-down independent of other forcings (e.g. land use change).

From each global model we highlight three variables: near-surface air temperature (tas, °C), total land carbon stock (cVeg, Pg C), and net ecosystem productivity (NEP, Pg C yr^{-1}). We focused on NEP (gross primary productivity—plant and heterotrophic respiration), because this represents the net carbon retained by the ecosystem and thus the rate of change of the carbon stock, only excluding carbon losses from disturbances like harvests and fires. We compare these variables to a reference period (anomalies, expressed as ΔT, cVeg and ΔNEP), to show changes relative to the historical baseline. To calculate the global temperature anomaly, the reference period is the pre-industrial period (1850–1900; common in climate reporting). cVeg and NEP were compared to 1985–2014 to depict the changes to the more recent past. Analyses were limited to the period up to 2100 because too few model simulations extended beyond this date to allow robust intercomparison. We then looked at consistency among models, using inter-model spread as an indicator of uncertainty.

In addition to the global analysis, we examined regional responses in two specific areas: Europe and central Africa (see figure S2 for the masks). Europe is a region with extensive data records and experiments, whereas in Africa data scarcity means models are the primary tool and it is essential to better understand how consistent they are. Therefore, these two study regions represent a data-rich and data-poor region. Not all models reported all variables or ran all scenarios; the availability of model output per scenario is summarised in table S2 and figure S1.

2.2. Systematic search of recovery in global change experiments

To compile experimental evidence on ecosystem carbon responses to global change, we screened the MESI database (Van Sundert *et al* 2023), which collates field-based global change experiments published up to 2022. We restricted our search to field experiments in natural ecosystems, excluding greenhouse, pot, and planted experiments. Since anthropogenic climate change manifests as a combination of many changes including elevated CO_2, higher temperatures, and regional precipitation shifts (IPCC 2021), we retained experiments manipulating elevated CO_2, warming, drought, or irrigation (individually or in combination). We further restricted response variables to carbon stocks or measures of net primary productivity (NPP). Ideally, we would compare experimental results to modelled NEP directly, as NEP integrates both productivity and heterotrophic respiration. However, few field experiments simultaneously quantify both variables. We therefore focus on NPP as the best available proxy, while acknowledging that it captures only part of the carbon cycle response. Applying these filters yielded 198 studies spanning 1994–2021.

To extend coverage beyond 2022, we conducted a structured Web of Science search including literature up to 31 December 2025. We used search terms combining treatment descriptors (warming, temperature, heating; precipitation, drought, rainfall; CO_2, FACE, eCO_2, enrichment experiment) with productivity terms (ANPP, BNPP, soil carbon, fine root increment, biomass increment, NEP). We included all studies reporting on global change experiments using the same inclusion criteria as for the MESI database. In addition, we performed a targeted search for studies explicitly framing their results around recovery, using the terms 'recovery,' 'rewetting,' 'removal,' or 'cooling' in combination with the same productivity terms. This secondary search was designed to capture studies that might not have appeared in the broader treatment-focused query. Together, the two searches yielded 58 additional studies on global change experiments.

From all 256 studies on global change experiments we extracted the study location (latitude, longitude), which we used to infer the ecoregion (Dinerstein *et al* 2017). We also extracted the treatment, or combinations of treatments, and treatment duration. We screened all studies for the inclusion of a recovery phase, defined as a period during which measurements continued after the treatment had ended. The database is available on Boeschoten 2026.

2.3. Modern-day analogues

To complement the experimental and modelling evidence with observations, we synthesised published literature on ecosystem productivity and carbon stock responses to major recent climate extremes. The first case study focused on the 2015–2016 El Niño event, which caused widespread drought and heat stress across tropical forests (Burton *et al* 2018). We also included papers on the 2023–2024 El Niño event. Reflecting known geographical biases in climate

research (Metcalfe *et al* 2025), fewer studies are available from Africa than from other tropical regions. We therefore report responses across the tropics while recognising that African forests may respond differently to climate change than the Amazon (Hubau *et al* 2020), an important consideration when linking these observations to the modelling case study. The second case study examined the 2018–2020 multi year drought in northwestern Europe, which strongly affected temperate forests and grasslands (Rakovec *et al* 2022). For each analogue, we reviewed studies reporting on ecosystem productivity during and after the extreme event, with a focus on the trajectory and completeness of recovery. These analogues were used to evaluate whether the recovery dynamics from the experimental work and the models are consistent with observed post-extreme responses.

2.4. Paleoclimate reconstructions

To extend the temporal frame beyond what experiments or modern observations can provide, and to get more insight into potential ecosystem shifts, we draw on past periods of elevated temperatures as another analogue for 21st century overshoot scenarios. The first is the Holocene Climatic Optimum (∼9000–5000 BP), a postglacial interval characterised by warmer and more favourable growing conditions, with temperatures around 0.5 °C–1.5 °C above the 20th century average in many regions and atmospheric CO_2 concentrations of about 280 ppm, followed by gradual cooling (Dawson *et al* 2025, Sweeney *et al* 2025). The second is the Paleocene–Eocene Thermal Maximum (PETM, ∼55.8 Ma), a more extreme event characterised by rapid global warming of roughly 5 °C over 10 000–20 000 years, followed by a return to background climate conditions over the subsequent approximately 200 000 years (Rogger *et al* 2025). Atmospheric CO_2 rose from roughly 870 ppm to a peak of ∼2200 ppm (Gutjahr *et al* 2017), from a pre-event background estimated at 840–1680 ppm (Meissner *et al* 2014).

For each period, we examine published evidence for ecosystem shifts during both the warming and subsequent cooling phases to assess whether recovery occurred and on what timescales. While primary productivity and carbon stocks cannot be directly quantified from paleoclimate records, these archives preserve signals of long-term vegetation change that offer a broader perspective on ecosystem resilience than models, experiments or modern observations alone can provide.

3. Results

3.1. ESM experiments show relative reversibility

None of the emission-driven model scenarios project a return of global temperatures below 1.5 °C warming by 2100 in the multi-model mean (figure 2(a), table S2). Still, all three scenarios considered here did display warming followed by partial cooling, making them relevant for overshoot analysis. The most explicit is SSP5-3.4-OS, which was designed as a strong overshoot scenario. It peaks at 2.96 °C warming in 2064 and then ends at 2.54 °C warming by the end of the century. SSP1-1.9 and SSP1-2.6 follow more gradual trajectories in which net negative emissions emerge from sustained mitigation rather than a sharp peak and decline. Consequently, these scenarios produce smaller overshoots, with peak warming of 2.03 °C and 2.25 °C, respectively. Only the SSP1-1.9 scenario returns below 2 °C warming by 2100, ending at 1.71 °C. SSP1-2.6 peaks later, in 2069, and then declines only minimally, with the multi-model mean ending at 2.2 °C warming. Even though individual models such as CanESM5, ACCESS-ESM1-5 and MPI-ESM1-2-LR showed a slightly more distinct peak-decline behaviour for this scenario, the multi-model mean is closer to a stabilisation scenario (figure 2). Across all scenarios, there is considerable model spread between the different ensemble members, with CanESM5 and CanESM5-1 consistently driving the upper bounds, while MPI-ESM1-2-LR and NorESM2-LM simulate comparatively lower warming across scenarios (figure S1).

Across all scenarios, the multi-model mean shows continued increases in global terrestrial carbon stocks through the mid-21st century, driven by elevated CO_2 concentrations and warming induced increases in productivity and growing season length (figure 2(b), Qiu *et al* 2023, Gier *et al* 2024). Carbon stocks continue to rise until approximately 2060, after which the multi-model mean ΔNet Ecosystem Production (ΔNEP; figure 2(c)) declines gradually across all overshoot scenarios and becomes negative under SSP1-1.9, indicating productivity below the historical average. Nevertheless, changes in ΔNEP remain relatively modest, reflecting compensating responses in net primary productivity (ΔNPP) and heterotrophic respiration (ΔRh; figure S3). In particular, ΔNPP decreases more directly following peak warming, whereas ΔRh remains comparatively stable because it is strongly linked to the existing carbon stock. As a result, ΔNEP declines after peak warming, but only gradually.

Despite the declining ΔNEP, absolute NEP remains positive under all scenarios, and none show a pronounced decrease in total land carbon stocks during the cooling phase (figure S4). Instead, carbon stocks stabilise or continue to increase slowly after peak warming, implying that much of the carbon accumulated during the warming phase is retained. However, this multi-model mean masks substantial uncertainty among individual models. Some simulate a persistently positive land carbon sink throughout the second half of the century, whereas others already project negative NEP under present day conditions and consequently simulate substantial declines in

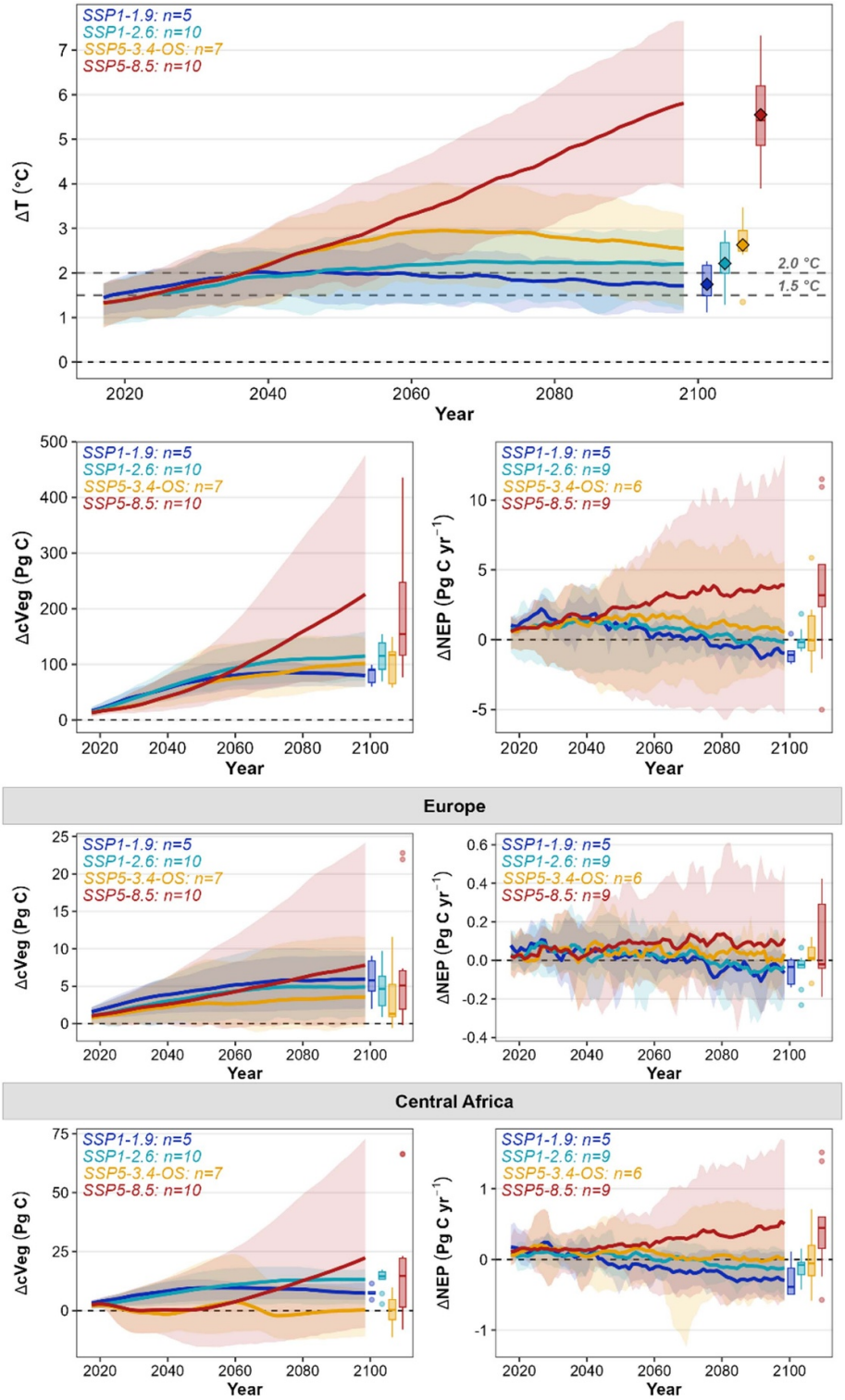


Figure 2. Multi-model mean projections of global and regional temperature and vegetation carbon dynamics for four emission-driven SSP scenarios (including land-use change). (a) Change in global mean temperature (ΔT) relative to pre-industrial levels. Horizontal dashed lines indicate the 1.5 °C and 2.0 °C targets. (b) Global change in vegetation carbon stock in vegetation (ΔcVeg) and (c) Net Ecosystem Production (ΔNEP), both relative to the contemporary baseline 1985–2014. (d), (e) Regional projections for Europe and (f), (g) Central Africa showing ΔcVeg and ΔNEP, respectively. Solid lines represent the multi-model mean for the scenarios: SSP1-1.9 (dark blue), SSP1-2.6 (light blue), SSP5-3.4-OS (yellow), and SSP5-8.5 (red). Shaded areas illustrate the spread across the model ensemble, with the number of members per scenario indicated in the top left. Across all plots, box plots show the median and interquartile range of end-of-century values per scenario. Please refer to figure S1 for the individual model projections and to S3 for additional model output of each scenario (ΔGPP, ΔNPP, ΔRh, ΔNEP, ΔNBP, ΔcVeg, ΔcSoil and ΔcLand).

vegetation carbon stocks (figures S1 and S4). These model-specific differences underscore the uncertain future of this carbon sink.

Regional projections broadly mirror the global pattern. In Africa, vegetation carbon stocks remain above recent-past values throughout the century under all scenarios (figure 2(d), compare to multi-model mean historical cLand of 133 ± 38.3 Pg C). However, in both SSP5 scenarios there is substantial forest loss projected up to around 2040, resulting in lower cVeg values compared to the two SSP1 scenarios, which do not include this disturbance. Because these forest losses are treated as disturbances, they are not reflected in ΔNEP. After 2040, cVeg increases again in both SSP5 scenarios, before stabilising and declining slightly following the peak in temperature and the reduction in ΔNEP under SSP5-3.4 OS. Notably, the overshoot pathway relies on large-scale carbon dioxide removal, partly achieved through afforestation and the accumulation of carbon on land (Meinshausen *et al* 2020), which may offset declines in terrestrial carbon stocks that would otherwise occur in response to climate change alone. Despite this, the multi-model mean ΔNEP falls below zero in all overshoot scenarios, indicating ecosystem productivity below the historical average.

Europe shows a similar overall response (figure 2(f), compare to multi-model mean historical cLand of 72 ± 41.7 Pg C), although the smaller land area and lower forest cover result in smaller absolute changes in carbon stocks. Across the region, terrestrial ecosystems maintain a positive NEP under all scenarios (figure S4), even as ΔNEP declines below the historical average during the second half of the century (figure 2(g)).

Compared to those emission-driven socioeconomic pathways, the concentration-driven 1pctCO2-cdr experiment involves a far more extreme rise in CO_2 and, correspondingly, in temperature. Global warming reaches almost 5 °C over the 140 year ramp-up phase (figure 3(a)). This idealised experiment demonstrates how the models predict reversibility in both global and regional cVeg when there is no land use change: cVeg increases in parallel with CO_2 and temperature, rather than being dampened by forest conversion to agricultural area as in the two SSP5 scenarios. Models predict an almost doubling of the global cVeg at peak warming, up to almost 1000 Pg C. After the peak, we see a hysteresis as the peak in cVeg comes later then the peak in temperature and CO_2. Then, by the end of the experiment, values return to almost the same level as at the start.

3.2. Limited experimental data on recovery after overshoot

Our systematic search identified 256 papers on global change experiments implementing elevated CO_2, warming, drought, or irrigation treatments, with drought studies comprising the majority (figure 4). Experiments are heavily concentrated in temperate ecosystems across Europe, China, and the United States, leaving major knowledge gaps for tropical and boreal ecosystems, especially in Africa (figure 4).

From all those studies, only 15 studies reported on a recovery phase. Just one study examined recovery following warming, combined with irrigation, in a grassland in Oklahoma (USA). Over the nine months of post-treatment monitoring, productivity remained suppressed, driven by persistently lower soil moisture in previously warmed plots (Sherry *et al* 2008). The one other irrigation experiment with a recovery phase also showed productivity increases during treatment in a temperate forest, followed by declines once watering stopped, suggesting physiological acclimation after twelve years of elevated water supply (Vitali *et al* 2024). No CO_2-enrichment experiment measured post-treatment responses.

Thirteen grass- and shrubland experiments on drought included a post-treatment recovery phase (figure 4). Each reported productivity declines during drought, scaling with drought intensity, followed by mixed outcomes upon re-wetting: some studies found full recovery or even overproduction (Albert *et al* 2011, Ru *et al* 2023, Schärer *et al* 2025), while others found negative legacy effects persisting for up to two years (Yahdjian and Sala 2006). Several studies also documented community shifts during recovery, with rapid grass regrowth compensating for slower recovery (Luo *et al* 2023, Ru *et al* 2023).

3.3. Modern day analogues of overshoot emphasise the importance of multiple stressors

Given the limited experimental evidence on post-treatment recovery, modern extreme events can serve as complementary analogues for ecosystem responses to climatic stress and subsequent recovery (Salomón *et al* 2022, Chambers *et al* 2025). These events have two key advantages: they operate at spatial scales far exceeding those of any manipulative experiment, and they capture co-occurring stressors, such as heat and drought (Yao *et al* 2023). At the same time, modern extreme events are shorter-lived than a potential overshoot period and they lack slower ramp up-ramp down phases. As a result, they can provide evidence of legacy effects and resilience to compound extremes, but lack the timescales at which a full overshoot scenario will play out.

3.3.1. Tropical forest responses to El Niño events

The 2015–2016 El Niño produced unprecedented heat and drought across the tropics, driving an estimated decline of 1.3 Pg C in aboveground carbon stocks between 2014 and 2017 due to persistent aboveground carbon losses in Africa (−0.8 to −1.1 Pg C) and America (−0.4 to −0.6 Pg C) (Wigneron *et al* 2020). Although photosynthesis recovered rapidly once rains returned (Santos *et al* 2018), structural

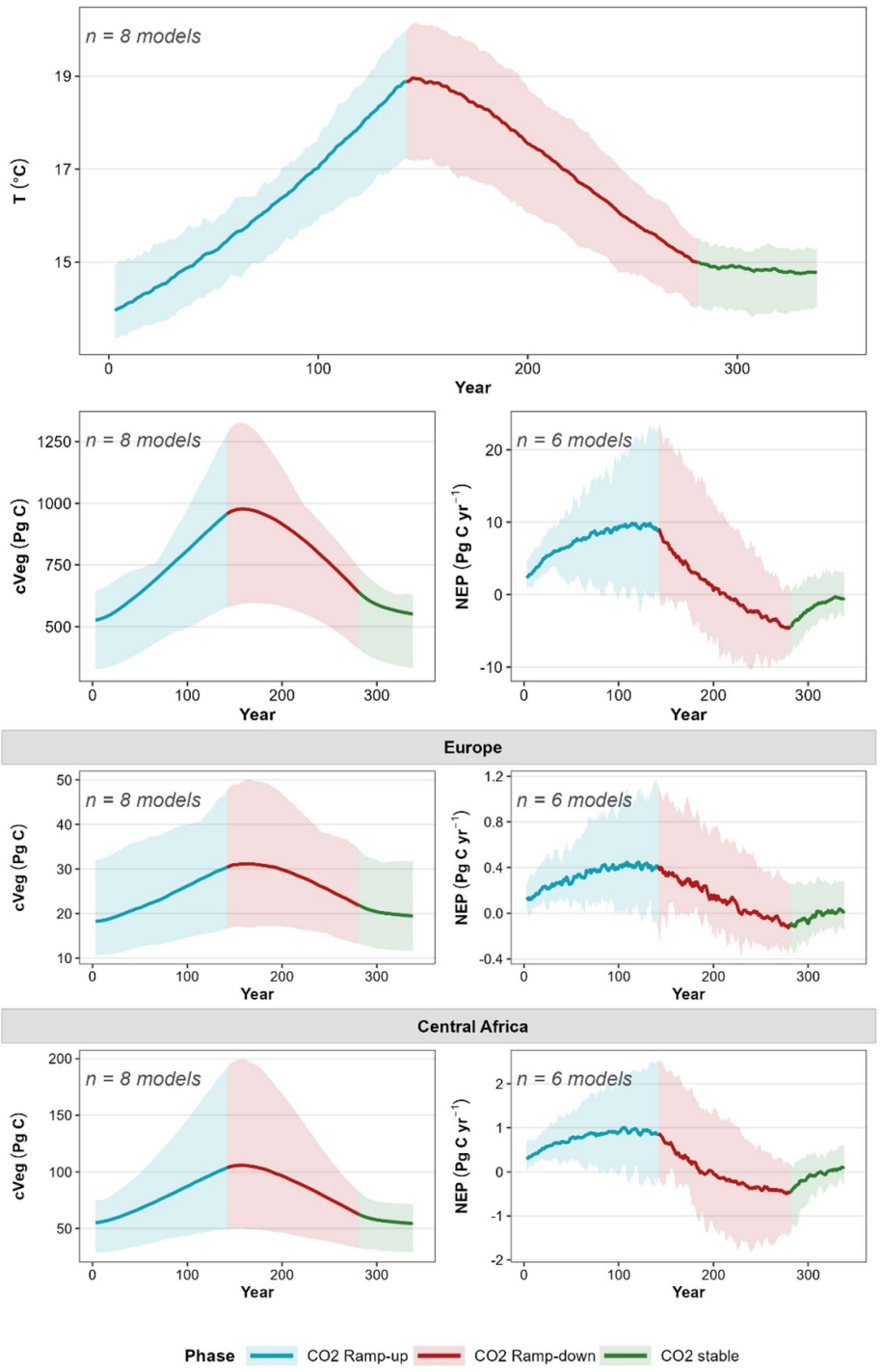


Figure 3. Multi-model mean projections of global and regional temperature and vegetation carbon dynamics of the concentration-driven 1pctCO2-cdr experiment (excluding land use change). (a) Global mean temperature (T), (b) Global change in vegetation carbon stock in vegetation (cVeg) and (c) Net Ecosystem Production (NEP) (d), (e) Regional projections for Europe and (f), (g) Central Africa showing cVeg and NEP, respectively. Solid lines represent the multi-model mean, coloured by phase. Blue is the CO_2 ramp-up phase, red the CO_2 ramp-down phase, and green the last CO_2 stable phase. Shaded areas illustrate the spread across the model ensemble, with the number of members with output per variable indicated in the top left. Note that only four models overlap with the SSP scenarios in figure 2. Please refer to figure S5 for the individual model projections and to S6 for additional model output of each scenario (ΔGPP, ΔNPP, ΔRh, ΔNEP, ΔNBP, ΔcVeg, ΔcSoil and ΔcLand).

recovery lagged behind. Estimates of aboveground carbon stock recovery vary substantially, from 40% recovery of affected forests by 2019 inferred from L-band microwave vegetation optical depth (Yang *et al* 2022), to full recovery by late 2020 based on microwave satellite data (Fan *et al* 2024), and full recovery times up to 2022 suggested by radar analyses (Bai *et al* 2026). Modelled productivity recovered to pre-drought levels across 77% of tropical forest area by 2020 (Wu *et al* 2025). This spread in estimates reflects genuine variation in what is being measured (photosynthetic activity, canopy structure, biomass),

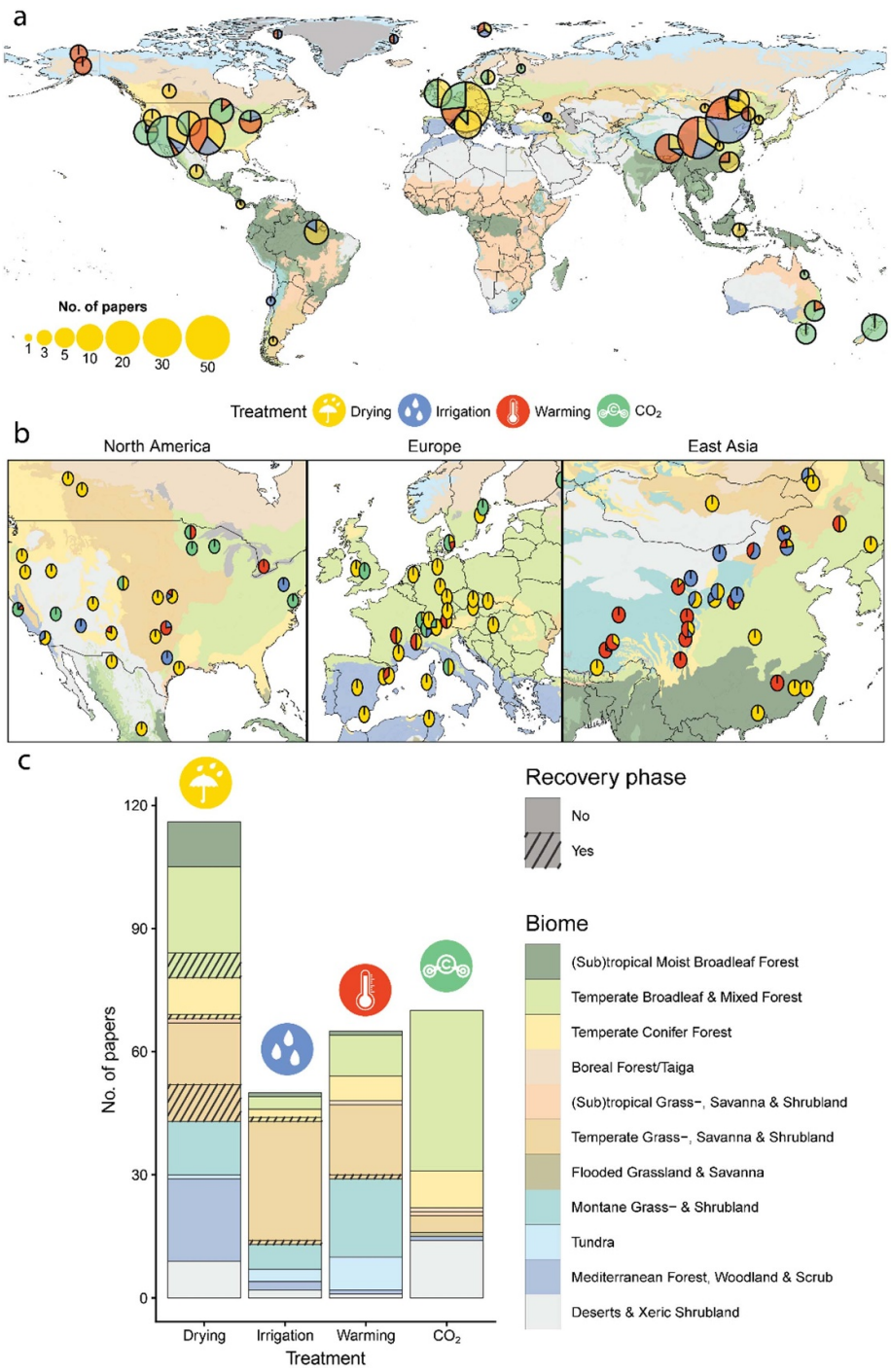


Figure 4. Global distribution and biome classification of climate change experiments. (a) Geographic distribution of experimental sites, where pie chart size reflects the number of studies (sites within 600 km are aggregated for visibility) and pie colours indicate the proportion of each treatment type: Drying (yellow), Irrigation (blue), Warming (red), and CO_2 (green). Country borders are sourced from the Rnaturalearth R package (Massicotte and South 2017) and may not reflect internationally recognised boundaries. (b) Close-up views of the three regions with the highest experimental density; note that marker size is not proportional to study count here to reduce overlap. (c) Number of studies per treatment type and biome, coloured by biome classification (see legend); hatching indicates experiments that included a recovery phase.

but collectively these studies underscore that even a single extreme drought can impose carbon losses that take many years to restore.

Additionally, recovery was spatially heterogeneous. It was slowest in heavily stressed and structurally degraded forests, and in transitional ecosystems at the forest-savanna boundary. In the Cerrado in Brazil, stem productivity declined by 58% during the drought event and rebounded only gradually (Matias Reis *et al* 2025). African forests showed greater resilience than Amazonian ones, with field and radar data suggesting a stronger capacity to return to pre-drought conditions (Malhi *et al* 2018, Bennett *et al* 2021, Berenguer *et al* 2021). Where

recovery did occur, it was partly facilitated by the elevated moisture typical of subsequent La Niña conditions, which compensated for productivity losses incurred during the drought (Takamura *et al* 2023, Zuidema *et al* 2025). However, repeated drought events progressively erode this capacity, with prior stress reducing a forest's ability to recover from subsequent disturbances (Tao *et al* 2022).

Although the 2023–2024 El Niño was weaker by standard indices, it coincided with record global temperatures and produced a tropical carbon sink anomaly comparable to 2015–2016, acting as a net carbon source in both years (Ke *et al* 2024, Du *et al* 2025). In Amazonia, canopy productivity reached record lows (Yang *et al* 2025, Buras *et al* 2026) and resilience indicators deteriorated markedly, suggesting a slowing of ecosystem dynamics (Bai *et al* 2026). The magnitude of these impacts despite a weaker El Niño highlights how background warming is amplifying the carbon-cycle effects of extreme events. Together, these two El Niño events illustrate that compound heat and drought produce carbon losses that are slow to reverse, that recovery depends heavily on subsequent climatic conditions, and that continued warming is likely progressively amplifying the impact of extremes.

3.3.2. Temperate ecosystem recovery to the 2018–2020 European droughts

The summers of 2018–2020 brought an unprecedented sequence of hot, dry years across Central Europe and the North Sea region, causing widespread forest dieback, bark beetle outbreaks, and productivity losses (Buras *et al* 2020, Schuldt *et al* 2020, Thonfeld *et al* 2022). As with the El Niño events, this period offers a natural experiment in compound heat and drought stress, and in the limits of ecosystem recovery when extreme events occur back to back (Zscheischler *et al* 2020).

The 2018 event was exceptional, with growing-season temperatures over 3.3 °C warmer than the long-term average across Austria, Germany, and Switzerland. Negative drought effects impacted productivity in an area roughly 1.5 times larger than in 2003, previously considered Europe's worst drought in 500 years (Buras *et al* 2020, Schuldt *et al* 2020). The strongest effects were concentrated north of the Alps, where less drought-adapted ecosystems suffered record heat and drying, while Mediterranean ecosystems were comparatively unaffected (Schuldt *et al* 2020, Senf and Seidl 2021).

Importantly, recovery between the consecutive droughts was incomplete. Legacy effects on productivity were detectable up to 2020 (Schuldt *et al* 2020, Senf and Seidl 2021, Sturm *et al* 2022), while incomplete hydraulic recovery increased tree vulnerability to secondary stressors such as bark beetles and fungal pathogens, contributing to continued mortality after the initial event. A Europe-wide assessment confirmed sustained tree cover loss even in 2021, by itself a climatological average year, and damage persisted through to 2022 (Knutzen *et al* 2025). As a result, some forests were reported to be a consistent net carbon source after 2018 at least up to 2023 (Haberstroh *et al* 2026).

These consecutive extreme droughts demonstrate how frequent extremes progressively increase ecosystem vulnerability (Ohlert *et al* 2025, Serrano-León *et al* 2025), as depleted hydraulic and carbohydrate reserves may not recover between events (McDowell *et al* 2008, Arend *et al* 2022). This progressive degradation resembles a form of tipping behaviour with direct relevance to overshoot scenarios: it suggests that post-overshoot recovery will not be linear, and that repeated extreme stress can erode both ecosystem resistance and resilience, impacting recovery timescales (Serrano-León *et al* 2025).

3.4. Paleoclimate analogues suggest asymmetric ecosystem responses during cooling phases

A first relevant paleo-analogue for a gradual overshoot-and-return scenario comes from Holocene vegetation dynamics in Europe and North America. Pollen-based reconstructions show that tree cover peaked around 6500 years BP during the mid-Holocene Climatic Optimum (∼9000–5000 BP) (Dawson *et al* 2025, Sweeney *et al* 2025), when orbital forcing produced summer temperatures in mid to high latitudes broadly comparable in magnitude, if not in rate, to currently projected near-term warming. Subsequent cooling was associated with a transition towards more open landscapes and declining tree cover across Europe (Thompson *et al* 2022, Dawson *et al* 2025). Although human land use from ∼6000 BP onward may have contributed to this vegetation shift, its early influence is considered limited, given that rapid population growth occurred only within the last 2000 years (Klein Goldewijk *et al* 2017, Sweeney *et al* 2025).

This pattern of reduced tree cover during cooling is further supported by model simulations of European forest dynamics following the abrupt 8200 BP cooling event, a period of depressed annual temperatures across the Northern Hemisphere caused by a weakened Atlantic Meridional Overturning Circulation. In response to this cooling, which lasted a few hundred years, grasses expanded across much of Europe (Li *et al* 2019). Notably, those simulations also demonstrated that similar climatic conditions can sustain divergent vegetation compositions depending on the prior state of the system, suggesting strong path-dependency in ecosystem recovery (Li *et al* 2019).

As an analogue for the risks of even higher warming, the (PETM, ∼55.8 Ma) provides a more extreme but instructive case. This ∼5 °C–6 °C global warming event, which unfolded over ∼10 000–20 000 years

and persisted for approximately 200 000 years, was associated with widespread terrestrial disruption. Existing plant communities partially collapsed and pioneer fern-dominated vegetation persisted for millennia across multiple continents (Korasidis *et al* 2022, Nelissen *et al* 2026). Regional floras reorganised through rapid range shifts of hundreds of kilometres within ∼10 000 years, followed by the return of most pre-event taxa, indicating local extirpation rather than widespread extinction (Wing *et al* 2005, Wing and Currano 2013) with floral expansions towards the poles (Korasidis *et al* 2022). Combined model simulations and vegetation reconstructions suggest that warming-induced migration and evolutionary adaptation of vegetation were insufficient to prevent a widespread loss of productivity (Rogger *et al* 2025). Recovery of biospheric carbon stocks was lagged by 70 000–100 000 years, producing a prolonged perturbation of the global carbon cycle (Rogger *et al* 2025). The PETM involved temperature anomalies exceeding a realistic modern-day overshoot scenario, with CO_2 concentrations rising from an estimated 840–1680 ppm (Meissner *et al* 2014) to a peak of ∼2200 ppm (Gutjahr *et al* 2017). Nevertheless, it demonstrates that rapid exceedance of ecological thresholds can produce vegetation state changes and carbon cycle feedbacks that outlast the climatic perturbation by orders of magnitude.

Results from the Palaeoclimate Model Intercomparison Project (PMIP4) (Brierley *et al* 2020) further showed the importance of correctly modelling vegetation dynamics, at least at the level of global vegetation distribution, for accurately estimating global warming. Their results show that capturing regional vegetation shifts and increases in woody cover is essential for simulated climates to match proxy-based climate data (Lu *et al* 2019, O'ishi *et al* 2021, Chen *et al* 2023). In contrast, models lacking dynamic vegetation distributions underestimated the magnitude of global temperature change in the paleoclimate reconstructions.

4. Discussion

Under current emission trajectories, getting anywhere close to the Paris Agreement targets will likely require an overshoot pathway (Cannon 2025, Van Vuuren *et al* 2026), in which global temperatures peak before being brought back down through active carbon dioxide removal. Our synthesis suggests, however, that our knowledge on the ecological reversibility during the cooling phase is extremely limited. While ESMs predict a trajectory where global terrestrial fluxes decrease during the cooling phase but stay positive, leading to relatively stable carbon stocks although with regional differences (Koven *et al* 2026, Swann *et al* 2026), the little evidence we have from short-term experimental studies, modern climate analogues and the paleorecord consistently points to ecosystem responses that are asymmetric, lagged, and shaped by persistent legacy effects (Anderegg *et al* 2015, Yu *et al* 2025, Deng *et al* 2026).

A fundamental challenge in assessing the cooling trajectory is the mismatch between the timescales of ecological recovery and those of the experiments designed to study it. Our systematic search found that only 15 of 256 global change studies included a recovery phase, and only one experiment ran for over five years. However, consecutive droughts produce stronger and more persistent losses than isolated events (Luo *et al* 2023, Zuidema *et al* 2025), suggesting the existence of a threshold beyond which return to pre-disturbance conditions becomes increasingly unlikely (Ohlert *et al* 2025). Additionally, none combined elevated CO_2, temperature change, and altered precipitation regimes simultaneously, reflecting the considerable logistical challenges involved in these studies. However, this matters because ecosystem responses to multiple drivers are frequently nonlinear, amplified, or even reversed relative to single-driver expectations (Sherry *et al* 2008, Gharun *et al* 2026).

Evidence from modern extreme events offers some insight into how interacting climatic drivers affect ecosystems at short timescales. They show that concurrent heat and drought produce damage that accumulates across years (Knutzen *et al* 2025, Ohlert *et al* 2025), recovery depends on disturbance intervals and ecosystem composition (Sachsenmaier *et al* 2024), and increasing extreme event frequency is progressively eroding baseline resilience (Bai *et al* 2026). With such events projected to intensify, ecosystems globally may be approaching transition thresholds, for example from forest to shrubland or savanna-like systems, from which recovery is far more difficult than maintaining the original state would have been (Flores *et al* 2024, Maes *et al* 2024, Wunderling *et al* 2026). However, a limitation of modern analogues is that extreme events occur under current CO_2 concentrations rather than the elevated levels that would accompany an overshoot. Since elevated CO_2 enhances water use efficiency (van der Sleen *et al* 2015, Walker *et al* 2021), ecosystems during an overshoot may be more drought-tolerant than modern analogues suggest. A second limitation is that overshoot conditions would persist for multiple years rather than occurring as isolated extreme events and have a slower ramp-up and ramp-down phase, allowing impacts to accumulate over time (Tao *et al* 2022). Lastly, extreme heat and drought events by themselves are projected to become more intense in a warmer climate (IPCC 2021), likely contributing to further declines in ecosystem resilience.

The paleorecord extends this perspective across longer timescales and larger temperature anomalies, though with the important caveat that these past warming periods took place under very different

circumstances, and unfolded far more slowly than current climate change, allowing more time for adaptation and evolutionary response (Korasidis *et al* 2022). Nevertheless, it offers valuable insight into the nature of ecosystem shifts under sustained climatic change, which are likely to be more pronounced under the unprecedentedly rapid warming now underway. Both the Holocene Climatic Optimum and the PETM illustrate that rapid exceedance of ecological thresholds can generate state changes and carbon cycle feedbacks that long outlast the climatic disturbance itself, because reversibility depends on whether thresholds have been crossed and whether the biotic context allows reassembly of prior communities (Dawson *et al* 2025, Nelissen *et al* 2026).

Current ESMs are limited by the scarcity of modern overshoot examples against which to develop and test their representations of hysteresis and state shifts. This model uncertainty is reflected, for example, in the lack of consistency between models in projecting carbon stocks in the Congo Basin, a region historically underrepresented in observational data. The current aboveground carbon stock in Congo Basin forests is estimated at 36 Pg C (Worden *et al* 2026; though note that their spatial extent is about half of the extent in this study). Yet the spread across model projections implies this stock could nearly double or lose around a third of its biomass by 2100, depending on the scenario and model. Disturbance regimes are similarly poorly captured: European forests are projected to face increasing disturbance from fire, bark beetle outbreaks, and wind damage under all warming scenarios, with both the frequency and occurrence of compound disturbances scaling with the degree of warming (Messori *et al* 2025, Grünig *et al* 2026). Large-scale disturbance converts mature, high-biomass forest to younger, structurally simpler stands with fundamentally different carbon dynamics, a legacy effect that current models do not adequately represent. Ecosystem degradation during both peak warming and the cooling phase could release additional CO_2 into the atmosphere (Rogger *et al* 2025), slowing further cooling in a feedback loop that current global climate projections rarely account for. This is especially visible in the concentration-driven experiment where we see an almost linear increase in the multi-model mean of cVeg, with no negative impacts of climate change. NEP only decreases when CO_2 concentrations go down again.

Future research should focus on these modelling and experimental gaps. The dedicated model intercomparison effort TIPMIP is aimed at improving the representation of tipping point dynamics in ESMs (Winkelmann *et al* 2025, Jones *et al* 2026). Additionally, the scenarios for the next phase of model intercomparison, CMIP7, now include more direct overshoot pathways like in CDRMIP and exclude the least plausible extremes of the CMIP6 range (Van Vuuren *et al* 2026). Vegetation representation in ESMs is also becoming more sophisticated and thus potentially more realistic, incorporating demographic processes, nutrient limitation, and more realistic disturbance regimes. On the experimental side, the large existing body of global change experiments (figure 4) could yield further insight if recovery phases were routinely included after treatments end. Targeted research filling geographical gaps, particularly in the tropics, will also be essential. In addition, Ecotron facilities offer a promising framework, as they allow researchers to study interacting drivers under controlled conditions across multiple climate scenarios (Rineau *et al* 2019, Roy *et al* 2021). They are especially relevant given the likelihood that ecosystems will face novel combinations of temperature and precipitation conditions, which can be tested in an integrated way in these facilities (Williams and Jackson 2007).

Taken together, these research lines suggest that the land carbon sink cannot be simply assumed to remain stable through the peak of a temperature overshoot, nor that productivity will respond symmetrically to declining temperatures (Koven *et al* 2022, Asaadi *et al* 2024). Less optimal growing conditions and lag effects of extreme events could lead to substantial reductions in productivity and the total carbon stock. We have too little research on overshoot scenarios to treat ecological reversibility as the default outcome in climate projections, even though this is how current ESMs respond to overshoot in a purely concentration-driven experiment. Further addressing this research gap requires global change experiments that explicitly incorporate recovery phases, alongside ESMs with more realistic representations of disturbance legacies, threshold dynamics, and compositional change. Without these, projections of land carbon uptake during the cooling phase of an overshoot remain uncertain.

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Data availability statement

The data that support the findings of this study will be openly available following an embargo at the following URL/DOI: https://doi.org/10.5281/zenodo.20529027.

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Conflict of interest

The authors declare no conflicts of interest regarding this work or its publication.

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